Case studies in network community detection

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Abstract

Community structure describes the organization of a network into subgraphs that contain a prevalence of edges within each subgraph and relatively few edges across boundaries between subgraphs. The development of community-detection methods has occurred across disciplines, with numerous and varied algorithms proposed to find communities. As we present in this Chapter via several case studies, community detection is not just an “end game” unto itself, but rather a step in the analysis of network data which is then useful for furthering research in the disciplinary domain of interest. These case-study examples arise from diverse applications, ranging from social and political science to neuroscience and genetics, and we have chosen them to demonstrate key aspects of community detection and to highlight that community detection, in practice, should be directed by the application at hand.

Most networks representing real-world systems display community structure, and many visualizations of networks lend themselves naturally to observations about groups of nodes that appear to be more connected to each other than to the rest of the network. One might be reasonably curious about why this is such a common feature across a great variety of real networks, and even more intriguingly, what do the groups mean? Considering examples from different disciplines, one can observe that these groups (or communities) often have important roles in the organization of a network. For example, in a social network where nodes represent individuals and edges describe friendships between them, communities can correspond to groups of people with shared interests (Granovetter, 1973; McPherson et al., 2001; Moody and White, 2003; Zachary, 1977). In the graph of the World Wide Web, where a directed edge between web pages represents a hyperlink from one to the other, communities often correspond to webpages with related topics (Flake et al., 2000). In brain networks of interconnected neurons or cortical areas, communities can correspond to specialized functional components such as visual and auditory systems (Sporns and Betzel, 2016). In networks representing interactions among proteins, communities can group together proteins that contribute to the same cellular function (Spirin and Mirny, 2003). Across each of these examples, the communities provide a new level of description of the network, and this intermediate (that is, “mesoscopic”) perspective between the microscopic (nodes) and macroscopic (the whole network) domains proves to be very useful in understanding the essential functionality and organizational principles of a network.

In particular, one of the motivations to identify communities in many of the aforementioned applications is that the network structure aligns with data attributes such as age, location, interests,
health, race, sex and so on. However, congruent with most community-detection algorithms, we refer to structural communities in which there is a prevalence of edges between nodes in the same community versus those between communities. Importantly, this notion is a topological property of the network and is agnostic to attributes. In principle, one can choose other definitions for what constitutes a community, and we note that for attributed (also called annotated) networks there is growing interest in developing community-detection algorithms that utilize both structural and attribute information (Binkiewicz et al., 2014; Bothorel et al., 2015; Newman and Clauset, 2016; Peel et al., 2017; Yang et al., 2013). While here we do not explore these possibilities, and focus our attention on communities in the topological sense, it is important to note that there is often positive correlation between community structure and attribute information due to homophily (Aral et al., 2009; McPherson et al., 2001)—that is, edges exist preferentially between nodes with similar attributes. Generally speaking, studying the interplay between attribute information and network structure is complicated due to confounding effects (Shalizi and Thomas, 2011).

Detecting communities in an automated manner is not a simple pursuit, first, because although the qualitative notions of communities may be intuitive, translating such ideas into an appropriate modeling framework can be challenging. In particular, various applications call for different notions of a community, each producing a different mesoscopic description of a network. Second, the computational complexity of community detection can be a fundamental issue; for example, the number of possible partitions of nodes into non-overlapping groups is non-polynomial in the size of the network (and allowing overlapping communities increases the number of possibilities), motivating important work on different heuristics for efficiently identifying communities. Such challenges make community detection one of the most complex—yet fascinating—areas of network science, with a huge and ever increasing number of different algorithms available in the literature.

We only indicate a few classes of community-detection methods here, referring the reader to comprehensive community-detection reviews by Porter, Onnela, and Mucha (2009); Fortunato (2010); and Fortunato and Hric (2016) (see also a recent review by Schaub et al., 2017, on the conceptual differences between different perspectives on community detection). While the ideas of community detection have been around in sociology for decades (see, e.g., Coleman, 1964; Freeman, 2004; Moody and White, 2003), the field has benefited from significant contributions across numerous disciplines, proposing a variety of methods and algorithms for automating community detection.

Graph partitioning (e.g., Barnes, 1982; Fiedler, 1973; Kernighan and Lin, 1970; Mahoney et al., 2012) spans a large literature across computer science and mathematics, aiming to divide a network into a specified number of groups so that some selected quantity is optimized, such as the number of edges between the groups (i.e., cut size).

Modularity maximization (Newman and Girvan, 2004), a different optimization approach for graph partitioning originating in the physics literature, aims to find the partition with the largest difference between the total weight of within-community edges and that expected under a null model—that is, a random-network model with selected properties. Modularity maximization typically leads to more balanced community sizes, can account for degree heterogeneity in the network, and does not require a priori specification of the number of communities. However, it is well-known to suffer from a resolution limit (Fortunato and Barthelemy, 2007), and it is not at all clear how to best interpret the different numbers of communities that can be obtained by varying resolution parameters (Arenas et al., 2008b; Reichardt and Bornholdt, 2006).

Statistical inference (e.g., Ball et al., 2011; Hastings, 2006; Karrer and Newman, 2011; Peixoto, 2013, 2014), arising from the statistics literature, typically aims to identify a parametrized generative model that describes the network (e.g., with maximum likelihood). For example, stochastic
block models (Fienberg and Wasserman, 1981; Holland et al., 1983; Snijders and Nowicki, 1997) assume for a given partition that the edge probability between nodes depends on their community memberships (see more details in a recent note by Abbe, 2017, on the current developments in community detection in the context of stochastic block models).

Cut size, modularity, and likelihood all define objective functions that measure the “goodness” of the partitions (or, in some cases, sets of communities that may or may not cover the network) and are generally NP-hard optimization problems. In particular, in most cases finding the conclusively best community assignment is effectively computationally equivalent to checking a non-vanishing fraction of all possibilities, which grows exponentially with system size. Fortunately, many algorithms have been developed to efficiently provide approximate solutions, including a variety of iterative (Blondel et al., 2008; Kernighan and Lin, 1970; Peixoto, 2014) and spectral (Barnes, 1982; Fiedler, 1973; Newman, 2006) methods.

At the same time, numerous heuristics have been developed for community detection that do not necessarily optimize a global objective function but nonetheless have proven to be useful. These often fall into two categories: agglomerative methods which are akin to hierarchical clustering (Hastie et al., 2001); and divisive methods, such as iteratively partitioning a network by some local measure (such as edge betweenness, Girvan and Newman, 2002).

A number of other community-detection methods stem from analyses of dynamical systems on a network, including the Potts model for spin systems (Reichardt and Bornholdt, 2004; Wu, 1982), random walks (Delvenne et al., 2010; Jeub et al., 2015; Pons and Latapy, 2005; Rosvall and Bergstrom, 2008; Zhou, 2003), and oscillator synchronization (Arenas et al., 2006; Li et al., 2008). Such approaches are directly applicable for studying these respective dynamical systems and in some cases are closely related or even equivalent to one of the above-mentioned quality functions (Delvenne et al., 2010; Fiedler, 1973; Rosvall and Bergstrom, 2008). Conversely, community structure can have a profound effect on dynamics taking place on networks [e.g., the spread of information across social networks (Aral et al., 2009; McPherson et al., 2001; Melnik et al., 2014; O’Sullivan et al., 2015; Ugander et al., 2012; Weng et al., 2013), random walks and heat flow (Delvenne et al., 2010; Mucha et al., 2010), cascades (Galstyan and Cohen, 2007; Gleeson, 2008), and synchronization (Arenas et al., 2006; Skardal and Restrepo, 2012)] and adopting a community-based perspective provides a useful vantage point to study these dynamics.

These are just a small sample of the many community-detection methods that have been developed, and we in no way intend this Chapter to be a comprehensive review of all methods. Rather, here we present examples from different scientific disciplines demonstrating the useful application of community detection. In particular, we aim to emphasize community detection as a tool for studying networks. Identifying communities is often just a first step in data analysis as it opens up many possibilities for further study. We illustrate this idea with a well-known example shown in Fig. 1, the Zachary Karate Club (Zachary, 1977).

The Karate Club network developed by Zachary (1977), through observing the interactions between members of a club during the two-year period 1970–1972, represents the friendships between 34 of the club members as an aggregated, weighted network. During this period, there was a club division (indicated by node colors and shapes in Fig. 1) due to a conflict between the club instructor and the president (nodes 1 and 34, respectively). Due in part to this “ground truth” division and the network’s small size and simple structure, the Zachary Karate Club has become a common example for demonstrating community-detection algorithms. Zachary demonstrated that most of the members chose to be in the subgroup best associated with their friends. Specifically, his use of a cut algorithm to define a split of the network into two subgroups almost perfectly reproduced the
real-life split of all but one of the members. Node 9 didn’t choose to join the president’s new club despite the larger number of ties that linked them, apparently because he was only three weeks away from completing a four-year quest for a black belt, requiring his allegiance to the instructor.

This seemingly odd behavior of node 9 highlights three important lessons: (I) adopting a community-based approach to network analysis provides a vantage point to ask new research questions; (II) one must be cautious when comparing the output of a community-detection algorithm to known information on the network (frequently referred to as “ground truth”), as the latter might include important additional information not captured by the network topology (Peel et al., 2017); and finally (III) applied community detection should incorporate domain knowledge to choose appropriate methodologies, develop application-specific techniques, and address domain-driven questions.

With these lessons in mind, the rest of this Chapter is organized by the following case studies. In section 1, we describe how communities have been used to help predict which memes go viral on Twitter. In section 2, we highlight political polarization in the U.S. Congress, demonstrating the use of communities to quantify polarization and identify node roles such as U.S. Senators that bridge the legislative space between political parties. In section 3, we present a study of the neuronal network of *C. elegans* in which multiresolution communities uncover groups of neurons with similar biological function. In section 4, we turn to a different neuroscience application that uses communities to compare human brain networks under different tasks and rest states. Finally, in section 5, we provide an example of how communities can help explain the evolution of genes important to Malaria. We selected these case study examples to highlight the utility of a community-driven approach to network analysis, drawing from these creative applications in which the modeling assumptions and algorithm choices elucidate important aspects of the data. We hope that our discussion will be thought provoking for those previously unfamiliar with this area and inspire further use of community detection for network analysis.
1 Virality prediction of social memes

Community structure affects social contagions and epidemics through structural trapping, meaning that a meme or virus spreads readily within a community (or communities, if the contagion arises in clusters) and tends to not spread (as quickly, if at all) from one community to another (Aral et al., 2009; McPherson et al., 2001; Melnik et al., 2014; Onnela et al., 2007; O'Sullivan et al., 2015; Ugander et al., 2012; Weng et al., 2013). That is, the contagion exhibits “community concentration” in which it is localized (i.e. concentrated) within one or more communities. In the context of epidemics, structural communities (which often reflect geographic constraints) can be represented by metapopulation models (Colizza and Vespignani, 2008; Melnik et al., 2014) that partition the human population into subgroups (broadly defined). Social contagions and epidemics share many mathematical and modeling similarities (Dietz, 1967; Goffman and Newill, 1964); however, their differences are also important. One crucial distinction is that social contagions are typically better modeled as complex contagions (Centola and Macy, 2007) in which a node’s (i.e. person’s) adoption of the contagion requires social reinforcement, e.g., as modeled by a threshold criteria (Granovetter, 1978). Whereas a biological epidemic can be transmitted through a single exposure, a person can require a certain amount of “contagion exposure” (e.g., number or fraction of contacts who have already adopted it) before adopting a social contagion themselves. Although subtle, this discriminating feature of social contagions and epidemics can significantly impact spreading patterns on networks (Centola, 2010; Centola and Macy, 2007; Melnik et al., 2013; O'Sullivan et al., 2015; Taylor et al., 2015; Weng et al., 2013).

Weng, Menczer, and Ahn (2013) study the spread of memes across the Twittersphere, concluding that homophily and social reinforcement collectively boost community concentration. Interestingly, they find this effect to differ for viral memes (those that spread vastly in the population) versus non-viral memes (those that do not reach high levels of popularity and are only shared by a small fraction of the population). The three main findings of their work are: (I) communities allow us to estimate how much the spreading pattern of a meme deviates from that of infectious diseases; (II) viral memes tend to spread more like epidemics than non-viral memes; and finally (III) the virality of memes can be predicted based on early spreading patterns in terms of community structure. We now describe further each of these results.

The authors built an unweighted, undirected network from Twitter data, encoding reciprocal following relationships between users. This network provided evidence of structural trapping for memes, defined as unique hashtags, that spread through tweets and retweets. They identified communities using two community-detection methods: Infomap (Rosvall and Bergstrom, 2008), an information-theoretic algorithm; and link clustering (Ahn et al., 2010), which identifies overlapping communities by clustering edges. By analyzing the flow of information, they found that memes are much more likely to spread across intra-community edges versus inter-community edges. Given that a variety of factors (e.g., homophily, social reinforcement, and use history) can contribute to this phenomenon, it is important to recognize that this feature of community structure alone is able to differentiate how important different edges might be in fostering the spread of memes.

To demonstrate that the local phenomenon of preferential spreading across intra-community edges contributes to the mesoscopic phenomenon of community concentration, the authors developed an entropy-based measure to quantify the extent to which the spreading of memes concentrates into communities. They compared this measure for their data set to that of four null models for social contagions: random spreading, a simple epidemic, a social reinforcement model, and an epidemic with homophily. By drawing this comparison, the authors observed community concen-
tration for non-viral epidemics to more-closely resemble complex contagions, whereas the spreading of viral memes more-closely resembled simple epidemics. In particular, viral memes exhibited less structural trapping (similar to epidemics), whereas non-viral memes exhibited stronger structural trapping (similar to complex contagions).

To further distinguish viral and non-viral memes, Weng et al. focused on the early stages of contagions and studied the average contagion exposure (i.e. the number of social contacts who are already adopters) for each adopter of a contagion. The authors compared their Twitter data set to the same four null models and again observed viral memes to more-closely resemble simple epidemics; namely, less exposure is required for transmission of a viral meme.

Motivated by the observation that community concentration and contagion exposure are informative features to gauge the virality of a meme, they then implemented a classification algorithm using random forests to predict whether or not a meme will go viral. To map virality prediction as a classification problem, they partitioned the set of memes into two classes (viral versus non-viral) so that they can specify the fraction of memes that are non-viral (considering virality both in terms of the number of retweeters and the total number of retweets). To study the benefit of using community structure information to improve virality prediction, they compared the resulting classification precision and recall scores for three classifiers: random guessing, community-blind prediction and community-based prediction. They found that incorporating information about community structure can greatly improve the prediction accuracy for the virality of memes.

## Congressional roll call

While the representation of Twitter following as a network is straightforward, direct connectivity is only one of many data types that can be represented by a network. Other common networks encode the similarity between, for example, people, text documents, or protein sequences. Here we consider communities found in network representations of roll-call voting similarity in the United States Congress, as constructed and studied by Waugh, Pei, Fowler, Mucha, and Porter (2009). These networks connect two members in a selected Congress (that is, the two-year period starting in the early January following the biennial Congressional elections) according to the similarity in their voting patterns. Waugh et al. (2009) defined edge weights equal to the fraction of bills that the two members voted the same way, yay or nay, among the total number of bills for which they were both present and voted (after removing nearly unanimous votes). This definition yielded weighted edges in a dense network; indeed, every member of Congress is connected in this definition to every other member in the same chamber with some positive weight unless they managed to never once vote the same way, while two members who always voted identically are connected with an edge of weight 1. Because the self-loops connecting each member of Congress to herself do not provide additional information, these were removed. This undirected roll-call-similarity network is a selected projection of the underlying bipartite (and signed) data that connects legislators with the bills that they voted on. This projection is useful for describing legislative activity because the community structures group together members of Congress who vote similarly, providing relatively accessible and intuitive examples of communities, independent of the political or policy content of the bills.

Waugh et al. (2009) studied community structure for these networks, providing a framework for thinking about the large-scale structure of Congressional legislative action in terms of political allegiances, whether or not those allegiances are well aligned with the nominally declared party memberships. In particular, they considered modularity, which measures the difference between
Figure 2: Roll call similarity adjacency matrices in the U.S. Senate as defined by Waugh et al. (2009) for the (left) 85th and (right) 108th Congresses, after reordering indices (Senators) with reorderMAT from the Brain Connectivity Toolbox (Rubinov and Sporns, 2010). The 85th Congress, January 3, 1957 – January 3, 1959, included the first federal civil rights legislation passed by Congress since Reconstruction (Wikipedia, 2017a). The modularity of this weighted network (that is, the maximum modularity obtained across observed partitions) is 0.091. In contrast, the modularity of the 108th Senate, January 3, 2003 – January 3, 2005, is 0.273, one of the highest values in any Senate. For comparison, two equal-sized blocks with perfect agreement within and zero agreement between blocks yields a modularity of 1/2 (up to a 1/N factor from removal of self loops).

Additional intuition about these networks and their changes over time can be obtained from visualizations, as demonstrated by the force-directed layouts of Andris et al. (2015) and the community-focused figure of Moody and Mucha (2013). Looking at the Senate roll call from 1975 to 2012, Moody and Mucha combined modularity for system-wide polarization of a Congress with groups of Senators in each Congress identified by a modified version of “convergence of iterated correlations” (CONCOR, Breiger et al., 1975; White et al., 1976). A feature of this grouping is that by construction it leaves some Senators in the political center unaffiliated with the party-centric groups, allowing for easy visualization of the hollowing out of legislative activity in the political center over time, along with increasing polarization. This simultaneous use of modularity and CONCOR in the visualization demonstrates the value of using multiple methods for identifying communities.
Because of the temporal nature of the roll call networks, community-detection methods that explicitly utilize the identifications across time have also been usefully applied. Whereas the Waugh et al. (2009) analysis and Moody and Mucha (2013) visualization detected communities within each two-year Congress independently (and then identify common Senators from one Congress to the next in the visualization), a “multilayer networks” framework can be used for studying networks that change dynamically over time, as well as a variety of other network generalizations (see, e.g., Kivelä et al. (2014). Mucha et al. (2010) used the properties of Laplacian dynamics to generalize the original definition of modularity to multilayer networks, using the Senate roll call as an instructive example for temporal networks, processing the data into the two-year single-Congress waves (called “slices” then but now more commonly thought of as “layers”). Naively, one could start by maximizing the modularity of each layer independently, but connecting those communities between layers then requires selection of a matching procedure that often leads to ambiguities. In contrast, the multilayer version directly allows for continuation of communities from one layer to the next and characterizing their flow across layers. In the simplest setting, the idea behind multilayer community detection introduces an interlayer coupling parameter, \( \omega \), describing the weight of the identity arcs linking corresponding nodes across layers. The multilayer modularity and the partitions found under fixed parameters then depend on \( \omega \). For \( \omega = 0 \), the single-layer modularity of each network layer is optimized independently. As \( \omega \) is increased, the coupling between layers encourages finding partitions that include greater spanning of communities across layers.

The partition highlighted and visualized in Mucha et al. (2010) includes communities that span multiple Congresses, with most of the single-Congress layers containing only two communities. The handful of layers with more than two communities mark key transitions in the two-party system, often with one group fading in favor of another (whether or not they name themselves differently). While the start of the American Civil War in 1861 is particularly obvious in the data, these transitions also occur near other major political moments or, in some cases, near the boundaries of the recognized “Party Systems” of the United States as studied in political science (see Wikipedia, 2017b). Alternative partitions of the data corresponding to different interlayer coupling parameter values were visualized by Mucha and Porter (2010), demonstrating how different features are highlighted by exploring the space of community detection parameters.

We note that similar network constructions have been used to study voting in the Congresses in Peru (Lee et al., 2017) and Brazil (Levorato and Frota, 2016), as well as the United Nations General Assembly (Macon et al., 2012). Community detection has also been used to study committee assignments (Porter et al., 2005, 2006, 2007) and cosponsorship (Zhang et al., 2007) in the U.S. Congress, and multilayer modularity in the multiplex setting was used by Cranmer et al. (2015) to measure the level of “fractionalization” in international relations.

3 Exploratory analysis of the C. elegans neural network

Many community-detection methods, including but not limited to many traditional modularity optimization algorithms, provide a user with a single partition of the network into communities along with the corresponding value of the objective function (e.g., modularity). The value of modularity itself can be valuable as in the example of the previous section and is frequently interpreted by users as an assessment of the meaningfulness of that partition, although caution is strongly recommended (see Bassett et al., 2013; Guimerà et al., 2004). There are two immediate problems with analyzing a network with a fixed resolution community-detection algorithm. First, some meaningful structures
could remain undetected (e.g. small cliques lumped together into one community) under modularity optimization at a single resolution (Reichardt and Bornholdt, 2006) due to resolution limits of modularity (Fortunato and Barthélemy, 2007), as well as detectability limits that apply to all polynomial-time community-detection methods (Nadakuditi and Newman, 2012). Second, when the purpose of community detection is data exploration, studying a single resolution (or scale) of community structure might lead to the conclusion that there is only one good way to partition that data (which is often misleading). Instead, being able to access multiple scales of resolution of the data can be crucial for identifying and understanding interesting phenomena that otherwise would have been unexplored.

One example that illustrates the importance of multi-resolution community detection is a study of the neural network of the nematode Caenorhabditis elegans. C. elegans is a free-living, transparent nematode that has become one of the most widely studied living organisms in biology. C. elegans was the first multicellular organism to have its whole genome sequenced and is currently still the only organism for which we have access to its whole connectome. The structural anatomy of C. elegans is approximately a cylinder of diameter 0.1 mm and length 1 mm. The structure of its neuronal wiring can be found in the Wormatlas database (Altun et al., 2002), consisting of 302 neurons, their locations, and the synapses between them as determined by serial section electron microscopy. The database also describes different functions in which each neuron is involved.

Arenas, Fernández, and Gómez (2008a) and Granell, Gómez, and Arenas (2011) studied the structure of the nematode from a complex networks perspective, illustrating that community analysis can help discern the interplay between the topology and functionality of neural networks. The network abstraction describes the nervous system of C. elegans as a directed, weighted network, where nodes represent neuronal cell bodies and edges represent synapses. The resulting network was analyzed via modularity optimization (using the original formulation of Newman and Girvan, 2004), yielding a partition that divided the neurons into five communities corresponding mainly to locations on the worm’s body. This result is not entirely surprising, as it indicates that synapses occur more often within identifiable spatially contiguous and determined regions as compared to a corresponding random-graph model (which is independent of spatial location). However, the authors were interested in analyzing the network at further resolution levels, in the hope that this would reveal new interesting features. To this end, Arenas, Fernández, and Gómez (2008b) proposed an algorithm using a modified version of the original modularity formulation, incorporating a tuning parameter to detect communities across the whole mesoscale. This was done by adding a self-loop of equal weight $r$ to all nodes in the network, a modification that only affects the diagonal of the adjacency matrix and therefore keeps the network connectivity unchanged (cf. the different resolution parameter approach introduced by Reichardt and Bornholdt, 2006). When the weight $r$ takes its minimum value, the maximum-modularity partition for this modified network is a single community including all nodes (the macroscale). Conversely, when the weight of the self-loop is tuned to its maximum value, the corresponding partition separates each node into its own community (the microscale). By tuning $r$ between these two extreme values, one can explore community structure at different resolutions. It is worth noting that as each modularity optimization is independent from the others, the obtained structure is not forced to follow a hierarchical structure.

To apply this algorithm to the C. elegans neural network, Granell et al. (2011) discretized the self-loop weight range into 1000 logarithmically spaced intervals, spanning $r \in [0, r_{\text{max}}]$. By considering $r > 0$, they tunably identified a greater number of communities (whose sizes decreased) with increasing $r$. The mesoscale is depicted in Fig. 3(A), where we can observe multiple important
Figure 3: Results of a multiresolution-community-detection algorithm for the *C. elegans* neural network. Panel A shows the number of detected communities for the modularity-optimizing partition at every value of the topological scale defined by the $\log(r - r_{\text{min}})$, where $r_{\text{min}}$ is the value of $r$ that maximizes the modified modularity measure for the macroscale-partition (i.e., the partition obtained with $r = 0$). Panel B visualizes the frequency matrix of the mesoscales of the *C. elegans*, thresholded at a value of 0.6.

resolution scales. The most persistent scale of community structure is highlighted by a circle in the figure, providing evidence that at this scale the communities are robustly detected. To simultaneously extract information across scales, they built a frequency matrix (or “consensus matrix”) encoding the number of times that two neurons were placed in the same community for the different $r$ values. By thresholding these frequencies, they were able to unravel sub-structural scales corresponding to groups of neurons involved in different functionalities at different scales. Figure 3(B) shows the frequency matrix thresholded at 0.6, a value chosen by fixing the sizes of the groups to be analyzed to ten neurons or less. The figure highlights the five large communities corresponding to optimizing the original modularity measure (i.e. $r = 0$), as well as the substructures within these five communities. In particular, the highlighted scales in Fig. 3(A) contributed most to the frequency matrix.

Trying to classify the functional role of neurons in *C. elegans* is extremely delicate because of their multifunctional aspects; that is, many neurons participate in different synaptic pathways resulting in different functionalities. However, with the previously obtained partition and the extensive description of each neuron in the Wormatlas database, Granell et al. (2011) proposed a tentative classification of some groups of neurons. The task involved assigning functions to groups of nodes that are persistently co-clustered across many scales of resolution. They identified nine groups of neurons that were both strongly persistent and small (specifically, they contained fewer than 10 neurons) and found these communities to be strongly associated to the following functional roles: (I) nose/head orientation movement; (II) head-withdrawal reflex, related to dorsal relaxation; (III) head-withdrawal reflex, related to ventral relaxation; (IV) olfactory and thermosensation reflex; (V) chemotaxis to lysine reflex; (VI) backward sinusoidal movement of the worm, related to touch stimulus; (VII) forward and backward autonomous sinusoidal movement of the worm; (VIII) relaxation state related to a sleep state; and (IX) a group containing neurons with functions that remain unknown. Their classification does not intend to be exact or final, but rather to provide biologists with useful information for future research.
As we have seen, the application of community-detection algorithms is a powerful approach to exploratory data analysis. Moreover, the use of a multiresolution approach identified structures beyond the expected grouping of neurons in different locations, and allowed discovery of groups of neurons that contribute to the same neurological function, providing a takeoff point for further research.

4 Comparing network architectures of the human brain at different states

Another type of neural-connectivity data is functional brain connectivity, which describes the statistical patterns of dynamic interactions among neurons or brain regions (Bullmore and Sporns, 2009). Unlike the “structural network” in the previous section (where the network represents the actual wiring between neurons), “functional networks” can be measured with a variety of neuroimaging or electrophysiological recording methods and can be measured while the brain is in a resting state or under stimulus (Sporns, 2013). The structural and functional brain networks of various model organisms (such as C. elegans mentioned in Section 3) and humans have been shown to organize into communities (usually called modules in this context) which often correspond to specialized functional components (Sporns and Betzel, 2016). Such a modular organization has been suggested as evolutionarily advantageous for several reasons. For instance, it conserves the wiring cost involved in anatomically connecting neurons to constitute circuits or networks, since the connections inside communities are often shorter (Bullmore and Sporns, 2012). Moreover, changes in the modular organization of the human brain have been recently shown to associate with aging and clinical disorders (Fornito et al., 2015).

However, community detection applied to a static single network can fail to capture more realistic situations where the data is temporal, originates from multiple sources or spans multiple spatial and/or temporal scales. To address this shortcoming, some community detection techniques have been recently extended for multilayer networks in which multiple networks form a multilayer stack as shown in Fig. 4A (see also the discussion in Section 2 on the use of multilayer networks in studying temporal Senate roll-call networks). In general, these layers can represent different time windows in an experiment, different individuals, or different experimental conditions.

Cole, Bassett, Power, Braver, and Petersen (2014) applied multilayer community detection to characterize the relationship between resting-state (i.e. subjects were asked to do nothing) and task-evoked (i.e. subjects were asked to perform a specific task such as pressing a button or answering a logic question) functional connectivity in the human brain. Subjects were asked to perform different kinds of tasks while fMRI was used to measure the temporal changes in brain activity across hundreds of brain regions. Then, for each task, they constructed a layer in a multilayer network using the Pearson correlations between the fMRI time series of all pairs of brain regions. The authors hypothesized that networks obtained from resting-state fMRI would reveal an intrinsic architecture that would also be present across a wide variety of task states (i.e. across networks obtained from fMRI measurements under different tasks), but also that some task-evoked connectivity changes unique to each task state would be evident.

To estimate both intrinsic and evoked architectures simultaneously, Cole et al. (2014) used the multilayer generalization of modularity (Mucha et al., 2010) to uncover communities spanning across layers. In this setting, the multilayer formulation across subjects connects every brain region in a given layer to itself in each of the other layers with an identity arc of edge weight $\omega$, called
Figure 4: Multilayer community detection applied to resting state and task-evoked functional brain networks (Reprinted figure with permission from Cole et al., 2014 ©2014 Elsevier Inc). Each layer in the multilayer network (schematic shown in panel A) represents the functional connectivity between brain regions under different tasks. The layers are coupled by identity arcs of weight $\omega$ connecting each node (brain region) in a given layer to itself in all other layers (dashed lines). Panels C-D show the similarity (measured by the standardized Rand coefficient) of each task partition to the resting-state partition reported in Power et al. (2011) (shown in panel B) as a function of $\omega$. As $\omega$ increases, the task partitions converge to a consensus partition similar to the resting-state community partition.

The authors used small values of the coupling parameter, $\omega$ to identify network communities elicited differentially across tasks, and large values of $\omega$ to identify consensus communities present across tasks. For a given $\omega$, they applied multilayer community detection and compared the partition obtained for each task layer with the resting-state partition reported by Power et al. (2011) (which used the Infomap community-detection method by Rosvall and Bergstrom, 2008). In particular, for every value of $\omega$, they performed 100 random optimizations and chose the one that was most similar on average to the other 99 optimizations as the representative partition. This is one example of a consensus algorithm, which is used to find stable results from a set of partitions delivered by stochastic methods, as encountered with some of the computational heuristics for modularity optimization.
The similarity between task-specific communities and resting-state communities is reported in Fig. 4C-D, shown as a function of weight $\omega$. Similarity was quantified by the z-score of the Rand coefficient, which counts the fraction of node pairs identified the same way by both partitions (either together in both or separate in both, see Traud et al., 2011). To ensure the robustness of the results, two data sets were used. One data set consisted of 64 tasks (each performed by 15 individuals) defined as distinct cognitive processes with minimal perceptual changes across tasks. The second data set involves seven tasks (each performed by 118 individuals) that were chosen to elicit the involvement of all major cognitive domains and brain systems. In both data sets, it was found that as $\omega$ increases, a single architecture emerged with high similarity to the resting-state network architecture. While multilayer community detection indeed encourages a single consensus partition at high coupling parameters, there is no guarantee that this partition would look like the resting-state partition. In other words, the network architecture present across many task states is also present during rest, implying an intrinsic network architecture.

Upon further examination, the authors identified a set of small (but likely functionally important) task-evoked connectivities that differed from the rest-state connectivities. To quantify these network changes, they calculated the percentage of connections that significantly (quantified by t-tests) changed from the rest state, revealing a prominent pattern of decreased within-community connectivity and increased between-community connectivity during task performance, which suggests a partial breakdown of network communities during task performance so that activity can better flow between systems with diverse functions.

Providing a mesoscale perspective on the organization of brain networks, multilayer community detection employed at different coupling parameters can be useful for network comparison. Here, the authors compared connectivity patterns between brain regions (representing the functional dependencies between their fMRI time series) under different tasks and a rest state, revealing an intrinsic community structure that was present across brain states as well as small (but consistent) changes in the community structures that were common across tasks.

5 A probabilistic network model for malaria parasite genes

In addition to the analysis of neuroscience data, community detection can be useful for analyzing other biological data. The nature of community detection applied to biological data is desirable for developing a mechanistic understanding of the underlying system. Here we highlight the work of Larremore, Clauset, and Buckee (2013), which used community detection to develop and computationally investigate a hypothesis about the nature of recombination in the sequences of the genes (called var genes) encoding proteins in the human malaria parasite *Plasmodium falciparum* genome. This work is novel and interesting because the authors used a network representation of their data, along with the communities found in this representation, to formulate and validate biological hypotheses.

Rich genetic diversity in the var genes of the human malaria parasite has been shown to contribute to the complexity of the epidemiology of the infection and disease. The parasite can change which of the var genes are expressed at any given time on the infected red blood cell, which prevents the antibody from recognizing and resisting the new protein. One diversity-generating mechanism is recombination, which is the exchange and shuffling of genetic information during mitosis and meiosis (Barry et al., 2007). The ability to understand genetic diversity is complicated by inadequate tools to uncover the phylogeny, or genetic relationship between sequences resulting from recombination events, in a scalable and statistically rigorous way. The typical analyses for evolutionary
data assume a tree-like relationship between events, which is unrealistic for recombination data. To address this challenge, Larremore et al. (2013) use a novel approach: they cast their problem in terms of a collection of networks. Then, they apply community detection to each of the networks and use the properties of the communities to generate hypotheses of the mechanisms behind the recombination process.

More specifically, to investigate the heterogeneity and the corresponding possible patterns in recombination events across a set of 307 sequences from the *var* gene, the authors restricted their analyses to 9 particular “highly variable regions” (HVR) within each of the 307 sequences. Then for each HVR, they constructed a network, where the nodes represented the 307 sequences and an edge was placed between a pair of nodes if they had evidence of a recombinant relationship, based on a notion of sequence similarity within the particular HVR. Communities were then identified in each of the 9 networks using a degree-corrected stochastic block model (SBM) approach (Karrer and Newman, 2011). In the SBM, the probability of an edge existing between a pair of nodes depends on their community assignments and hence nodes within a community are connected to each other and to other communities in a characteristic way. For a network with $N$ nodes and $K$ communities, the SBM is parametrized by an $N$-length array $\mathbf{z}$, where $z_i$ gives the community assignment for node $i$, and a $K \times K$ matrix, $\mathbf{\Theta}$, where $\theta_{ij}$ (together with the node degrees) specifies the probability of an edge existing between nodes in communities $i$ and $j$. In the process of fitting the SBM, one learns the parameters $\mathbf{\Theta}$ and $\mathbf{z}$ that are most likely to describe the data, and hence these parameters can then be used to sample networks from the model. In this analysis, sampling from the model was useful because it allowed the authors to create synthetic networks to computationally validate their hypotheses about the constraints influencing recombination.

After identifying communities within each HVR network, as shown in Fig. 5 the authors used two summary statistics to formulate their biological hypothesis. First, the variation of information (Meila, 2005) was used to compare the community assignments of nodes (i.e. each of the 307
sequences) across the 9 HVR networks. They observed that each network had a prominent community structure (i.e. far from random) and that the community assignments between networks were quite distinct. These observations motivated the hypothesis that recombination events occur in constrained ways, leading to a strong community structure, and that one should analyze HVR networks individually instead of building a consensus network that aggregates the HVR networks. Next, they used assortativity (see, e.g. Newman [2002]) to overlay the network structure with various known biological features of the sequences, such as var gene length. Specifically, assortativity quantifies the tendency of nodes of the same type (e.g. same gene length) to be connected in the network. They observed that three HVR networks had community structure correlating strongly with two biological features (i.e. nodes of the same biological label tend to group together), while three other HVR networks with highly heterogenous community structure were unaligned with any of the known biology. These observations allowed for the formulation of the hypothesis that the HVRs that are unrelated to each other also promote recombination under unrelated constraints and are responsible for fostering genetic diversity to avoid immune evasion.

Given the ability to find communities within each HVR network and the lack of similarity in community structure between HVR networks, Larremore et al. [2013] were able to formulate and test hypotheses for the diversity-generating mechanisms of var genes, and this would have been difficult using standard phylogenetic approaches or without adopting a community-based perspective. The application of the stochastic block model to this task provided a statistically grounded approach for testing the plausibility of the model.

**Concluding comments**

Through five representative case studies from diverse application domains, we have demonstrated the utility of community detection in data-analysis tasks such as prediction (see Section [1]), node role classification and temporal evolution (see Section [2]), multi-scale functional analysis (see Section [3]), network comparison (see Section [4]), and data representation for probabilistic model construction (see Section [5]). Our goal here was to provide the reader with an application-driven perspective on the various uses of community detection while highlighting application-specific goals and motivations for identifying communities in networks. We have by no means covered even a small fraction of the activity in community detection with the above examples, and many others could have been used [see, for example, recent applications in Hi-C data analysis (Cabreros et al., 2016), network security (Ding et al., 2012) and understanding of animal societies (Rubenstein et al., 2015)]. We hope that our presentation encourages readers to think about how community detection might be useful in their own work.

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