REVIEW

Temporal dynamics and network analysis

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Summary

1. Network analysis is widely used in diverse fields and can be a powerful framework for studying the structure of biological systems. Temporal dynamics are a key issue for many ecological and evolutionary questions. These dynamics include both changes in network topology and flow on the network. Network analyses that ignore or do not adequately account for the temporal dynamics can result in inappropriate inferences.

2. We suggest that existing methods are currently under-utilized in many ecological and evolutionary network analyses and that the broader incorporation of these methods will considerably advance the current field. Our goal is to introduce ecologists and evolutionary biologists interested in studying network dynamics to extant ideas and methodological approaches, at a level appropriate for those new to the field.

3. We present an overview of time-ordered networks, which provide a framework for analysing network dynamics that addresses multiple inferential issues and permits novel types of temporally informed network analyses. We review available methods and software, discuss the utility and considerations of different approaches, provide a worked example analysis and highlight new research opportunities in ecology and evolutionary biology.

Key-words: dynamics, flow, graph theory, network, time aggregated, time ordered, time-scale

Introduction

Network analysis is of current and growing importance in diverse fields including ecology and evolutionary biology. Many biological systems consist of interconnected units and can be usefully modelled as networks, which are mathematical constructs describing a set of edges between vertices (Albert & Barabasi 2002; Proulx, Promislow & Phillips 2005; Diestel 2010; Newman 2010). The identity of each varies with the system and question of interest – for example, vertices can be genes, proteins, neurons, individual organisms, species, geographic regions, etc. and edges can represent regulatory interactions, binding affinities, synapses, social associations, predation, gene flow and so on (Dunne, Williams & Martinez 2002; Proulx, Promislow & Phillips 2005; May 2006; Bascompte & Jordano 2007; Wey *et al.* 2008; Sih, Hanser & Mchugh 2009; Bascompte 2010). Network *topology* refers to the structure of edges and vertices and can be quantified with a range of statistics about the pattern of connections among

vertices. Processes of *flow* can occur on these edges, representing transfers of resources, disease, information, etc. Network theory provides a basis for analysing outcomes that depend on network topology or flow and is thus a powerful framework for testing hypotheses about biological interactions by measuring and comparing network variation.

Questions of network dynamics are of key interest for many ecological and evolutionary systems, for example, how and why the topology of the network changes over time, how these changes affect the flow of resources (or disease) through the network, and the nature and importance of feedbacks between flow processes and topological change. However, network dynamics can be quantitatively challenging and difficult to address and are largely unaccounted for in most extant network analyses (James, Croft & Krause 2009; Sih, Hanser & Mchugh 2009; Bascompte 2010).

In the current standard framework, networks are usually taken as representations of a system aggregated over a certain limited time interval. It is difficult to ask questions about how and why a system changes over time using this static abstraction, which is based on several critical assumptions. Specifi-

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cally, this approach assumes that the network's topology is fixed; processes of flow are at a dynamic steady state; edges represent persistent interactions; interactions are sufficiently stable to address the question of interest; and there is sufficient sampling so that the structure of the network is accurately and completely known. Together, these assumptions imply that the chosen representation of interactions is sufficient to evaluate equilibrium situations, but breaking them, which occurs in many real networks, can lead to a range of serious inferential problems (Box 1). Many networks involve dynamics but have so far been analysed using methods more appropriate for static systems. Thus, while these assumptions permit some simple and fast analyses, an explicitly dynamic approach can be more useful.

Here, we review current approaches that address the need for incorporating temporal dynamics into network analysis of observational data in ecology and evolutionary biology. Our goal is to introduce ecologists and evolutionary biologists interested in network dynamics but that may currently be unfamiliar with the concepts and techniques already available. We survey basic concepts that are important in dynamic network analysis as well as recent advances in a range of disciplines and their applications in ecology and evolutionary biology. Furthermore, we discuss considerations in determining the appropriate network representations for the dynamics of interest and highlight important ecological and evolutionary questions that can be understood as network dynamics questions at different time-scales. These concepts are brought together via the *time-*

Box 1. Common inferential problems can arise when different time-scales are important to networks. Here, we highlight four common types of problems.

> **a.** Standard static network analyses measure a set of interactions with the implicit assumption that edges in a network are permanent associations. If instead, interactions are brief, rarely connected vertices may appear connected more often than they should be, changing the topology of the network. Varying the window over which to aggregate interactions into a network can produce a range of topologies and resulting inferences. Too short of a window, and no individuals are connected; too long of a window, and perhaps all individuals incorrectly appear connected (James, Croft & Krause 2009; Blonder & Dornhaus 2011). Alternatively, weighting edges by interaction probabilities can represent true levels of connectivity.
> **b.** If networks change more rapidly than an investigator samples (e.g. if the dashed edge in the illustration changes state during sampling of interactions), dramatic changes in topological dynamics can occur (Stumpf, Wiuf & May 2005; de Silva *et al.* 2006; Franks *et al.* 2009). Edges may not be persistent, well defined or adequately sampled at the time-scales of interest.
> **c.** Simulated removal or addition of edges and vertices often neglect topological dynamics of a network. Investigators may incorrectly assume that networks do not change their structure in response to a perturbation (Albert, Jeong & Barabasi 2000). Many networks rewire edges in response to perturbation, potentially even at time-scales relevant to flow dynamics. Removal simulations that do not include rewiring should be considered critically if rewiring could occur at relevant time-scales.
> **d.** The ordering of events is important to flow dynamics on a network and can affect inference about resource flow processes. Interactions that are aggregated into a network may suggest that individuals are connected to each other. However, the ordering and timing of interactions imply that some paths are causally impossible, and some paths that appear short in terms of number of edges may be long in time delay (Holme 2005; Chan, Holmes & Rabadan 2010; Blonder & Dornhaus 2011). In this example, the shortest-length path from A to D is A-B-D, but the shortest-time path is actually A–B–C–D. Also, until Saturday, A can spread a resource to D, but D cannot spread a resource to A. Neither inference is possible without knowledge of the ordering of events.
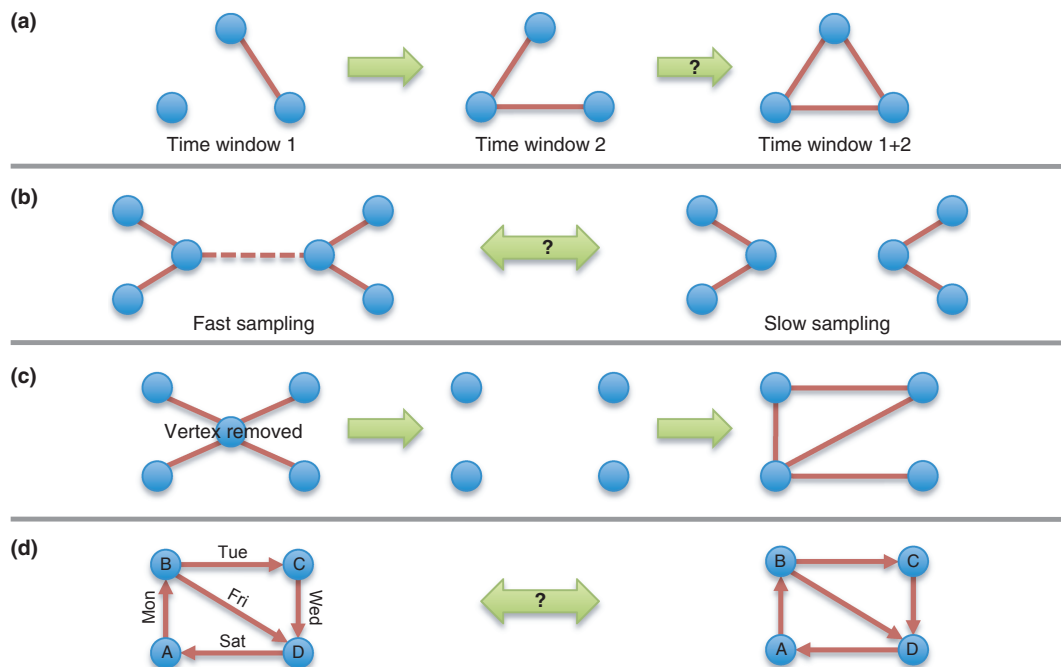
ordered network framework, which unifies dynamics at multiple time-scales, resolves common inferential problems and enables many new types of analyses. We provide a guide to time-ordered network analysis that includes computational resources, work through an example application and identify research areas where this framework may be valuable.

Two types of dynamics: topology and flow

Our concept of the network, and what it represents, depends on two key types of dynamics: flow processes on the network and changes in the underlying topology of the network. Flow dynamics are how resources, contacts, information, disease, etc. are propagated between network vertices, for a given set of vertices and edges. Topological dynamics are how the network structure changes through variation in the identity or weight of edges (sometimes known as 'rewiring'). Systems may exhibit one or both types of dynamics, and questions of interest will determine the appropriate focus. For example, evolutionary and seasonal changes in the interactions between multiple species in a pollination network (Bascompte & Jordano 2007; Petanidou *et al*. 2008) are topological dynamics. Alternatively, resource exchanges between plants and animals (e.g. biomass in a food web (Jarre-Teichmann & Pauly 1993) or disease in a population (Rothenberg *et al*. 1998)) would represent flow dynamics.

The relative times-cales of underlying processes can be important to understanding both topological and flow dynamics. Topology can influence flow, and also flow can influence topology. If both are occurring on a similar time-scale, feedbacks between the two may exist. In the example of disease transmission on a social network, contracting the disease (the result of flow processes) can result in changes to interactions with others (Croft *et al*. 2011a), either through changes in the sick individual's behaviour or through changes in response of others to that individual and thus to the topology of the network (Fefferman & Ng 2007; Bansal *et al*. 2010; Romano *et al*. 2010). Networks that exhibit coupling and strong feedback between the two time-scales are sometimes considered 'adaptive' or 'co-evolutionary' (Gross & Blasius 2008).

Time-ordered networks as a unifying framework

A framework for analysing network dynamics that unifies topology and flow dynamics is available through the concepts of *time-ordered* networks and *time-aggregated* networks (Kempe, Kleinberg & Kumar 2002). Both types of networks can be used to study different aspects of topological and flow dynamics, as shown below. This framework encompasses many extant approaches to network dynamics and can be used not only to avoid the critical issues discussed earlier (Box 1) but also to enable novel and temporally informed analyses. References to extant studies, computational tools and future opportunities are organized thematically in Table 1 and cited from within the text. Additionally, the free R package 'timeordered' implements many of these analyses, using any data that

list the identities of vertices and edge occurrence time for each interaction. We provide an example analysis of ant colonies using time-ordered networks that highlights the power of this framework (Box 3).

TIME-ORDERED NETWORKS

For many network phenomena, the order, duration and timing of events can be critical (Box 1d) (Moody 2002). Time-ordered networks represent data observed for a set of interactions that occur at certain times, thereby retaining complete information on the ordering, duration and timing of events. Graphically, vertices in a time-ordered network can be represented as a series of static networks with edges distributed over the time dimension. Vertices always move forward in time, and edges between vertices are visualized as arrows drawn at the start and stop time steps for an interaction (Box 2a). The arrows can be bidirectional if the interaction is undirected (i.e. A interacts with B implies B interacts with A). Thus, the time-ordered network is a complete record of all observed interactions at all time points which describes all flow and topology changes. Time-ordered networks have also been called temporal networks (Holme & Saramäki 2011), temporal graphs (Kostakos 2009), dynamic networks (Carley 2003; Lahiri *et al*. 2008) or dynamic graphs (Berger-Wolf & Saia 2006).

Mathematically, time-ordered networks are directed acyclic graphs (Diestel 2010). In the graph, a 'temporary vertex' is created at the start and stop time for each interaction and assigned a label corresponding to the identity of the corresponding vertex in the static network. Thus, in the time-ordered network, a single vertex in a static network (e.g. Individual 1) will be represented by multiple 'temporary vertices' (e.g. Individual 1, at time t_1; Individual 1, at t_2). Next, an edge is created between 'temporary vertices' at the start and stop time of each interaction, and a directed edge is created that connects the 'temporary vertex' to itself at the stop time for one interaction and the start time for the next interaction. If certain vertices do not exist at some time points, the investigator may choose to either keep the vertex in the network without recording any further interactions (e.g. an animal that has temporarily left the area of observation) or instantiate a new time-ordered network without this vertex being present (e.g. an animal that has died and will never interact again). The latter approach may be more appropriate when using statistics such as the network diameter that are sensitive to global connectivity or extra zeros.

Time-ordered networks can be used to answer many descriptive questions about flow dynamics (Table 1, F2). For example, how fast (if at all) can a resource propagate from one vertex to another? Determining these causally permitted pathways of resource flow is possible with time-ordered networks by tracing any line that follows a non-decreasing path in time (Kempe, Kleinberg & Kumar 2002). An example is shown as a dotted yellow line in Box 2a. In Box 1d, we show how for several apparently connected vertices, A can transmit a resource to C via B only by interacting with B before B interacts with C. Similarly, bounds on resource flow can be determined by determining shortest-time or shortest-

Table 1. Multiple research questions in ecology and evolutionary biology could be addressed with network dynamics approaches. This table highlights shared questions, key references and available computational resources

Problem	Key biology references	Methods references and software	Available free software	Example future applications
Topological dynamics (T)				
T1. Measuring response of network to external factor or perturbation	Extinctions in food webs (Dunne & Williams 2009), ecological degradation in food-web degradation (Coll, Lotze & Romanuk 2008; Staniczenko *et al.* 2010), temporal variability in plant–pollinator systems (Alarcon, Waser & Ollerton 2008) and in food webs (Ings *et al.* 1993) and other eco (Walters, Christensen & Pauly 1997) logical networks (Olff *et al.* 2009), yeast regulatory gene networks under variable environments (Luscombe *et al.* 2004), primate social networks (Flack *et al.* 2006), marmot dispersal (Blumstein, Wey & Tang 2009).	Time series and regression methods applied to time-dependent statistics (this manuscript)	statnet (R), dynamicnetwork (R), SIENA (R)	Conservation: what will be the impacts of one species' extinction on others?
T2. Prediction of future network state from current network state	Plant–animal mutualistic networks (Bascompte & Jordano 2007), food-web assembly (Williams & Martinez 2000) invasion success (Romanuk *et al.* 2009) stability (Thebault & Fontaine 2010).	Assessment of causality (Seth & Edelman 2007), structure prediction (Liben-Nowell & Kleinberg 2003; Lahiri & Berger-Wolf 2007; Snijders, Koskinen & Schweinberger 2010; Dunlavy, Kolda & Acar 2011; Lü & Zhou 2011)	MSBVAR (R)	Mutualism: is the identity of specialist pollinators consistent between years?
T3. Model selection and hypothesis testing	Social insect networks (Blonder & Dornhaus 2011)	Stochastic actor-based models (SAM) (Snijders, Van de Bunt & Steglich 2010), resampling (Croft *et al.* 2011b) (this manuscript)	SIENA (R), timeordered (R)	Evolution: do newly evolved proteins interact preferentially with functionally central proteins?
T4. Identification of temporally persistent network structures and of variation between groups	Community membership in bat fission–fusion societies (Kerth, Perony & Schweitzer 2011), queen–worker differentiation in ant social networks (Blonder & Dornhaus 2011), persistence of primate social associations (Henzi *et al.* 2009)	Community detection algorithms (Tantipathananandh, Berger-Wolf & Kempe 2007; Berger-Wolf, Tantipathananandh & Kempe 2010; Mucha *et al.* 2010), resampling of time-dependent network statistics for different network subsets (Newman 2010; Croft *et al.* 2011b), lagged association rates (Whitehead 2009)	CommDy, SIENA (R)	Animal behaviour: over what time-scales is group membership consistent?
Flow dynamics (F)				
F1. Model selection and hypothesis testing	Social learning ((Kendal *et al.* 2010)	Resampling (this manuscript), network-based diffusion analysis (Franz & Nunn 2009; Hoppitt, Boogert & Laland 2010), stochastic actor-based models (Snijders, Van de Bunt & Steglich 2010)	timeordered (R), NBDA (R), SIENA (R)	Social behaviour: do females share information faster than males?

Table 1. (Continued)

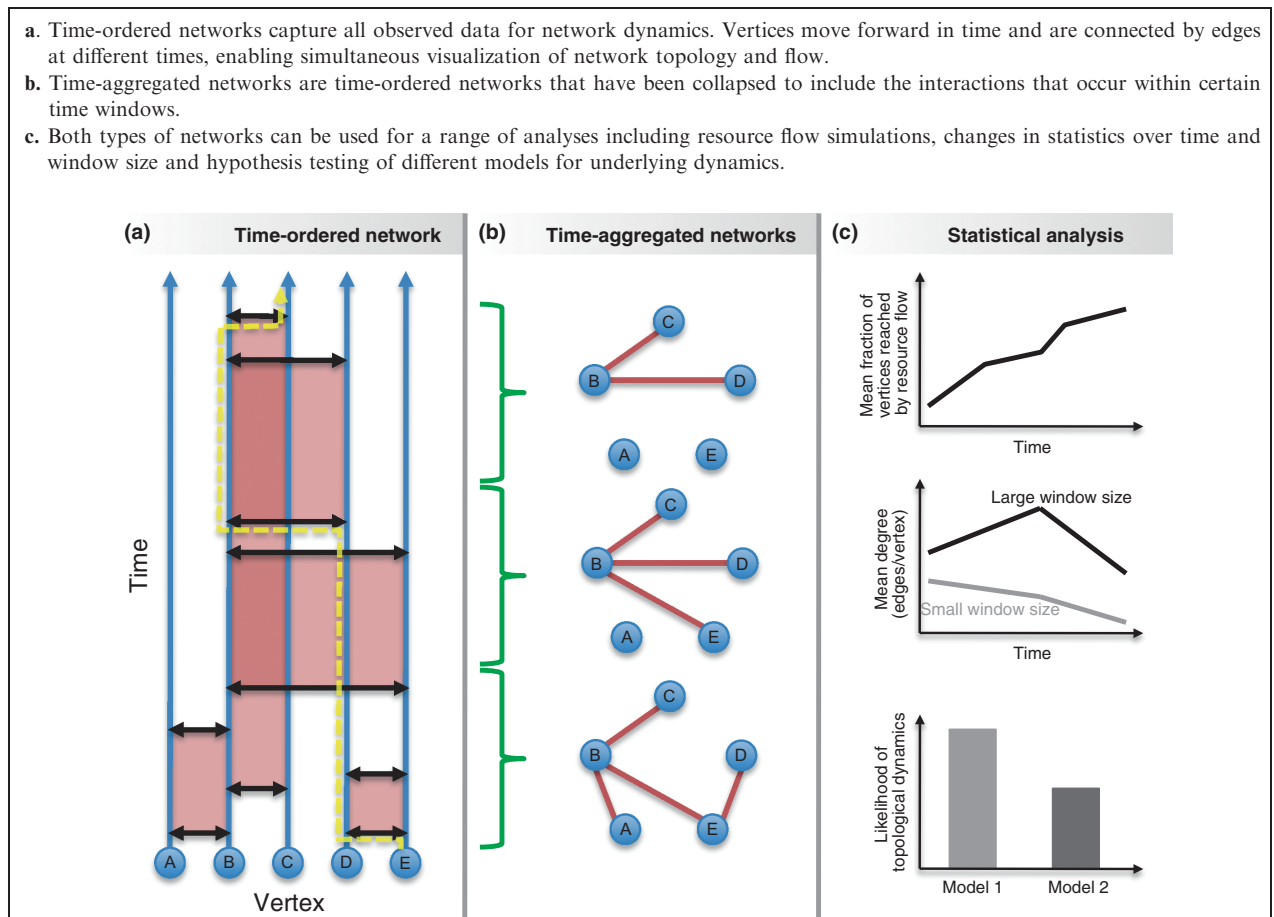| Problem	Key biology references	Methods references and software	Available free software	Example future applications
F2. Observation or manipulation of resource flows	Flow of individuals between populations (May 2006; Fletcher et al. 2011), food between animals (Otterstatter and Thomson 2007; Naug 2008; Sendova-Franks et al. 2009; Romano et al. 2010), biomass between species in a food web (Jarre-Teichmann & Pauly 1993), disease between people (Chan, Holmes & Rabadan 2010; Romano et al. 2010), information between people (Centola 2010, 2011)	Food-web dynamics (Walters, Christensen & Pauly 1997)	timeordered (R)	Trophic interactions: do generalist predators have a disproportionate effect on population dynamics?
F3. Identification of nodes or processes important for maximizing or minimizing flow	Spread of disease (Volz & Meyers 2007; Salathé & Jones 2010).	Maximizing influence in social networks (Kempe, Kleinberg & Tardos 2003) (this manuscript), finding influential individuals (Prakash et al. 2011)	timeordered (R)	Social behaviour: does information flow most rapidly through high-status individuals?
F4. Simulation of resource flow	Resource or information transfer in social insects (Naug 2008; Blonder & Dornhaus 2011; Pinter-Wollman et al. 2011), social learning (Kendal et al. 2010)	Simulation of flow on shortest paths (Holme 2005) (this manuscript) or stochastically via any allowed path (Onnela et al. 2007; Lahiri et al. 2008; Tang et al. 2010), network-based diffusion analysis	statnet (R), dynamicnetwork (R), epinet (R), timeordered (R)	Disease dynamics: is the spread of an epidemic dependent on the order in which animals contact each other?
F5. Prediction of stable outcomes of games or individual-based models	Evolution of cooperation (Ifti, Killingback & Doebeli 2004; Ohtsuki et al. 2006; Szolnoki & Perc 2009), gene interactions and adaptive landscapes (Kauffman & Johnsen 1991; Kauffman et al. 2003), origin of macroecological pattern (O'Dwyer & Green 2010), cellular automata models for spatial distribution of vegetation (Scanlon et al. 2007) and species invasions (Eppstein & Molofsky 2007).	Cellular automata models ((Wolfram 2002) and agent-based models (Frantz & Carley 2009; Yates et al. 2009)	NetLogo	Ecology: how do interactions between individual plants lead to landscape-scale vegetation patterning?
Coupled dynamics (C)				
C1. Measurement of time delays and resource flows	Social insect networks (Blonder & Dornhaus 2011)	Reachability of nodes (Holme 2005), waiting times between interactions (Barabasi 2005; Karsai et al. 2010; Tang et al. 2010), vector clock latencies establishing bounds on minimum time delays for resources to propagate between nodes (Kossinets, Kleinberg & Watts 2008)	timeordered (R)	Metapopulations: what limits gene flow between different regions?
C2. Prediction of outcomes of games or of network stable states	Games where agents may change the number and identity of the partners they interact with (Lieberman, Hauert & Nowak 2005; Bryden et al. 2011; Fehl, van der Post & Semmann 2011; Rand, Arbesman & Christakis 2011)	Adaptive networks (Gross & Blasius 2008), behavioural networks (Sih, Hanser & Mchugh 2009), stability analysis (Gross, D'Lima & Blasius 2006; Holme & Newman 2006)		Evolutionary theory: when can cooperation between multiple agents persist?

Table 1. (Continued)

Problem	Key biology references	Methods references and software	Available free software	Example future applications
C3. Response to perturbation	Behaviour shifts during epidemics (Rothenberg et al. 1998; Gross, D'Lima & Blasius 2006; Shaw & Schwartz 2008; Funk et al. 2009; Volz & Meyers 2009; Bansal et al. 2010), variable species interactions in food webs because of changes in resource flow (Uchida & Drossel 2007; Ings et al. 2009; Staniczenko et al. 2010; Valdovinos et al. 2010)	Stochastic actor-based models (Snijders, Van de Bunt & Steglich 2010)	statnet (R), dynamicnetwork (R), SIENA (R)	Disease dynamics: does individual behaviour shift after infection?
C4. Consequences of individual mobility on proximity networks	Social insect (Pinter-Wollman et al. 2011; Jeanson 2012) or animal (Flack et al. 2006; Couzin 2009; Onnela et al. 2010) networks	Null models of proximity network properties (Blonder & Dornhaus 2011; Bode, Wood & Franks 2011)		Animal behaviour: how do the movement patterns of individuals affect the spread of information in the group?
C5. Control of network	Human cooperation (Rand, Arbesman & Christakis 2011), Food webs (Sahasrabudhe & Motter 2011), genomic networks and organismal development (Abdallah 2011)	Control theory (Zecevic & Siljak 2010; Liu, Slotine & Barabasi 2011)		Food webs: if a specialist predator goes extinct, can the removal of a second species permit the persistence of a third species of interest?

unique-vertices paths between individuals. For example, a question like 'At least how many unique individuals does a resource pass through when moving from A to C?' is important for questions about network efficiency or the importance of certain individuals in determining resource flow. One can also identify key vertices for resource-spreading processes by computing standard network metrics on a time-ordered network (Table 1, F3). For example, a high betweenness centrality of a 'temporary vertex' (number of shortest paths in the network passing through this vertex) indicates that this vertex mediates many resource flow paths at this time point.

Summary statistics of time-ordered networks also provide insight into dynamic properties of the system (Table 1, F4, C1). These metrics can be made explicitly dependent on absolute time and time intervals and thus can provide more insight into processes underlying networks than static metrics. One useful metric is the mean time delay between two random vertices over a certain time window. For example, a short average time for resource flows between some individuals may indicate membership in a common group, or identifying an individual through which many shortest-unique-vertices paths pass can indicate that this individual plays a preferred role in mediating resource flows. Also, if this time delay is only short for the first half of the data collection interval and later becomes longer, we may conclude that the underlying dynamic process is changing; this group no longer plays a preferred role in resource flow processes. We further describe applications of such statistics in the worked example (Box 3). Note that the details of resource flow on the time-ordered network should depend on the resource type – for example, some resources like food are passed on but not retained while others like disease are passed on and retained. This means that the dynamics of resource flow processes may shift from a transfer to a broadcast process. Using the correct metric for each type of flow process is critical; we refer the reader to (Borgatti 2005) for a comprehensive perspective on this issue.

Simulations or observations of flow dynamics occurring on networks with fixed topology can be described using time-ordered networks (Table 1, F4, C2). For a network with fixed topology whose edges represent potential interactions that depend on the details of the system, the occurrence and ordering of actual interactions can be completely described by a time-ordered network. The approaches described in previous sections can then be used to make time-dependent descriptions and inferences about the system. This approach may also be valuable for individual-based or cellular automata models (Wolfram 2002) where network topology is fixed – for example, in a cellular automata model of pollen flow between multiple patches with unchanging connectivity, one could simulate the activity of different pollen carriers and test the hypothesis that plants with more conspecific neighbours had higher rates of resource flow. An area of active application is in social learning, where network-based diffusion analysis (Franz & Nunn 2009; Hoppitt, Boogert & Laland 2010) is used to assess how the social structure of a group predicts the rate of acquisition of a new behaviour in group members. This general approach

Box 2. Time-ordered and time-aggregated networks provide complementary approaches to describing networks and making inferences.

> **a**. Time-ordered networks capture all observed data for network dynamics. Vertices move forward in time and are connected by edges at different times, enabling simultaneous visualization of network topology and flow.
>
> **b**. Time-aggregated networks are time-ordered networks that have been collapsed to include the interactions that occur within certain time windows.
>
> **c**. Both types of networks can be used for a range of analyses including resource flow simulations, changes in statistics over time and window size and hypothesis testing of different models for underlying dynamics.

of fitting multiple competing models of flow on a fixed network to observed patterns of flow would likely be applicable in other areas.

Similarly, proximity networks have been another valuable area for the application of time-ordered networks (Table 1, C4). These networks are relevant to a wide range of animal groups because they describe interactions between mobile individuals (vertices) where edges are created when individuals are near each other and are destroyed as individuals move apart. Here, time-ordered networks can describe group dynamics, and observed data can be easily compared to networks constructed from null models of individuals' motion.

Time-ordered networks can also provide insight into patterns in the processes of network rewiring after perturbation by detecting new temporally variable or persistent structures or by characterizing changes in flow (Table 1, C3). For example, in a food web, energy flows may appear to become more compartmentalized during some seasons (Jarre-Teichmann & Pauly 1993); time-ordered network analyses can provide a rigorous test of this hypothesis.

Most powerfully, time-ordered networks enable new types of null modelling of both topological and flow dynamics that permit inferences to be made (Table 1, F1). Resampling of time-ordered networks is a powerful approach in which certain correlations within observed data are randomized while others are preserved – for example, identities of interaction partners or times of interactions. This approach is useful for understanding the processes controlling a network phenomenon and for hypothesis testing without needing to meet the assumptions of more standard statistics (Franks *et al.* 2009; James, Croft & Krause 2009; Karsai *et al.* 2010). For example, one can determine whether resources flow between two vertices significantly faster than expected by simulating a large set of networks that differ from the observed data only by randomization of the times at which interactions were observed. If the observed shortest path length between the focal vertices is indeed shorter than in some fraction (e.g. 95%) of the simulated networks, then there are processes causing temporal correlations between interactions. As with any re-sampling procedure, investigators must be careful to break only correlations in the structure of interest while maintaining all other structures in the data set (Holme 2005). We show how these approaches can be applied in the worked example (Box 3).

TIME-AGGREGATED NETWORKS

A benefit of time-ordered networks is that they can be flexibly decomposed into multiple time-aggregated networks based on selected time windows, which can be analysed with standard

Box 3. An example analysis using time-ordered (a–c) and time-aggregated (d–f) networks. Many common questions can be quickly answered using network dynamics approaches. Here, we use data from a study of interactions between individually marked *Temnothorax rugatulus* ants (Blonder & Dornhaus 2011). The code for these analyses uses the *timeordered* R package which is available from http://cran.r-project.org/web/packages/timeordered/index.html.

a. The interactions between ants can be visualized as a time-ordered network. Shortest-length paths for resource flow can be easily calculated; one such path between two individuals is shown in red.

b. Resource flows can be traced. Here, resources are simulated as being transferred during every interaction. The hypothesis that resources originating from the ant queen spread significantly faster than those from worker ants is falsified ($P = 0.23$) by comparing the distributions of the 'fraction of workers reached' at $\Delta t = 1000$ s.

c. The effect of time-ordered network structure on network statistics can be quantified. For example, the importance of the ordering of events to time delays for resource flows can be measured by calculating the observed network-mean vector clock latency at $t = 1440$ s and comparing it to the distribution of latencies for a network where the ordering of interactions has been resampled. Here, the observed network has significantly greater latencies ($P = 0$ for 1000 randomizations) than the networks with random ordering of interactions, indicating that network structure retards the flow of resources.

d. The time-ordered network can be collapsed to several time-aggregated networks; here, nine networks with the same size of time window are shown.

e. Network statistics can be computed for different sets of time-aggregated networks. Here, the degree distribution is shown for the nine networks shown above (left), four networks with larger time windows (centre) and one network whose time window spans the observation period (right). The observed properties of the degree distribution are highly sensitive to the time interval and window size, potentially changing inferences.

f. Time-series analyses of time-aggregated network statistics can be used for hypothesis testing or pattern identification. Here, colony activity level is hypothesized to drive network closeness centrality. The cross-correlation between these time series is highest ($\rho = 0.91$) at zero time-lag, indicating a potentially strong and immediate causal relationship between activity level and closeness centrality.
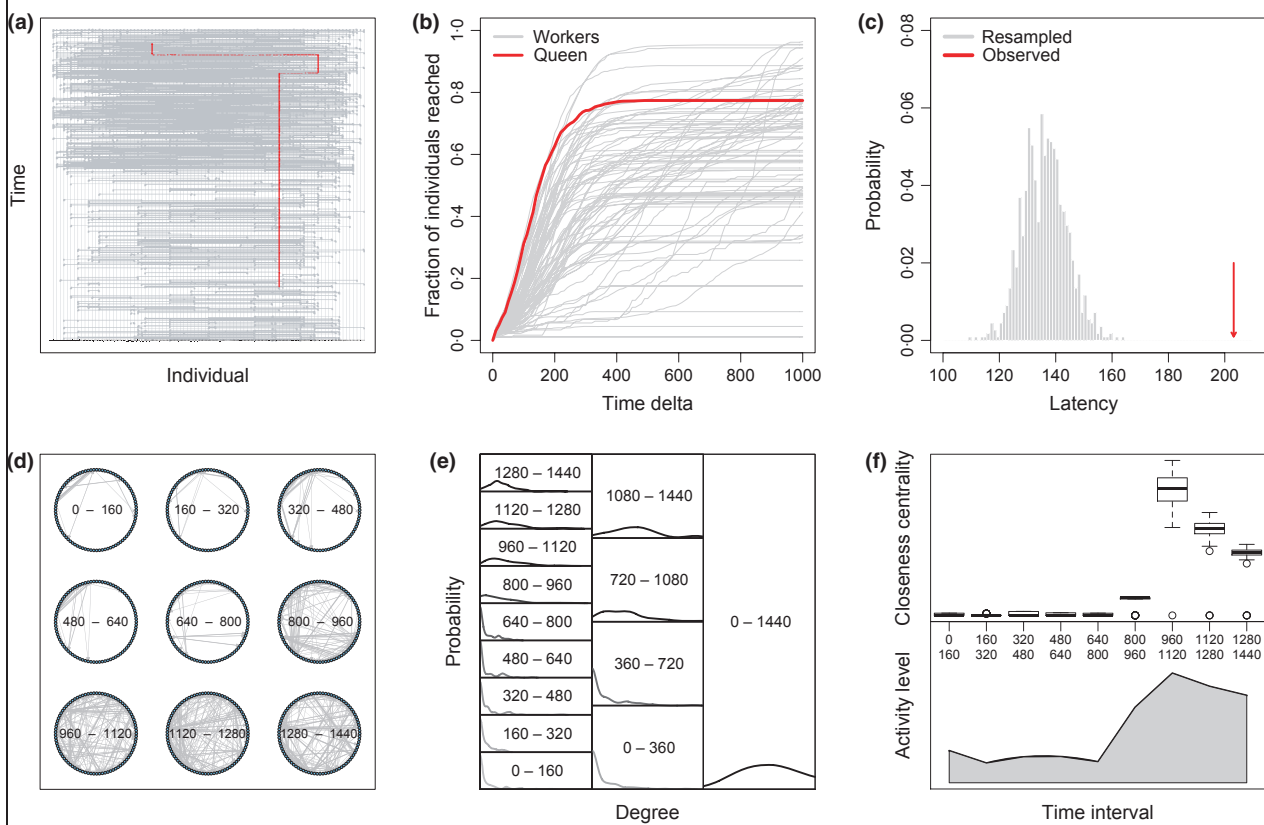
methods. Essentially, this approach reduces the time-ordered data into a series of static networks. To generate *time-aggregated* networks, one subsets the time-ordered network at different start and stop time points and then projects along the time axis to retain any interactions that begin or stop within the window (Clauset & Eagle 2007) (Box 2b). They are sometimes called panels, waves, or longitudinal data (Robins *et al.* 2007; Snijders, Van de Bunt & Steglich 2010). Time-aggregated networks are identical to the networks studied using standard approaches, except that they are associated with a given window of time. This explicit consideration of time allows one to directly investigate how this time window impacts inferences about the network (Yeung *et al.* 2011). Nearly, all extant network data are time aggregated.

Using time-ordered networks to generate time-aggregated networks lets us study topological dynamics by redefining net-

work statistics as functions of time window or of total aggregation time. In Box 2c, we have sketched three examples: a resource flow metric (fraction of vertices reached at a given time delay), a topological metric (mean degree on each time-aggregated network, for two different window sizes) and a likelihood-based comparison of two models for underlying topological dynamics. The dynamics of these time-aggregated networks can then be analysed at multiple time points. Investigators can then use existing network statistics that have been made explicitly time dependent (Blüthgen, Menzel & Blüthgen 2006; Fefferman & Ng 2007; Yeung *et al.* 2011) – for example, mean degree (edges per vertex) as a function of time and window size (Box 2c). For example, in an animal social network, a consistently high diameter (the longest minimum-length path between any two individuals) may indicate an un-mixed population, while an oscillating diameter might indicate fission–fusion dynamics. Similarly, observing asymptotic behaviour of statistics over increasing window size (Holme 2005; Leskovec, Kleinberg & Faloutsos 2005) can also provide insight into underlying dynamics of a system.

Time-dependent network statistics are also useful for assessing changes in topology or topological dynamics in response to an external factor (Table 1, T1, C1) – for example, climate change or experimental perturbation. Besides being of theoretical interest for understanding how populations evolve, these questions have applied implications in the face of accelerated anthropogenic changes. Here, standard time series and regression methods should be used to relate network statistics of time-ordered or time-aggregated networks to these external factors (Madden & Clutton-Brock 2009). One could assess a system's responsiveness by measuring time delays between perturbation and the response of a network statistic using the cross-correlation between time series, or detect periodic behaviour in a system using Fourier analysis to compute the spectral density of the network statistic's time series. For example, aquatic food webs can show multi-year time delays between forcing because of fishing and response in network topology (Walters, Christensen & Pauly 1997). A related approach enables the determination of cause and effect in these networks. Using the formalism of Granger causality (Table 1, T2), one can construct time series of network statistics and use them to determine whether one set of events causes another set of events. This approach may be very useful for detecting sources of variation in apparently complex networks.

Model selection and hypothesis testing (inference of the underlying rules for dynamics) are now possible (Table 1, T3). Resampling methods for time-ordered networks have been described in the previous section and can also be used with multiple time-aggregated networks (Croft *et al.* 2011b). For example, consider a set of time-aggregated networks describing social interactions between animals. One could test whether the mean degree of one group of vertices (e.g. the males) is consistently significantly higher than in another group (e.g. the females) at multiple time points by randomizing the identities of all vertices in each time-aggregated network and comparing the randomized mean degree for each group to the observed values. Instead, to test whether this mean degree changed over

time for each group, one could compare observed degrees to those found in networks where interaction times had been randomized across all time-aggregated networks.

More advanced inference tools for time-aggregated networks also exist (Table 1, T3). The new field of stochastic actor-based models (Snijders, Van de Bunt & Steglich 2010) (and their extension to temporally variable situations (Hanneke & Xing 2009)) will be highly useful for inference because of its strong statistical basis. In these models, the time-aggregated network's future state is the outcome of a Markov process depending on both the state of the network, the state of variables associated with each vertex and also of variables associated with each pair of vertices. The network evolves as probabilistically selected vertices independently rewire their edges. The parameters associated with this rewiring are allowed to change over different time intervals. For example, animal behaviour investigators might ask whether certain individuals preferentially interact with other individuals that have more extant connections and also avoid less-connected individuals. Alternatively, we can also predict the network's future state or ask whether there are frequent causal linkages (Table 1, T2). The detection of periodic or frequent temporal structures is an area of ongoing research with many usable tools. For example, does A interacting with B always imply that B subsequently interacts with C? Or are A, B and C consistently connected to each other via triangle motifs (Alon 2007)? These developing approaches are available in ready-to-use software packages and provide a strong basis for understanding process in network dynamics (Berger-Wolf, Tantipathananandh & Kempe 2010; Lahiri & Berger-Wolf 2010; Wackersreuther *et al.* 2010; Kovanen *et al.* 2011). An advantage of these actor-driven models is that they enable the investigator to assess the relative contribution of different network attributes to the overall network's structure and dynamics and the comparison of different hypotheses for network dynamics (Snijders, Koskinen & Schweinberger 2010). However, analysis of weighted networks is currently not possible, so the issue of choosing a time window for aggregation remains relevant.

Lastly, time-aggregated networks can be used to identify community structure within a network. Methods do exist to detect community structure within a single-static network (Newman 2010), but more robust approaches using multiple time-aggregated networks (Table 1, T4) can detect groups that are persistent over several time intervals and identify individuals that leave or join each group. Thus, these methods make it possible to assess the dynamics of groups – their membership, formation and dissolution – across time points, with applications for a range of questions. For example, one can measure the stability of different animal groups (e.g. politicians (Mucha *et al.* 2010)) or empirically identify ecological guilds that are consistent over multiple seasons. However, a limitation of these methods is that the available approaches come with a diverse set of assumptions. Some approaches automatically determine the number of groups in the data, while others require the investigator to specify this parameter. Thus, a range of results can be obtained from different community detection algorithms.

CONSIDERATIONS FOR BOTH KINDS OF NETWORKS

A strength of time-ordered and time-aggregated networks is that the temporal dependence of network-based inference is made explicit. For time-aggregated networks, different conclusions will necessarily be reached depending on the particular time window over which interactions are aggregated and the size of that window (compare Box 1a). Thus, determining the appropriate window used to define a network is critical. Choosing the correct window size can be done by measuring lag times between association events (lagged association rates) (Whitehead 1997, 2009; Clauset & Eagle 2007). Alternatively, window size can be chosen by determining when time series of network statistics constructed from different temporal subsets of the data become stationary(Sulo, Tanya & Robert 2011). A final approach is to use prior knowledge about natural timescales in the system (Lahiri *et al.* 2008; Cattuto *et al.* 2010): for example, for a pollinator network, 1 year may be a natural window size if the network re-forms annually, but 1 day may be a better window size if seasonal changes in interactions occur (Baldock *et al.* 2010). If the investigator believes the network is at a dynamic steady state, it could be appropriate to use a very long window size and weighted edges corresponding to interaction probabilities. This could be necessary, for example, in animal societies where all individuals can interact with all other individuals but some interactions are always more likely (Blonder & Dornhaus 2011). Unfortunately there is currently no consensus on the best method for choosing a window size.

Time-ordered networks highlight the need to assess the importance of investigator sampling rate to observed network properties (Blüthgen 2010) (compare to Box 1b). Networks can be very sensitive to missing data (Fletcher *et al.* 2011), and there are currently no widely agreed-upon methods for correcting sampling issues (Stumpf, Wiuf & May 2005; Kim & Jeong 2007) although some approaches work better than others (Kurant, Markopoulou & Thiran 2011; Maiya & Berger-Wolf 2011). Many studies have shown that common topological and flow statistics may have both high variance and bias when networks are not completely sampled (Kossinets 2006; de Silva *et al.* 2006). This problem may also arise when sampled edge weights do not converge to a central value – that is, when the underlying process generating these networks changes in time. While it is not possible to avoid this problem, time-ordered networks make it possible to detect insufficient sampling via rarefaction procedures. Consider a statistic of interest, computed from a time-ordered network. Rarefy the network by randomly removing individual edges. If the statistic of interest does not converge to a fixed value, the number of randomly removed edges decreases (i.e. the amount of rarefaction reaches zero), then one should be wary of analysing the data as-is and instead increase the sampling rate (Clauset & Eagle 2007). For example, in a study of resource flow between animals, a time-aggregated network diameter that does not converge under rarefaction indicates that edges that could dramatically change network connectivity are being undersampled. One approximate rule based on the Shannon–Nyquist sampling theorem (Shannon 1949) is to ensure sampling rates are at least twice that of the fastest dynamics of interest. More recent work on graph entropy rates (a metric of the difference from random of the information in a graph) provides a formal approach to determine the minimum sampling rate required to ensure that the information lost does not exceed an investigator-specified bound (Haddadi *et al.* 2011).

Applications and opportunities for network dynamics

Network dynamics are relevant to a range of research questions in ecology and evolutionary biology. We have reviewed a shared set of conceptual issues, common problems and methodological solutions centred on network dynamics, and have proposed an observational data-driven framework based on time-ordered networks. The power of this framework lies in its ability (i) to transform observed or simulated interaction data into mathematical structures that describe dynamics at multiple time-scales, (ii) to highlight the temporal issues that are relevant to these questions, and (iii) to open a large number of research questions to a unified set of descriptive and inferential statistics. Note that this framework does not propose explicit mathematical models for processes generating network dynamics (e.g. as used in epidemiology (Bansal *et al.* 2010; Pinar, Seshadri & Kolda 2011; Seshadri, Pinar & Kolda 2011)) – rather, it provides a common mathematical and statistical language for networks based on real data that can then be studied in the context of these models.

Several research areas show high potential for the application of this framework, which we have surveyed in Table 1. For example, the structure of transport networks found in many organisms (Heaton *et al.* 2010; Katifori, Szöllősi & Magnasco 2010; Tero *et al.* 2010) is rarely examined with methods from network dynamics. A time-ordered network perspective would be useful for assessing processes of network growth and development and for comparing properties of networks across organisms. Secondly, time-ordered networks could be used to understand species coexistence by providing a framework for testing hypotheses about changes in connectivity over time and for predicting future interactions between species. Although a network dynamics perspective has been used in studying spatial effects related to landscape fragmentation and metapopulations (Urban & Keitt 2001; Dale & Fortin 2010), many research opportunities remain. For example, community assembly could be studied using time-ordered networks constructed from paleo-records of temporally resolved species interactions and co-occurrence. Third, understanding how to directly control network dynamics will also have many practical implications (Table 1, C5). The control theory of network dynamics provides principles to obtain and maintain a desired future network state through targeted manipulations of current network state and the connectivity of focal individuals. For example, what management decisions should be taken to ensure the temporal persistence of multiple prey species for an endangered predator? Are there mathematically necessary tradeoffs between the robustness and performance of management strategies? Control theory of time-ordered networks is a

new area of research (Zecevic & Siljak 2010; Abdallah 2011; Liu, Slotine & Barabasi 2011) that is only beginning to be applied to biology. Significant progress could be made using these network approaches for the conservation of diversity and the preservation of ecosystem functioning (Bascompte & Jordano 2007; Sahasrabudhe & Motter 2011), and for better controlling diseases (Salathé & Jones 2010). Time-ordered networks can provide a natural framework for tracing changes in network state and for identifying vertices and temporal patterns that may be relevant for controlling the system.

Lastly, many apparently complex systems may be more parsimoniously described and thus understood using time-ordered networks. In many networks, flow dynamics and topological dynamics occur on similar time-scales. In these systems, the topology of the network influences flow on the network, and vice-versa, leading to strong couplings between processes and patterns at different scales. These networks exhibit many interesting properties including phase transitions between states, symmetry breaking where similar vertices spontaneously diverge into topologically distinct populations with different functions and identities, sudden synchronization of behaviour or topology for multiple vertices, nonlinear shifts in waiting times and flow processes and strong interactions between simple local dynamics and global whole-network dynamics (Gross & Blasius 2008; Funk, Salathe & Jansen 2010). The ubiquity of these phenomena suggests that many temporally variable systems could be understood in terms of the couplings between the topology and flow of their underlying networks. While the time-ordered network framework does not directly propose different models that could explain these couplings, it does provide a natural framework for describing these couplings and for then comparing the validity of different generative models (e.g. with stochastic actor-based models that couple processes of flow and topological dynamics (Snijders, Van de Bunt & Steglich 2010)). Thus, many biological phenomena – for example, multiple stable animal community states, complex patterns of disease spread or surprising population dynamics of multiple species – may only be understood if we can develop models that can link local and global-scale network dynamics at a range of time-scales.

Challenges for the future

Despite the current popularity of network analysis, dynamic approaches remain rare in ecology and evolutionary biology. Fortunately, it is now becoming possible for biologists to take advantage of many recent conceptual and methodological advances (Table 1). However, several challenges still remain before dynamic analyses become more accessible. Some relevant questions cannot be addressed with current methods. For example, the general prediction of future network structure with or without perturbation is now only possible under the limiting assumption that the network is in some dynamic steady state (Snijders, Van de Bunt & Steglich 2010). Many applied studies of metapopulations or multi-species interactions where perturbations are of interest would be improved by an advance in this area. Similarly, understanding couplings

between multiple time-scales in a network remains difficult. For instance, how do rapidly occurring small-scale processes feed into global-scale processes and patterns, and vice versa? How do events at one time impact events at a later time? Being able to scale up limited observations to make inferences about entire networks over time would be tremendously useful when data collection is expensive or impractical.

The analysis of network dynamics – time-ordered and otherwise – still suffers from a limited set of inferential statistical tools. Although it is clear that accounting for time-ordering and for temporal dynamics is critical for many issues in ecology and evolution, only the few methods we have described currently exist to compare models, carry out hypothesis testing or detect within- and between-group variation. There is not yet a general analytical statistical framework for the analysis of time-ordered networks describing coupled processes. We also call for the development of even more resources to teach and implement the methods described. Although several free software packages exist (Table 1), there is still a gap between tools usable by investigators new to network analysis and theoretical advances made in the field. Fortunately, recent books (Croft, James & Krause 2008; Newman 2010) and reviews (Gross & Blasius 2008; Snijders, Van de Bunt & Steglich 2010) are making these mathematics more accessible. The interested reader should also be aware of recent perspectives from the physics (Holme & Saramäki 2011), computer science (Santoro *et al.* 2011) and engineering communities (Kuhn & Oshman 2011).

Time-ordered network analysis is only possible when sufficient temporally resolved data are available. Generating complete and accurate records of interactions at multiple time points can be very difficult, but should become a priority. For example, food webs rarely contain more than a few hundred species, and even more rarely assess their empirical change over seasons and years (Jarre-Teichmann & Pauly 1993). Community networks involving a much smaller subset of easily observed species (e.g. plant–pollinator interactions), however, can include relatively dense data on time-ordered networks (Bascompte & Jordano 2007). Similarly, good data are available for animals social networks that are visually observed semi-continuously (e.g. primates in a research centre (Flack *et al.* 2006), ant colonies in the lab (Blonder & Dornhaus 2011)) or lizards remotely tracked semi-continuously in the field (Godfrey *et al.* 2012). However, the situation is more difficult in animal groups analyses where individuals are rarely observed (e.g., dolphins or meerkats in the wild (Lusseau *et al.* 2003; Drewe, Madden & Pearce 2009) or pollinators on plants (Bascompte & Jordano 2007)). In these cases, network analyses are often based on one or a few time-aggregated networks. However, time-ordered network analyses could be highly insightful in systems where data coverage does not yet exist. While methods are available to correct for sampling and observation issues in time-aggregated networks (Lusseau, Whitehead & Gero 2008), we are aware of no tools for time-ordered networks. It is also unclear how much missing data is acceptable in time-ordered network analysis. Thus, an open challenge is to develop better tools for missing data and also to obtain support for

long-term and high-coverage studies of the dynamics of a range of systems. Advances in electronic sensors and video-tracking may provide a way forward (Cattuto *et al.* 2010; Pinter-Wollman *et al.* 2011; Jeanson 2012). Only with such data will we realize the full potential of network dynamics to answer a range of fundamental and applied questions. Comparative studies of networks across time-scales and systems may reveal general principles in the organization of biological networks and would permit robust comparisons with theoretically optimal networks and human-engineered networks.

In sum, the broader consideration and application of network dynamics has great potential to push forward our understanding of biological interactions. Temporal dynamics are found in all natural systems and underlie many broad scientific questions. By extending theory and data to account for temporal dynamics, we can couple a powerful time-ordered network framework to a much wider range of systems and questions.

Acknowledgements

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Glossary

Coupled dynamics: the simultaneous change of a network's topology and the flow of resources on it, involving strong feedbacks between these two processes at the same time-scale.

Degree: the number of edges for a given vertex, potentially indicating the importance of a vertex in a network. The frequency distribution of degree can indicate underlying dynamic processes.

Edge: a link between two vertices in a network, indicating a persistent interaction, an instantiation of an interaction or a probability of an interaction. Edges may be weighted to denote interaction strength.

Flow dynamics: the movement of resources (energy, disease, information, etc.) on a network over time. Topological dynamics of the network must be slower than flow dynamics.

Time-aggregated network: a network constructed by combining all interactions observed over some time window. Most networks are time aggregated.

Time-ordered network: a network that represents exactly all of the dynamic observations made by an investigator. Time-ordered networks indicate the multiple time-scales inherent to a biological system, can be used to study flow dynamics and can be collapsed to time-aggregated networks to study topological dynamics.

Topological dynamics: changes in the edges or vertices of a network over time.

Vertex: an individual object in a network that represents the biological phenomenon of interest.

Window size: An interval of time over which observed interactions are aggregated into a network. Many descriptive statistics like degree depend strongly on window size.