Layers of latency in social networks and their implications for comparative analyses

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Abstract

Animal social structures are remarkably diverse, encompassing relationships that range from strong, lifelong bonds to weaker, more transient connections. Understanding the drivers of this variation is a key question in behavioural ecology and has been the focus of numerous studies linking social structure to ecological, demographic, and life history patterns within groups, populations, and species. Equipped with this information, researchers are now turning to investigations of social structure that are comparative in nature. However, comparing social networks remains a considerable logistical and analytical challenge. Here, we present the *layers of latency framework*, which outlines how observed social networks are linked to the two underlying latent networks that are of interest for most research questions: the real social network (the actual pattern of social interactions), and the social preferences network driving these interactions. This conceptual framework provides a clear and unified approach to understand *when* and *why* differences in network properties and sampling protocols can introduce discrepancies between observed and latent networks, potentially biasing or confounding statistical inference. We then use this conceptual framework to outline some of the central challenges to comparing animal social networks, focusing on differences between networks in behaviour type, sampling effort, sampling type, network size and network scale. For each of these focus points, we describe why and how they create challenges for comparative analyses, and we suggest potential directions for solutions. The layers of latency framework can help researchers to identify networks and features they can (or cannot) compare. In doing so, this framework facilitates advances in cross-species social network studies with the potential to generate new and important insights into the ecological and evolutionary drivers of variation in social structure across the animal kingdom.

Keywords

comparative analysis; network analysis; social network; social system; social evolution; generative models; latent networks; Bayesian methods

Introduction

The animal kingdom features a remarkable diversity of social systems, from solitary individuals to large cooperative groups (Clutton-Brock, 2016; Rubenstein & Abbot, 2017). Yet, our understanding of the ecological and evolutionary causes and consequences of this diversity remains incomplete (Kappeler et al., 2019; Kurvers et al., 2014). Comparing animal populations facing distinct environmental challenges can provide insights into the influence of ecological variables such as predation and food availability on social patterns (Barsbai et al., 2021; Krause & Ruxton, 2002; Lukas & Clutton-Brock, 2018), and reciprocally, how these social patterns impact ecological factors, such as pathogen transmission (Albery et al., 2021; Bansal et al., 2007; White et al., 2017). Comparative analyses can also reveal how social systems evolve alongside life history traits (Silk & Hodgson, 2021) and interact with demographic mechanisms (Clements et al., 2022; Shizuka & Johnson, 2020).

As a result of countless long-term efforts to collect social data (Clutton-Brock, 2021; Sheldon et al., 2022), numerous animal social datasets exist, capturing social structure across diverse species and environments. With the emergence of large databases bringing together these data across taxa (e.g. MacaqueNet, De Moor et al., 2023; Animal Social Network Repository (ASNR), Sah et al., 2019; DomArchive, Strauss et al., 2022), attention has turned to the statistical methods with which such datasets can be compared (Albery et al., 2024; Ellis et al., 2021).

Comparative social network analysis offers a holistic approach to draw inference about the drivers and consequences of animal social structure (Albery et al. 2023;

Croft et al., 2016; Pinter-Wollman et al., 2013; Webber & Vander Wal, 2019). By explicitly representing social structure as an emergent property of social interactions between individuals (Hinde, 1976), social network analysis can be used to ask questions about social evolution at the level of individuals, dyads, social groups and populations. However, despite the value of comparative social network analysis, only a relatively small body of literature compares social networks across species and taxonomic groups (Albery et al., 2024). A major reason for the lack of such studies is the viability of comparing networks that are generated using different methodologies, and that may diverge widely in key properties such as network size and behaviour types (Faust & Skvoretz, 2002; Ogino et al. 2023; Pinter-Wollman et al., 2013).

Here, we offer an overview of five key challenges that create disparities between social networks and provide guidance on what to consider when designing comparative analyses to minimise these challenges. A common theme to these challenges is that the observed networks we compare are most often different from the underlying, latent (i.e. unobservable) networks we want to make inferences about. We therefore begin by introducing the *layers of latency framework* that provides a unified representation of how different biological and observational processes interact to influence the social structures we observe. A clear understanding of how these processes contribute to variation in observed social networks will help researchers to make principled decisions on how best to compare networks. While we introduce the *layers of latency framework* in the context of comparing networks, it contains valuable concepts for all social network analyses, be they comparative or not.

The layers of latency framework

One key issue in network analysis is that observed networks often do not directly, or exclusively, correspond to the biological phenomenon of interest. This lack of correspondence is due to two primary reasons. Firstly, the social networks we quantify are usually based on only a subset of interactions – those that have been recorded – and an observed network is therefore an estimation, not exact representation, of the complete or "real" patterning of interactions (Handcock & Gile, 2010). Secondly, even when all interactions that happen in a group are recorded, they are unlikely to correspond directly to individual preferences regarding social partners because of constraints that hinder individuals in realising their preferred relationships. For example, if all individuals in a group prefer high-ranking individuals as partners, only a subset of those individuals may have that preference realised because the time high-ranking individuals have available to socialise is limited (Seyfarth, 1977). Instead, some individuals might end up interacting with their second, third, or even last choice of partner.

To provide a structured way of thinking about this, we present the *layers of latency framework*, which represents social structure as a hierarchy of networks: an *observed social network* to which researchers have access, and two layers of latent networks -

the *real social network* and the underlying *social preference network* (Fig. 1). An *observed network* represents a sample of the *real network*. The *real network* is the actual pattern of all interactions or associations between individuals. In turn, the *real network* is itself a (likely partial) realisation of the individuals' social preferences. These preferences can also be represented as a network (e.g. a directed network representing the strength of preference that each individual has for others): the *social preference network*.

Mismatches between an *observed network* and the two latent networks (or indeed between the two latent networks) are the result of two main processes: *sampling biases* and *constraints* (Fig. 1). Common examples of *sampling biases* include cases where certain individuals or interactions are better sampled than others (Altmann, 1974; Bateson & Martin, 2021). For example, a researcher using biologgers to record proximity between pairs of animals may not be able to afford to put a biologger on every individual, or a researcher visually observing social interactions cannot simultaneously watch all individuals at once. *Constraints* include factors that prevent individuals from realising their social preferences. These constraints may come from different sources, including incompatible preferences between potential partners, social factors such as dominance structure, and environmental constraints such as spatial distances and barriers in the physical environment (Fisher et al., 2021; Webber & Vander Wal, 2018).

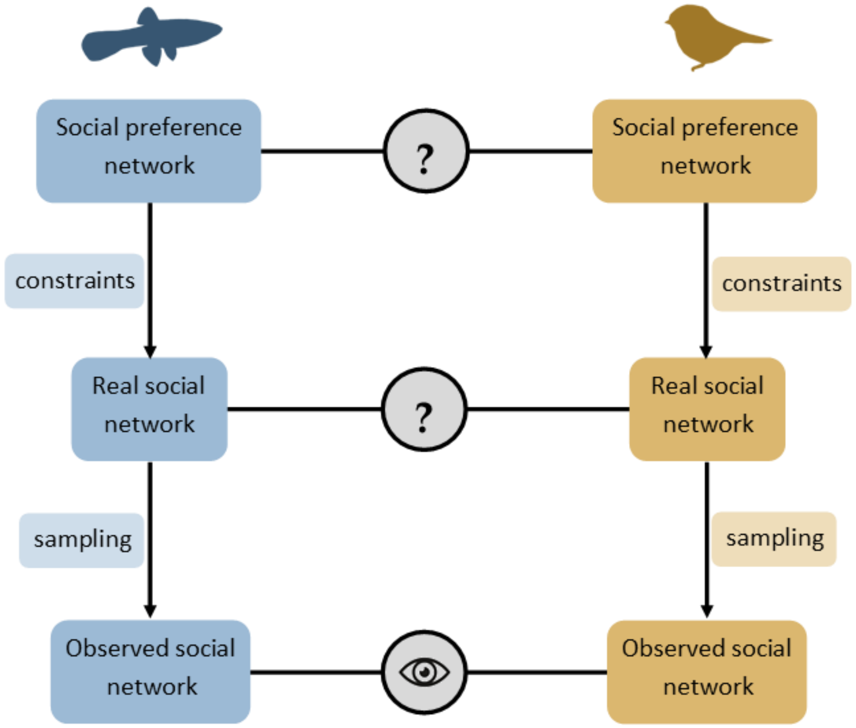


Fig 1. The *layers of latency framework*. Social structure can be considered a hierarchy of networks: an *observed social network* to which researchers have access, and two layers of latent networks - the *real social network* and the *social preference network*. When we compare networks across species (e.g. here a fish and a bird), we typically compare *observed social networks* (the eye icon), but our research questions typically concern differences between *real social networks* or between *social preference networks* (the question mark icons). To ensure that analyses of the *observed networks* accurately reflect the latent networks of interest, it is important to consider the factors along the path from the relevant question mark to the eye that could result in differences between the *observed* and the *real* and *social preference networks*. This includes accounting for *sampling biases* when the focus is on comparing *real social networks* and accounting for both *sampling biases* and *constraints* when comparing *social preference networks*.

Research questions are almost always about the latent network layers rather than the *observed network* (Lundberg et al., 2021). The *social preference network* is usually the level of interest when researchers seek to understand the *causes* of social behaviours, such as how kinship, age and sex impact partner choice, or the role of life history or ecology in shaping the types of social relationships individuals form (Chakrabarti et al., 2020; De Moor et al., 2020; Silk & Hodgson, 2021; Siracusa et al. 2022, Smith, 2014; Snyder-Mackler et al., 2016). On the other hand, the *real social network* is usually the level of interest for investigations into the *consequences* of social behaviours, such as the influence of social structure on disease or information transmission (Aplin et al., 2012; Collier et al., 2022; Silk & Fefferman, 2021) and on fitness outcomes (Ellis et al., 2017; Ellis et al., 2019; Riehl & Strong, 2018; Sabol et al., 2020; Strauss & Holekamp, 2019). However, analyses are typically run on the level of the *observed network* (Fig 1). Understanding which latent network layer is of interest for a given question, and how an *observed network* relates to that latent layer is therefore essential for reliable social network analyses.

Challenges of comparative social network analysis

BOX 1: MOVING BETWEEN LAYERS

Recent developments in Bayesian network analysis provide methods to move between the network layers depicted in Fig. 1 (De Bacco et al., 2023; Hart et al., 2023; Redhead et al., 2023). These generative modelling approaches estimate the latent network layers based on the observed data, while incorporating information about the processes that generate the *observed networks*. This information is used to quantify how well the *observed network* is expected to reflect the underlying latent network, which is translated into uncertainties in the estimated edge weights (Ross et al. 2023). For instance, within the BISoN framework (Hart et al., 2023), network metrics are calculated from draws of the Bayesian posterior distribution of the latent *real network* edge weights, while accounting for sampling effort. Doing so generates a posterior distribution of network metric values (instead of a single value, or point estimate), therefore explicitly including uncertainty in the metric estimates, where higher sampling effort leads to narrower distributions. Once network metric posteriors have been generated, they can be passed to downstream statistical analyses thereby carrying uncertainty forward into statistical analyses, such that networks with higher observation effort carry more weight on inference.

These methodological developments hold great promise for comparative social network analysis. They enable researchers to make inferences at the latent network level relevant to specific research questions, while also explicitly accounting for differences between networks that could potentially confound or bias comparisons (Fig 1). However, such models require information on the *generative processes* giving rise to the *observed neworks*, which include both biological (e.g., *social preferences* and social and/or physical *constraints* in realising those preferences) and observational (e.g., sampling protocols and effort) factors. Understanding these generative processes is still very much in development in animal social network analysis (Brask et al. 2023; Hobson et al. 2021), and is an area where significant methodological advancements are needed to fully enable reliable comparative social network analysis. The *layers of latency framework* offers a clear and structured approach to understanding these generative processes. It makes explicit how the *observed networks* used in research are generated by underlying *social preferences* and are modulated by *constraints* and *sampling biases*.

Comparative social network analysis faces significant challenges due to the variability in how networks are constructed. Networks can be based on different behaviours, sampled using diverse data collection methods with varying degrees of effort, and sampled at different biological scales (Albery et al., 2024; Canteloup et al., 2020; Davis et al., 2018; Faust & Skvoretz, 2002). These differences can create disparities between the *observed networks*, reflecting *sampling biases* and *constraints* rather than true differences, thus confounding comparative analysis (Gagliardi et al., 2023; Ogino et al., 2023).

Here, we consider five key challenges in comparative social network analysis: comparing networks that differ in 1) behaviour type, 2) sampling method, 3) sampling effort, 4) network size, and 5) biological scale. We summarise these challenges in Table 1 and discuss in greater detail how these differences introduce *sampling biases* and *constraints*, generating discrepancies between the observed and latent networks and affecting the comparisons of observed networks. Additionally, we provide guidance on how best to handle each of these challenges.

While we present these challenges independently here for clarity, it is key to note that these challenges are closely linked (Fig. S2). For example, the size of the *real network* (in combination with the research questions being addressed) may influence the scale at which sampling is undertaken, which can then influence the size of the *observed network*.

Table 1: Summary of five key challenges faced when comparing animal social networks.

Challenge	Description
Behaviour type	Networks vary in the behaviours used to construct them. Whether networks based on different (or the same) behaviours can be compared depends on the biological functions of the behaviours in the given populations and the research question.
Sampling effort	Sampling effort can vary substantially between networks, influencing how reliably an *observed network* represents the *real network*. Bayesian models that estimate the *real network* from observed data can account for sampling effort as uncertainty in the estimated network properties (Box 1).
Sampling type	Networks constructed using various sampling methodologies pose two main challenges: 1) different sampling protocols generate different sampling biases, and 2) how edge weights are quantified may not be directly comparable. Recent methodological advancements, such as mixture models and Bayesian models that estimate the *real* or *social preference network* from an *observed network* while explicitly accounting for sampling type, offer promising solutions (Box 1).
Network size	Networks can vary substantially in their size, which can influence network structure. Whether or not to account for network size depends on whether network size is central to the relationship between network structure and biological variables of interest. If controlling for network size is warranted, doing so correctly can be challenging as it requires knowledge of the generative

	process underlying the network (Box 1), which determines how size impacts the network property of interest.
Network scale	Networks can be sampled at various scales, resulting in *observed networks* representing different parts of *real networks*. The scale of sampling significantly influences network structure, making networks sampled at different scales generally incomparable, particularly for global network properties. Bayesian models that impute missing data for networks sampled at smaller scales may provide a solution, but they necessitate an understanding of the generative process underlying the network at the larger scale (Box 1).

1. Differences in behaviour type

The first factor determining the comparability of networks is the type of behaviour used to construct them. For most comparative analysis, networks compared should be constructed on behaviours with similar biological functions, therefore reflecting similar *social preferences* or representing *real networks* with similar outcomes. While it might seem obvious that an affiliation network based on huddling should not be directly compared to an agonism network based on physical aggression, determining which behaviours *can* be compared often requires more nuanced considerations. For example, various behaviours have been used to quantify social relationships in different studies and species, ranging from direct interactions such as grooming and allopreening, to spatial associations and co-membership of a group (Webber &

Vander Wal, 2019). Whether these behaviours can be considered to represent the same biological function is contingent on the research question and the biology of the study species to be compared (Carter et al. 2015, Farine & Whitehead, 2015). In addition, the same behaviour can serve different functions in different systems and might reflect different information depending on the context. For instance, pairs of animals sitting within a 5m range of one another could be indicative of a close association in wild populations, whereas that same distance might not carry the same information in a captive population where individuals have less space over which to spread.

Moreover, behaviours will differ in how strongly individuals are *constrained* in realising their *social preferences*. For example, certain behaviours like sex and grooming are often difficult to direct at more than one partner at a time. In contrast, individuals can sit near or vocalise to multiple partners at once and as such these types of behaviours are likely to be less constrained by limitations related to social preferences. Similarly, environmental constraints are more likely to impact behaviours that involve physical contact than behaviours that do not. Different behaviours are also influenced by *sampling biases* to different extents, so that an *observed network* of one behaviour might better represent the *real network* than another behaviour. Rare or less visible behaviours tend to be more heavily affected by *sampling biases* (Martin & Bateson, 2021). Moreover, the degree of *sampling bias* can vary for the same behaviours depending on the system or context. For example, recording aggression in a terrestrial species may be easier than in an aquatic one. Consequently, a smaller proportion of interactions may be observed for the aquatic species compared to the terrestrial one.

Considerations for comparing networks

Any comparative study whose question depends on comparing ‘like to like’ will need to carefully evaluate whether the networks are constructed based on behaviours with comparable biological functions and facing similar *sampling biases* and *constraints* in their given context (or whether differences can be accounted for in the analyses). This is important because behaviours should either reflect similar *social preferences* or represent a *real network* with similar outcomes. Determining which behaviour types can be reliably compared is a critical first step in comparative social network analysis, which requires thoughtful consideration tailored to the specific research question and informed by knowledge of the species' biology under study.

2. Differences in sampling effort

Sampling effort can significantly impact how reliably an *observed network* represents the *real network*, with increasing effort improving reliability (Farine & Strandburg-Peshkin, 2015; Franks et al. 2021). Accounting for uncertainty in the estimated network metrics is important for any social network analysis but becomes especially crucial when comparing networks constructed with varying sampling efforts. These networks inherently differ in the uncertainty surrounding their observed edge weights and consequently any estimated network metrics. Failing to account for this uncertainty might lead to wrong conclusions. For instance, in a network constructed based on just one hour of observation, a dyad may appear to spend most of their time together. Yet, this estimate could be a highly uncertain representation of this dyad's edge in the *real network*. Extending to 100 hours of sampling effort would provide a more accurate estimate of the weight of this edge in the *real network* and would lower the level of uncertainty around that estimate. Comparing a low observation effort network to a high observation effort network might falsely suggest that individuals in the low observation network spend more time together compared to those in the high observation network, but in reality the difference is due to sampling effort rather than actual differences in behaviour. One effective solution to address the challenge of variable sampling effort when comparing networks is to use models that estimate the *real network* based on the *observed network* as a latent structure, with an explicit degree of uncertainty (Box 1).

Considerations for comparing networks

When comparing networks, researchers should account for differences in sampling effort, which can strongly impact how well an *observed network* represents the *real network*. An effective solution to do so is to consider the *real network* as a latent structure, which is estimated with a degree of uncertainty, determined by the observation effort. Recent frameworks provide tools to estimate the *real network* from an *observed network*, while explicitly estimating uncertainty in the estimated latent network based on sampling effort (Box 1).

3. Differences in sampling type

Many challenges are associated with comparing networks constructed using different sampling methodologies (Albery et al., 2024). The two we focus on here are differences in sampling protocol and differences in how data are summarised into edge weights.

Different sampling protocols can impact how an *observed network* relates to the *real network*. Some of the most commonly used sampling protocols include focal continuous sampling (recording social interactions and/or associations, referred to collectively as 'interactions' from here on, that include a given individual for a set amount of time), group scan sampling (recording the social interactions of each individual in a group instantaneously at regular time intervals) and gambit of the group sampling (recording group compositions during repeated surveys, where individuals observed in the same group are taken to be associating with each other; Altmann, 1974; Whitehead, 2008). More recently, technologies such as camera traps, biologgers, or drones have been used to observe and record animal behaviour remotely (Webber & Vander Wal, 2019). Each of these sampling protocols have inherent biases in the interactions that are recorded (Altmann 1974). For instance, focal continuous sampling provides rich, detailed data on the focal individual and its social partners for a given time but overlooks social interactions between all other individuals during that time. Similarly, sampling using biologgers is often limited to a subset of individuals in the group because of their high cost and deployment schedules (e.g., not all animals can have a biologger deployed at the same date). Sampling the whole group at regular time intervals (using scan sampling or camera traps), on the other hand, can capture the overall occurrence of interactions across group members to a greater extent, but misses interactions occurring between sampling intervals.

A second challenge is that networks are built based on different measures of edge weights, which are not always directly comparable and can even sometimes represent different aspects of the *social preference network*. Raw data on social interactions typically comes from a count of the number of interactions and/or the duration of each interaction observed (Martin and Bateson, Altmann 1974). Which of these raw data are used is determined, in part, by the selected sampling protocol, although certain protocols permit the collection of multiple types of raw data. Edge weights may then be represented as the rate of social interactions per unit of time (rates, the count of the number of social interactions over observation time), as the proportion of observation time two individuals spend engaged in a social interaction (proportions), or as the likelihood of a social interaction occurring between two individuals within a specific time frame (probabilities, the ratio of samples during which an interaction is recorded over the total samples). Probabilities and proportions are both unitless measurements bound between zero and one. Rates, on the other hand, are the expected number of events per unit time (e.g. associations per hour), with a lower bound of zero and no upper bound. Because the probability of being in a particular state at a point in time is equal to the proportion of time spent in that state, a unit increase in a probability is equivalent to a unit increase in a proportion, allowing direct comparisons between probabilities and proportions, all else being equal. However, comparing probabilities or proportions to rates is not as simple, as there is no natural way to interpret these two distributions of data on the same scale. This also relates to a more conceptual point: how often individuals interact with a given partner (rates), and how much of their social time they spend on a given partner (proportions/probabilities) are meaningful aspects of the *social preference network*, which do not necessarily carry the same information (Dunbar, 1976). For instance, animals might interact frequently for brief amounts of time with certain types of partners and interact less often but for long amounts of time with others.

Selecting an appropriate interaction index can help mitigate issues related to sampling type to a certain extent. Various indices have been devised to address different *sampling biases*, making networks built from different sampling protocols more comparable (Franks et al., 2010). Moreover, some network metrics, such as unweighted network metrics, or metrics that are expressed relative to the mean edge weight of the group, are less sensitive to differences in sampling type. In addition, using a standardisation such as Z-scoring makes edge weights (or derived measures of network structure) interpretable in terms of standard deviations, thereby making rates and proportions/probabilities more comparable. However, these approaches do not account for the different *sampling biases* inherent to these distinct sampling processes, which may introduce disparities between an *observed network* and the *real network*. Nor do they account for how different measures of edge weights might capture different aspects of the *social preference network*.

Alternatively, mixture models can be used to identify similar interaction levels in the *observed network*, creating categories of individuals that share strong, intermediate or weak social relationships (i.e. estimating the *social preference network*; Ellis et al., 2021; Weiss et al., 2019). These categories are robust to variation in sampling type and can therefore readily be compared. Finally, the sampling process can be integrated into analytical models that estimate the *real network* based on an *observed network* (Box 1). Bayesian models have been developed to reconstruct latent networks by explicitly incorporating assumptions about how the sampling process impacts the relationship between an *observed network* and the *real* or even the *social preference network* (Young et al., 2020).

Considerations for comparing networks

When comparing networks derived from various sampling methods, two main factors need to be considered: 1) biases in the recorded social interactions due to differing sampling protocols, and 2) differences in how edge weights are measured. Although employing suitable indices and Z-scoring edge weights can alleviate some of these concerns, these approaches do not account for the disparities between an *observed network* and the *real* or *social preferences network* that differences in sampling can generate (Fig. 1). Recent methodological advancements, including mixture models and models that estimate the *real network* as a latent structure while accounting for the sampling process offer promising avenues to navigate these challenges effectively (Box 1).

4. Differences in network size

Network size, or the number of nodes in a network, varies substantially in animal societies ranging from only a few individuals to large assemblages of several hundred individuals (Webber & Vander Wal, 2019). This variation is shaped in part by differences in social organisation, dispersal patterns, ranging behaviour and/or territoriality (Kappeler, 2019). In addition, *observed networks* can include different subsets of the underlying *real network*, driven by researchers' choices regarding who is observed (for instance focusing only on adults or on habituated individuals). Observed network size therefore depends on the features of the social system being investigated (which determine *real network* size) as well as the decisions made by researchers when designing their study (which determine what subset of the *real network* is observed). Here we consider what different network sizes mean for the comparability of network structures. We explore the effects of sampling different subsets of *real networks* in the next section (*Differences in network scale across networks*).

Comparing networks of different sizes is a complex challenge because network size can greatly influence other aspects of network structure in non-trivial ways. The effect of network size on social structure depends on the nature of the underlying process generating the network (Box 1, Boccaletti et al., 2006; Hobson et al., 2021), and is often not the same for different measures of network structure (Anderson et al., 1999; Naug, 2009). Therefore, controlling for network size (e.g. dividing network metrics by network size, or adding network size as a control predictor in analyses) does not always fully account for size effects, and may even introduce biases.

The first question to consider when comparing networks of different sizes is *whether it is appropriate* to control for network size. Biological factors may influence key aspects of network structure through their effects on network size (at least in part). Network size can therefore be considered an important feature of social structure itself. For example, if an individual's risk of being infected by a pathogen depends on its number of social partners, then being in a larger group can help explain higher exposure risk. In these cases, conditioning network comparisons on network size would mask effects of biological importance (Fig. 2A). However, for other research questions it may be necessary to condition on network size to make meaningful biological comparisons. For example, to test the hypothesis that forest-living species (typically living in smaller groups) have denser social networks than those in open habitats (typically living in larger groups), conditioning on network size is necessary to demonstrate that habitat influences network structure (density) in a manner that is not solely driven by the relationship between habitat and network size (Fig 2B).

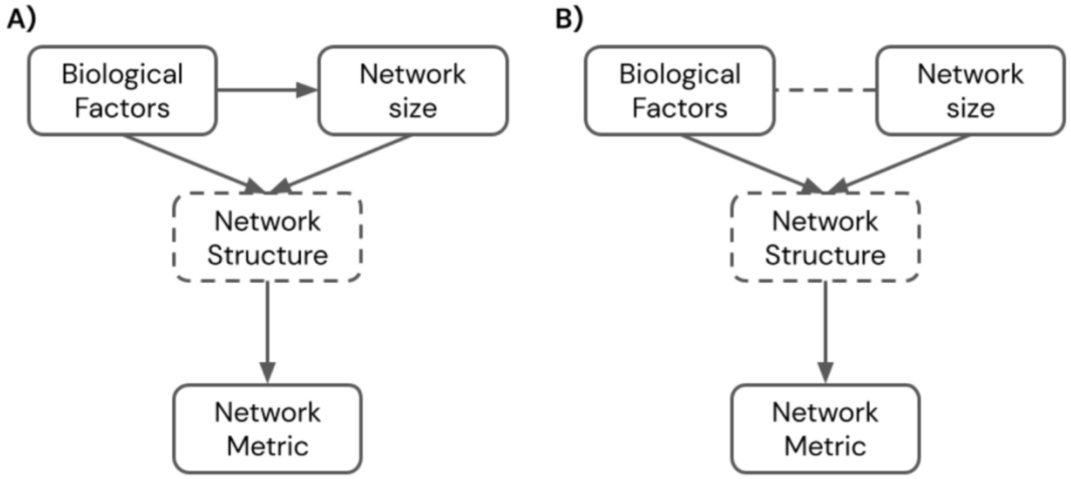


Figure 2: Potential causal mechanisms linking network size to structure. Note that 'network' here refers to the *real network* (Fig 1). The solid arrows represent causal relationships. The dashed line between biological factors and network size in panel B indicates a potential non-causal association. The dashed boxes indicate that the structure of the *real network* is a latent, unobservable variable, which can be quantified, but not entirely captured by a network metric, i.e. a measure of network structure. In A, biological factors affect network structure partially via network size, and controlling for network size would mask some of the influence of biological factors on network size. In B, biological factors do not influence network size, but through exogenous variables, biological factors and network size may be correlated. Unless network size can be effectively controlled for, the overall impact of biological processes on network structure cannot be estimated, as network size is a possible confound. In both cases, potential confounds act on the network structure itself, not on the network metric. As long as the chosen network metric is an accurate quantification of network structure, potential challenges do not lie with the metric, but with underlying causal assumptions.

The next question to consider is *how to control* for differences in network size. Even when controlling for network size is appropriate for a specific question, doing so in a way that correctly removes size effects can be difficult. The relationship between size and network structure depends on the process that generates the network, and these processes are often unknown (Box 1, Brask et al. 2023). For instance, unweighted network density (the ratio of actual to potential connections in a network) is divergently impacted by network size, depending on the process that generates the network (Fig. 3). If individuals choose their interaction partners at random with a fixed probability, then network density stays the same regardless of the size of the network. In contrast, if individuals preferentially interact with their most popular groupmates and each individual forms a fixed number of relationships, then the density of the network declines exponentially with its size. Similarly, the strength of social relationships can depend on network size in different ways. If individuals get more partners when the network is larger but are restricted in the amount of time they have available to socialise, relationship strength will decrease with network size. In contrast, relationship strength can be independent of network size if individuals keep a constant number of partners regardless of network size, or if they get more partners and also increase the amount of time they spend socialising (so that they can spend the same amount of time with each of their partners even when their number of partners increases). Each of these scenarios require different approaches to correctly remove the effect of network size (Hobson et al., 2021). That is, if the networks to be compared have emerged from different generative processes, then correctly controlling for size may involve a different control procedure for each network.

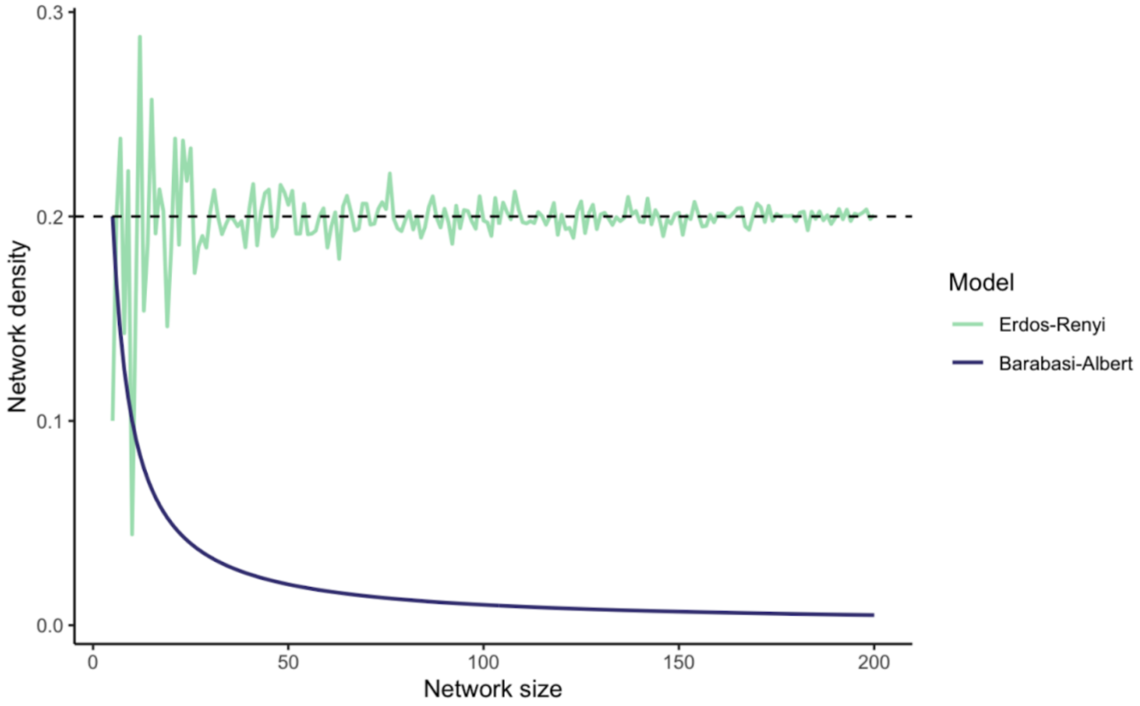


Figure 3: Measures of network structure can be influenced by network size in different ways, depending on the underlying processes that generate the network. In this example we compare how unweighted network density depends on network size for networks generated from two different processes. If individuals choose their interaction partners at random ('random attachment', captured by the Erdős-Rényi model, Erdős & Rényi 1959) with a fixed probability (e.g. each pair of individuals has a 20% chance of interacting) then the network density stays the same regardless of the size of the network. In contrast, if individuals preferentially interact with their most popular groupmates and each individual contributes with a fixed number of edges ('preferential attachment', captured by the Barabási-Albert model, Barabási & Albert 1999), then the density of the network declines exponentially with its size.

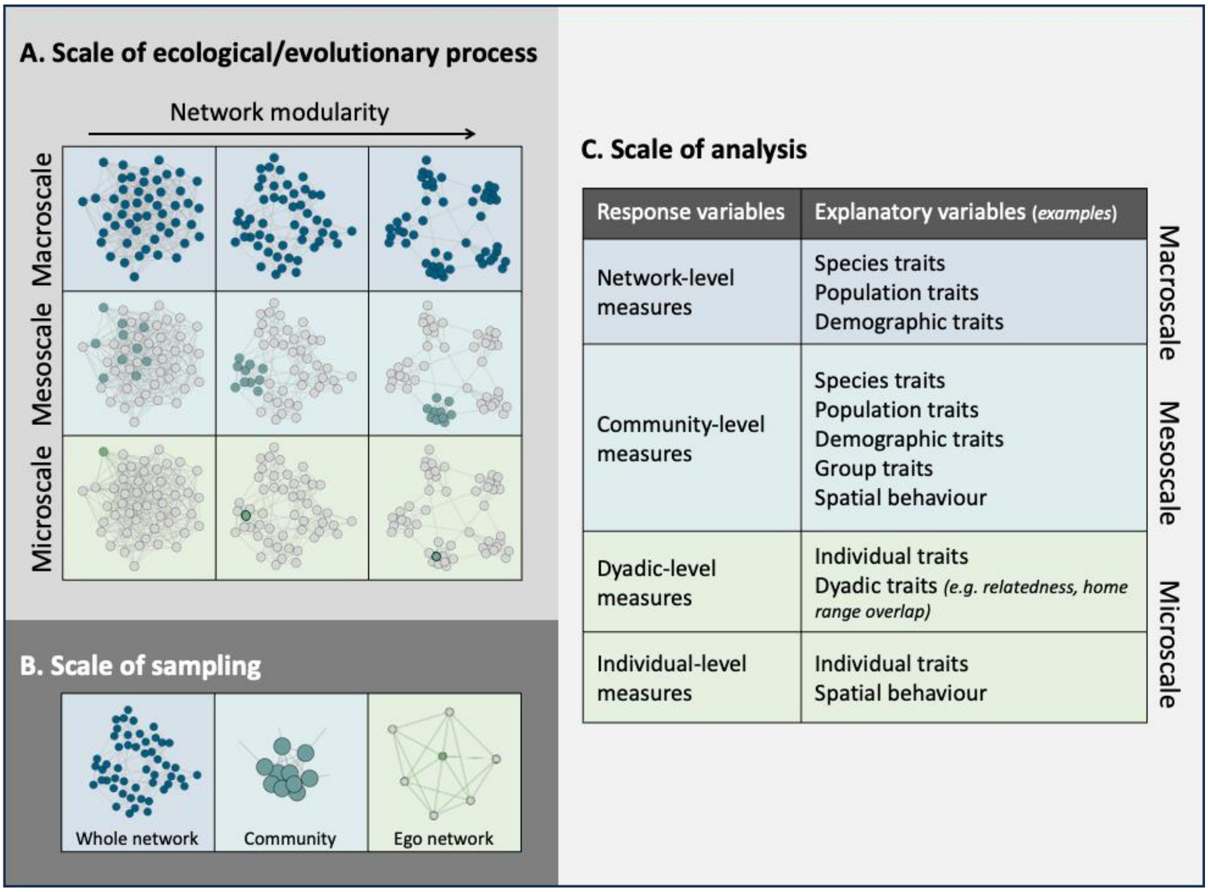
Properly accounting for network size in comparative network analysis is often difficult, if not impossible, unless valid assumptions are established about the underlying processes that generate the network (Hobson et al. 2021). Understanding *generative processes* in animal social networks is an area that still needs substantial methodological progress (Box 1, Brask et al. 2023), but one where the *layers of latency framework* may be particularly helpful. By explicitly considering the *social preferences* driving a given network, we can better understand the expected relationship between network size and relationship strength within the system. This in turn, can inform the design of simulations to predict how network structure varies with changes in size and guide decisions on whether and how to account for network size in subsequent analyses.

Considerations for comparing networks

When comparing networks, differences in network size are almost inevitable. Whether and how to account for differences in network size is a long-standing challenge in network science, and solutions are often context-dependent. When network size is central to how network structure relates to biological variables of interest, conditioning on network size could mask important effects. When biological factors do not directly influence network size, or when biological effects that go through network size are not of interest, conditioning on network size is warranted. To condition properly requires an understanding of the *generative processes* (i.e. the *social preferences* and *constraints*) underlying the networks, to understand the relationship between network size and measures of network structure (Box 1). As this information is often absent, we suggest restricting comparisons to networks of similar size, or where it is reasonable to assume similar underlying *generative processes* and similar relationships between network size and other components of network structure.

5. Differences in network scale

Networks can be studied at different social and spatial scales, depending on the ecological or evolutionary process of interest and limitations in data collection. For instance, in some cases a single group may be studied, in others the entire population. As a result, *observed networks* can represent samples of the *real network* at different scales, which can introduce biases in comparative analyses if they are not conducted with appropriate caution (Fig. 4).



Response variables	Explanatory variables *(examples)*
Network-level measures	Species traits Population traits Demographic traits
Community-level measures	Species traits Population traits Demographic traits Group traits Spatial behaviour
Dyadic-level measures	Individual traits Dyadic traits *(e.g. relatedness, home range overlap)*
Individual-level measures	Individual traits Spatial behaviour

Figure 4. An illustration of the challenges of scale in social network analyses. A. Social network analyses address diverse questions related to various ecological and evolutionary processes for which different scales of network structure are important. Networks can vary considerably between species across these scales. For instance, in species that cluster into groups, network modularity (illustrated), is higher at the population-level (macroscale) than the group-level (mesoscale). B. Research teams make decisions about the scale at which to sample networks based on biological properties of their study system, their research question and time and budget constraints. C. Research teams make decisions about the scale of analysis, focusing on measures that may capture the structure of their sampled network as a whole down to measurements that quantify the network position of single individuals. Any mismatches in the scales at which networks are sampled can generate challenges for subsequent comparative analyses.

The extent to which comparing across network scales poses a challenge depends on the scale of analysis required to answer the question of interest (Fig. 4). Measures of network structure that are being compared can vary from measures of the connectedness of individuals (microscale), to measures of the structure of the whole network (macroscale). Meso- and macroscale (whole) network metrics are likely to be particularly susceptible to differences in the scale of sampling between datasets (Ogino et al. 2023). For example, comparing network density (a macroscale measure) from a single social group with that of an entire population can be misleading because the scale of observation affects network density. Individuals within a single group are typically more strongly connected to each other, leading to higher density, while a population-level network includes multiple loosely connected groups, resulting in lower overall density. In contrast, microscale (individual-level) metrics of networks are often less affected by scale and will be more reflective of values in the *real networks* (including non-sampled individuals). However, this will vary according to the *generative processes* underlying the network structure and the specific choice of individual-level metric. For example, in species where individuals interact with others outside their group, an individual will have much higher betweenness centrality when a population- rather than group-level network is considered.

In some cases, it may be possible to compare networks sampled at different scales by sub-sampling from the network sampled at a larger scale. But this process is untested and fraught with complex decisions on how best to subsample (e.g., see the previous section *Differences in network size across networks*). Another potential solution is to estimate the *real network* as a latent structure from an *observed network* by using imputation to “fill in” missing parts of networks sampled at a smaller scale (Box 1, Young et al., 2020). Doing so requires information about the *generative processes* underlying the network, which currently are not well developed (Box 1). For example, in many studies focused on within-group networks, interactions with members of other groups may not be recorded or may occur so infrequently that they remain unobserved. This means we know little about the *social preferences* and *constraints* generating networks beyond the scale of the group. In these cases, it would be impossible to reliably infer the *real network* beyond the scale of the original study.

Considerations for comparing networks

Networks can be sampled across various scales, and *observed networks* representing different scales usually cannot directly be compared. One solution is to use methodological advancements that can impute missing data to reconstruct the *real network* at a larger scale. However, reliable imputation requires an understanding of the *generative processes* underlying the networks, including the processes that drive interactions beyond the scale that was sampled (Box 1). As this understanding is most often lacking, we suggest comparisons be restricted to cases where it is reasonable to assume networks have been sampled at a similar scale.

Discussion

Comparative social network analysis offers huge potential to answer fundamental questions in ecology and evolution, but this approach comes with a set of major challenges that are yet to be fully resolved (Albery et al., 2023). In this paper, we present the *layers of latency framework* that explains how observed animal social networks are related to the latent social structures and processes of interest to researchers. We then outline five key challenges in comparative analyses of social networks. Using the *layers of latency framework* as a base, we consider how these challenges can lead to erroneous conclusions, and we discuss the current state of solutions to mitigate these challenges. By doing so, we have aimed to offer guidance on factors to consider before embarking on comparative social network analyses and to inspire further developments of methodological tools that enable these types of analysis to be conducted robustly and to their full potential.

In addition to giving potential solutions for each specific challenge in the sections above, our summary of our overall current guidance for comparative network analysis is:

- Identify the latent network layer to which your research question applies (Fig. 1) - are you interested in the *real network*, or the *social preference network*? This will shape your analytical decisions going forward.

- Be clear about the limitations of any approach used. Different networks may have been affected by different inherent *constraints* and *sampling biases*, and this can influence observed differences between them.
- Consider whether and how differences between networks to be compared can be addressed analytically. Bayesian methodological developments offer promising solutions, by estimating the *real*, or even the *social preference network*, while explicitly accounting for key differences in compared networks (Box 1). Maintain uncertainty when moving between network layers, and propagate this uncertainty into subsequent comparisons.
- Consider the *generative processes* that link the latent networks to the observed network for different sampling methodologies and/or datasets (Box 1). Understanding these processes can help identify how to account for methodological differences to make different networks comparable or can help (careful) imputation of missing information.

The *layers of latency framework* highlights future theoretical and methodological work that will be central to facilitating analyses that make inferences about latent network layers (both for comparative network analyses and more generally). Moving between network layers necessitates detailed knowledge of the key processes that influence the emergent structure of animal social networks (Box 1). While such knowledge is available for some particularly well-studied species, a combination of theoretical modelling and empirical analyses will often be necessary to identify patterns that can be used to pinpoint the generative processes underlying animal social networks. New statistical tools will then be required to efficiently estimate the latent networks, as well as to tailor existing observation models (e.g. from capture-recapture models) to social network contexts (Silk & Gimenez, 2023). These steps forward will benefit greatly from interdisciplinary collaborations between behavioural ecologists, statisticians, and network scientists (Brask et al., 2021).

We hope the challenges and potential solutions presented here will help to move the field towards a more comprehensive suite of tools for comparing social networks. With further development, comparative social network analysis could become an accessible, reliable and powerful approach to answer long-standing questions in ecology and evolution. We hope that this paper provides a better understanding of the key challenges facing researchers applying these approaches, and some potential ways to address them. Good luck!

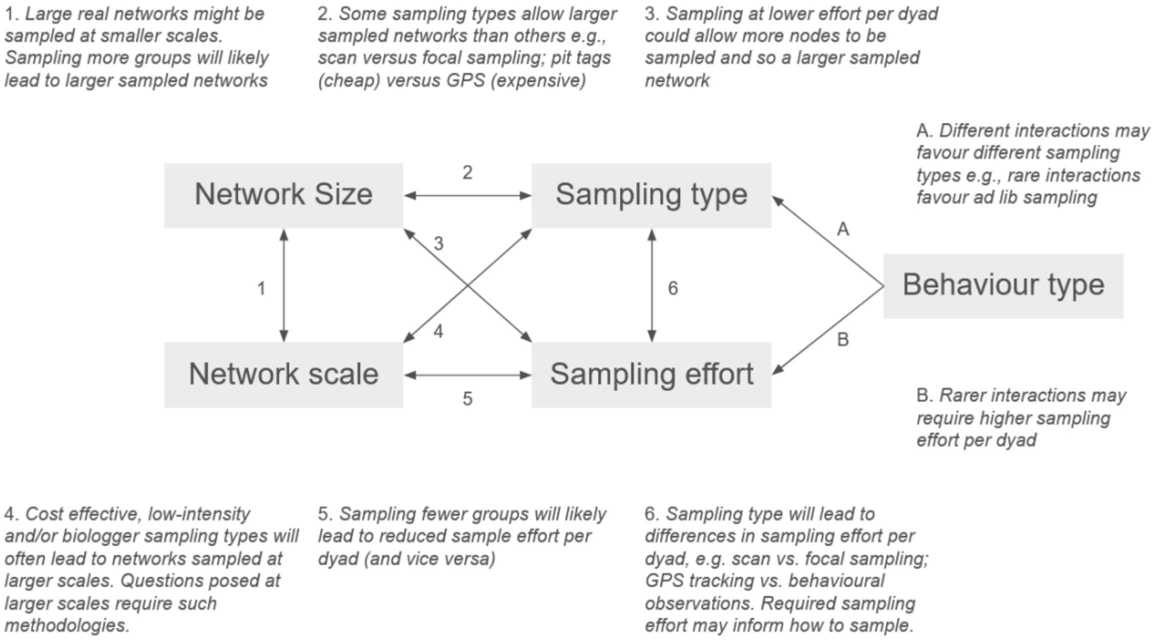


Figure S2. Links between the five key challenges faced when comparing social networks

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