

# Comparative approaches in social network ecology

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**Editor:** Ferenc Jordan**Abstract**

Social systems vary enormously across the animal kingdom, with important implications for ecological and evolutionary processes such as infectious disease dynamics, anti-predator defence, and the evolution of cooperation. Comparing social network structures between species offers a promising route to help disentangle the ecological and evolutionary processes that shape this diversity. Comparative analyses of networks like these are challenging and have been used relatively little in ecology, but are becoming increasingly feasible as the number of empirical datasets expands. Here, we provide an overview of multispecies comparative social network studies in ecology and evolution. We identify a range of advancements that these studies have made and key challenges that they face, and we use these to guide methodological and empirical suggestions for future research. Overall, we hope to motivate wider publication and analysis of open social network datasets in animal ecology.

**KEYWORDS**

comparative analysis, disease dynamics, group stability, meta-analysis, network analysis, pathogen spread, social dominance, social networks, social system

## INTRODUCTION

The social lives of animals vary immensely and across many axes (Hinde, 1976; Hobson et al., 2019; Prox & Farine, 2020; Whitehead, 1997). In some species, individuals live predominantly solitary lives, only interacting with others sporadically, while others form spectacular aggregations of many thousands. Similarly, while some species live in stable groups and form social bonds that last a lifetime (Bruck, 2013; Dakin & Ryder, 2020; Mitani, 2009), other social preferences can be weaker and the identity of social partners relatively unimportant. Variation among social systems is closely tied to ecological and evolutionary pressures faced by different populations (Cantor, Maldonado-Chaparro,

et al., 2021; Evans et al., 2020; He et al., 2019; Kurvers et al., 2014). Variation in well-studied benefits (e.g., access to information and avoidance of predation) and costs (e.g., competition, parasitism) of social interactions across species therefore creates associations between particular social systems and specific environments (Leu et al., 2016) or taxonomic groups (Chak et al., 2017). However, given the ecological environment can also cause variation in social structure within populations (e.g., Jordán et al., 2021), it is important to decompose intra- and interspecific variation in social structure. Because social structure alters the course of evolution (Fisher & McAdam, 2017, 2019), determines the outcome of ecological processes like disease spread (Keeling & Eames, 2005; White et al., 2017) and

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potentially influences a species' resilience to global change (Fisher et al., 2021), understanding drivers of interspecific variation in social structure has important implications and applications. Comparative approaches are popular ways for researchers examining the evolutionary ecology of sociality to understand these processes (Kappeler & Pozzi, 2019; Lukas & Clutton-Brock, 2013; Lukas & Huchard, 2014).

Nevertheless, there are substantial challenges in applying comparative approaches in socioecology, of which a major one is classifying or quantifying variation in social systems. Recent work (e.g., Lang & Farine, 2017; Prox & Farine, 2020) has begun to provide higher-dimensional classifications of sociality, but there remain limitations in the power and universality of these approaches, as qualitative classifications only provide coarse approximations. Furthermore, in many contexts, it is the specific pattern of interactions that plays a role rather than the type of social system *per se*. With the popularisation of social network analyses in behavioural ecology, the time is ripe to apply more quantitative cross-species comparisons that address diverse questions around interspecific variation in social structure and dynamics.

Social networks are an integral part of a behavioural ecologist's toolkit (Farine & Whitehead, 2015; Webber & Vander Wal, 2019). By linking individual behaviour to group- and population-level structure and outcomes (Figure 2), they have helped study diverse aspects of animal behaviour including dominance (Hobson, Mønster, & DeDeo, 2021; Shizuka & McDonald, 2012), cultural evolution (Cantor, Chimento, et al., 2021; Voelkl & Noë, 2008) and epidemiology (Bansal et al., 2007; Keeling & Eames, 2005; White et al., 2017). Applications of network approaches in socioecology have grown rapidly and now encompass substantial geographic and taxonomic diversity, albeit with remaining biases (Webber & Vander Wal, 2019).

Despite the growth in animal social network analyses, few studies have undertaken multispecies comparisons of social networks or used meta-analytic approaches to test broader evolutionary or ecological patterns. Nevertheless, multispecies analyses of social networks have multiple advantages for comparative analysis in social ecology, offering valuable tools to summarise the diversity of animal social systems and tease apart interspecific variation in social structure. These benefits emerge from network descriptions providing: diverse measures to succinctly quantify different aspects of social structure; the ability to quantify fine-scale variation in social systems beyond features like group size; and a way to unify analyses across social scales, from individual- to group-, and population-level features. For example, network approaches have moved discussion about sociality and the costs of parasitism beyond group size to factor in the combined effects of group structure and individual social relationships (Briard & Ezenwa, 2021; Nunn et al., 2015). This provides insight into the strategies with which animal societies balance the trade-offs between parasitism and the

benefits of sociality. Similarly, network approaches' ability to quantify social structure across scales has revealed multilevel social systems in taxonomically diverse species, demonstrating variation in the mechanisms underlying these structures (Camerlenghi et al., 2022; Papageorgiou et al., 2019). Two main issues have limited comparative analyses of social networks: (i) it is challenging to compare the structure of networks of different sizes (Faust, 2006), especially when they are generated by different behavioural processes (Hobson, Silk, et al., 2021), and (ii) there has been a shortage of animal social network datasets available to compare.

With the recent development of multispecies repositories of social network data (Box 1) and an increasingly advanced statistical toolkit, there is now the potential to overcome these issues and exploit comparative social network analyses in ecology and evolution. Here, we review existing studies that have undertaken such analyses. We then identify outstanding challenges to successfully employing comparative and meta-analytic approaches with social network data, suggesting potential solutions and highlighting specific areas in need of methodological research, as well as identifying promising areas for future empirical research. Overall, our paper provides a roadmap for conducting these analyses and aims to inspire the development of new statistical tools to increase their accessibility, as well as motivating the collection and publication of further open social network datasets.

## THE CURRENT STATE OF COMPARATIVE NETWORK ANALYSIS

### The data

As of 3 November 2022, we uncovered 49 studies that compared multiple species' social networks, spanning 16 years (2007–2022; Table S1). Initially, these studies typically compared a small number of species and networks; however, over time, these numbers have increased exponentially (Figure 2). While some studies still compare only a few species, there are now many that incorporate several hundred networks encompassing dozens of species—three of which also included humans. These larger studies often featured replication of several networks within each species, (potentially) allowing estimation of within- and between-species variation in network structure. On three occasions researchers developed (or are developing) substantial publicly available databases (Box 1). Otherwise, larger studies tended to produce their network datasets through literature searches and independently contacting researchers to request data (Nunn et al., 2015; Rocha et al., 2021), or by aggregating datasets that the authors themselves collected (Bhadra et al., 2009; Pasquaretta et al., 2014). Given the few independent datasets, substantial reuse of

## BOX 1 Social network repositories

A recent development is the creation of large-scale, publicly available databases of social network data (Table 1). We introduce three databases for non-human animal social networks here and draw attention to similar efforts for human networks too.

TABLE 1 Summary of existing social network databases.

Database	Number of networks	Number of species	Behaviours	Access
ASNR	790	76	Dominance; Foraging; Grooming; Group membership; Non-physical social interaction; Physical contact; Social projection bipartite; Spatial proximity; Trophallaxis; Mixed	<a href="https://bansallab.github.io/asnr/">https://bansallab.github.io/asnr/</a>
MacaqueNet	761	14	Spatial proximity Body contact; Grooming; Contact aggression; Non-contact aggression	<a href="https://macaquetnet.github.io/database/">https://macaquetnet.github.io/database/</a>
DomArchive	436	135	Dominance interactions; Submissive interactions; Aggression (151 subtypes identified)	<a href="https://github.com/DomArchive/DomArchive">https://github.com/DomArchive/DomArchive</a>
SocioPatterns	14	2	Proximity	<a href="http://www.sociopatterns.org/datasets/">http://www.sociopatterns.org/datasets/</a>

### Animal Social Network Repository (ASNR)

The animal social network repository (ASNR; Sah et al., 2019) was first published online in 2016, although has been regularly updated since then. It has subsequently been used by seven of the studies in our review. Of all the current social network datasets, the ASNR captures the greatest taxonomic diversity, including insects, fish, birds, reptiles and mammals. Data are currently stored as adjacency matrices. It also incorporates substantial variation in network size and the types of behaviour monitored. However, care is needed when exploiting the ASNR as it also includes networks measured in different ways and over varied social and temporal scales, as well as incorporating both free-living and captive populations.

### DomArchive

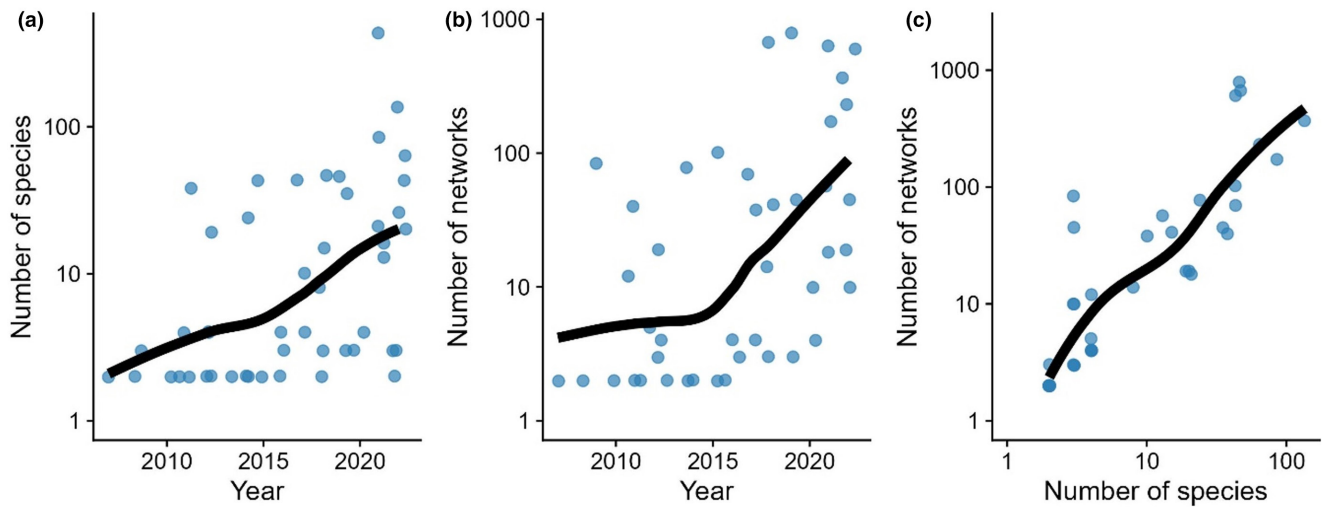
DomArchive is a newly available database of dominance interactions (Strauss et al., 2022), exploiting the long-term focus on social dominance in the animal behaviour literature. The majority of data are available as adjacency matrices (sociomatrices), with a subset stored instead as edge lists. The types of interaction incorporate a wide range of aggressive, formal dominance or submissive behaviours as well as related behaviours such as threats, avoidance and social displacement. The data available will be directly relevant to questions related to social stability and group function.

### MacaqueNet

MacaqueNet (De Moor et al., 2023) is a social network database focused on macaques (*Macaca* sp.) curated for the purpose of comparative analyses in primatology and behavioural ecology. By concentrating on a well-studied genus that shares similar social behaviours, MacaqueNet offers an exciting opportunity for tackling research questions related to group living with fewer of the pitfalls of larger datasets. As is the case for the ASNR, all data stored in MacaqueNet are formatted consistently so fully ready for comparative analyses (although note that data collection methods and edge weights can still differ between studies).

### Human contact network databases

The SocioPatterns team have collected a range of proximity network datasets using Bluetooth loggers (e.g., primary school (Stehlé et al., 2011); scientific conference (Cattuto et al., 2010); Kenyan village (Kiti et al., 2016); hospital (Vanhems et al., 2013)) in addition to one similar dataset from wild baboons. Data are provided as edge lists, and if aggregated as adjacency matrices would be directly comparable with networks connected using similar methods from the ASNR.



**FIGURE 1** Coverage of our identified comparative social network studies. (a) increase in number of species over time; (b) increase in number of compared networks over time; (c) positive correlation between the number of species investigated and the number of compared networks. Each point represents one of 49 studies; the line represents a Loess smooth fitted to the data. The rug on either axis displays the distribution of the data.

said datasets, and growing exploitation of the animal social network repository (ASNR; [Box 1](#)), there has been encouragingly little duplication of effort in producing network meta-datasets. In the near future, researchers carrying out comparative behavioural analyses will be well-placed to use much of the available data, rather than encountering issues with dataset harmonisation and unification—as has been the case with datasets of host–pathogen associations (e.g., [Gibb et al., 2021](#)).

### Taxonomic skew

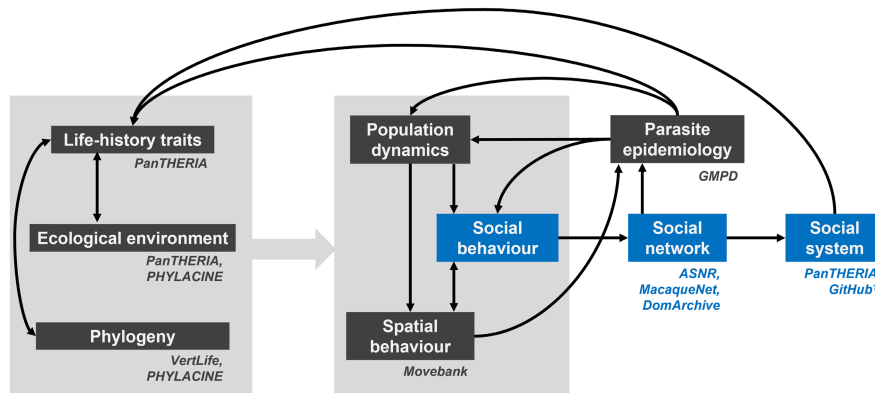
Many studies (19/49; 39%) focused primarily or entirely on primates, with a particular focus on macaques (*Macaca* sp., e.g., [Sueur et al., 2011](#); [Ciani et al., 2012](#); [Balasubramaniam et al., 2020](#)). Otherwise, there was broad coverage of different taxonomic classes, including fish ([Roose et al., 2022](#)), hymenoptera ([Bhadra et al., 2009](#)) and elephants ([de Silva & Wittemyer, 2012](#)), as well as large-scale studies that included diverse vertebrate classes and some invertebrates ([Rocha et al., 2021](#); [Sah et al., 2017](#)). It is unclear how this taxonomic skew could influence the results of pan-dataset analyses.

### Species-level analyses

Many comparative papers (11/49=22%) examined how species' traits correlated with their social network topology with others doing so qualitatively. For example, several analyses linked primates' cognition or behaviour with the structure of their networks ([Pasquaretta et al., 2014](#); [Sueur et al., 2011](#)). Conversely, two studies used the ASNR to examine how species' contact network structures were associated with their parasite communities, focusing on parasite species richness ([Poulin & Filion, 2021](#)) or the evolution of parasite species transmitted over the focal host's contact networks ([Collier et al., 2022](#)). These studies incorporated external databases of host–parasite associations ([Stephens et al., 2017](#)) and human parasite traits ([European Centre for Disease Control, 2016](#); [Richardson et al., 2001](#)), as illustrated in [Figure 1](#).

### Generative models

Two papers (2/49=4%) developed generative models for social network formation, which they validated using multispecies network datasets. For example, [Ilany and Akcay \(2016\)](#) developed a model for network formation



**FIGURE 2** Conceptual overview of the value of how comparative social network analyses fit within a broader framework for social ecology and evolution. We illustrate selected relationships between species- and individual-level traits and social network structure and draw attention to key comparative databases for the main traits illustrated. Github<sup>1</sup> refers to <https://github.com/CharlotteAnaisOLIVIER/Social-organizational-of-primates>.

by social inheritance, validating their predicted networks using data from four species.

## Methodological studies

Several studies (6/49=12%) used animal social network meta-datasets to illustrate new methods or confirm trends in network science or related fields. These included identifying novel scaling trends (Ojer & Pastor-Satorras, 2022; Rocha et al., 2021; Ward, 2021), producing new approaches (McDonald & Hobson, 2018; Ojer & Pastor-Satorras, 2022; Shizuka & Farine, 2016; Ward, 2021) or deriving new network traits (Péron, 2023).

## Dynamical simulations

A particularly common approach (13/49 studies; 27%) to comparative social network analysis was the simulation of transmission dynamics (e.g., Collier et al., 2022; Fountain-Jones et al., 2022; Nunn et al., 2015; Romano et al., 2018; Sah et al., 2017, 2018). This approach may be so popular because, so far, networks have been used to test general ideas for a broad set of potential pathogens. This reduces the importance of disparity in data collection methods and timescales, as (to some extent) the networks are providing a substrate to test ideas in network epidemiology rather than to provide broader ecological insights. These approaches have also often used unweighted (binary) versions of networks, mitigating the impact of variable edge weighting across different studies (see below).

## Individual-level meta-analyses

Finally, among our identified studies, there was only one (1/49=2%) ‘true’ meta-analysis—that is, one that did not

use raw data, but rather analysed a series of model estimates published in other studies (Briard & Ezenwa, 2021). All other papers derived network-level traits and carried out species-level comparative analyses. We capture the distinction between these approaches in [Box 2](#).

## BIOLOGICAL OVERVIEW OF COMPARATIVE NETWORK STUDIES

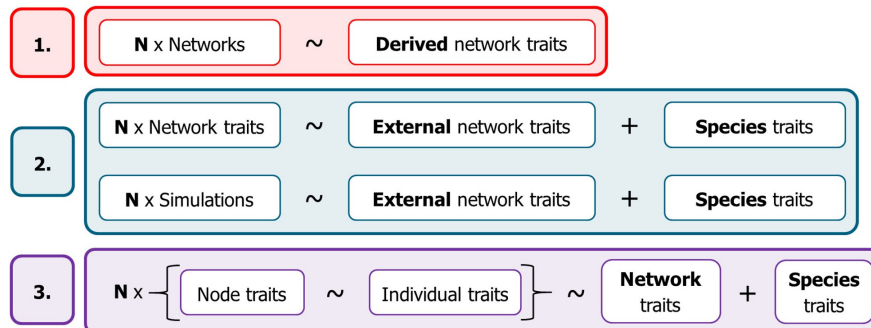
The 49 studies we found tackle diverse research questions across multiple ecological disciplines. We identify the major themes addressed so far, providing a synthesis within each theme based on the objectives and findings of comparative network studies.

### In behavioural ecology

Comparative network analyses in behavioural ecology (23 studies) have predominantly been used to provide insights into the structure and dynamics of animal groups, addressing these questions across social scales. Frequently, it has been applied to quantify population-level social structure for taxonomically similar species (e.g., bats: (August et al., 2014); elephants: (de Silva & Wittemyer, 2012); and equids: (Rubenstein et al., 2015; Sundaresan et al., 2007)). In these cases, using a comparative approach can reveal fine-scale differences in social structure that were previously undetected (e.g., Sundaresan et al., 2007). These studies have often demonstrated how ecological differences between closely related species explain variation in network structure. For example, different social network structures between Australian snubfin *Orcaella heinsohni* and Indo-Pacific humpback dolphins *Sousa chinensis* were attributed to differences in diet, prey availability and feeding behaviour (Parra et al., 2011). Similarly, the role of mating systems

## BOX 2 Classifying comparative network analyses.

A diverse set of comparative approaches are possible using social network datasets. Here, we provide a framework to distinguish between different approaches (Figure 3).



**FIGURE 3** Overview of different types of comparative analyses that can be applied to social network datasets. (1) Network-level analyses that connect network-derived traits with the structure of the network themselves. (2) Network-level analyses that connect network-derived traits or simulation outputs with other traits of the networks and the species that comprise them. (3) Node-level analyses across N networks that involve connecting node and individual-level traits within each system (inside brackets) and then connecting these estimates with species- and network-level traits in a meta-analytical context.

### Comparisons of network properties

The first approach involves comparing the topology of different networks as an outcome of other network properties (e.g., network size). This is common in network science where understanding the generative processes underlying network formation is a major focus (e.g., Ojer & Pastor-Satorras, 2022; Rocha et al., 2021; Ward, 2021). However, it is also of interest to ecologists, such as with studies that test the relationship between network size and modularity (Griffin & Nunn, 2012).

### Species-level comparative approaches

A second type is a conventional species-level comparative approach, in which a network property of interest is fitted as a response variable with a series of species-level traits as explanatory variables, and potentially alongside a phylogeny to control for non-independence among closely related species. The appropriate use of random effects can allow multiple observations to be used for a given species. We subdivide species-level approaches by the outcome variable of interest.

#### Using network topology

Often the outcome of interest is a property of the network itself (e.g., degree heterogeneity, modularity). For example, a researcher might want to ask: How does the modularity of affiliative networks in animal groups vary with environmental harshness? These types of questions will be common in behavioural ecology, for example, in contributing discussions around the role of social complexity in cognitive evolution (Barrett et al., 2007) or linking network structure to demographic factors (Shizuka & Johnson, 2020).

#### Using the outcome of dynamical processes

The outcome of interest could also be the ecological consequences of network structure, necessitating additional steps prior to the comparative analysis. For example, studies in disease ecology often conduct simulations of pathogen spread and then use features of the resulting outbreaks as variables in comparative analyses (e.g., Collier et al., 2022; Fountain-Jones et al., 2022; Nunn et al., 2015; Sah et al., 2017). Similar approaches are useful in understanding the consequences of social structure for information spread and behaviour change (Evans et al., 2020).

### Individual-level meta-analyses

The final category is a meta-analytic approach looking at how relationships between social interaction patterns and conditional traits vary among species. For example, Briard and Ezenwa (Briard & Ezenwa, 2021) showed an overall positive association between social centrality and parasite burden across 210 effect sizes covering 16 host species, but they could not explain variation in this relationship using other host traits. While this study was in the context of disease ecology, there is no reason similar methodologies could not be applied to other questions of interest such as the relationship between social network position and fitness (Silk, 2007; Snyder-Mackler et al., 2020).

We provide a schematic (Figure 3) to display model construction for these three main types of comparative network analyses: (1) analyses examining the relationship between *different* network traits across a range of studies (e.g., How does modularity depend on network or group size? How does network efficiency depend on degree heterogeneity?); (2) analyses of network properties (either topological or the outcome of dynamical processes operating on the network) as an outcome of both network traits and species traits (e.g., How does modularity depend on group size and longevity? How does mean outbreak size depend on fragmentation and body size?); (3) a full meta-analysis to test how relationships between network traits and individual traits vary across species and networks (e.g., Does the relationship weighted degree and fitness depend on species life-history and network modularity?).

(Matsuda et al., 2012) and variation in individual traits, such as cognitive capabilities (Pasquaretta et al., 2014), have also been investigated. One underused approach is applying comparative network analyses to find general rules for animal social structure. For example, Rocha et al. (2021) found a potential power law relationship between group size and social connectivity, with evidence that it varied depending on social interaction type.

At a finer social scale, comparative network analyses have also been used for within-group social dynamics, including dominance hierarchies (Balasubramaniam et al., 2018; Hobson, Mønster, & DeDeo, 2021) and social stability (Sueur et al., 2010, 2011). Here comparing between species can identify general patterns in within-group interactions. For example, (Hobson, Mønster, & DeDeo, 2021) compared dominance networks across 172 groups from 85 species to show most species distributed aggressive interactions evenly across all lower-ranked individuals rather than on either close competitors or the weakest individuals. This has implications for quantifying individual variation in the costs and benefits of social strategies. Comparative studies in macaques (*Macaca* sp.) have investigated how social networks influence fission–fusion dynamics and collective behaviour, for example, demonstrating how the importance of kinship differs between socially tolerant and intolerant species (Sueur et al., 2010). These types of study naturally extend into collective behaviour, including group fission events and departures (Sueur & Petit, 2008). Correspondingly, comparative network approaches have also been used in theoretical models of collective behaviour by demonstrating how more differentiated relationships in within-group social networks lead to reduced when modelling flocking dynamics (Ojer & Pastor-Satorras, 2022).

### In conservation and applied animal behaviour

Comparative social network analyses have also occasionally been used in applied ecology and conservation (five studies), moving beyond group-based analyses to simultaneously incorporate the importance of social relationships and the wider social environment in these contexts. For example, in the context of human–wildlife interactions, Balasubramaniam et al. (2020) showed differences among macaque species in how within-group social network centrality was associated with the tendency to interact with humans, with implications for pathogen spread. In the context of conservation welfare, comparative network analyses have revealed long-term social bonds in captive population that could inform husbandry decisions (Rose & Croft, 2017) or evaluated impacts of environmental enrichment (Dufour et al., 2011).

### In disease ecology

Comparative social network analyses in disease ecology (15 studies) have quantified the role of both individuals and emergent group- or population-level social structures in infectious disease transmission. They have also provided a more generalisable understanding of epidemiologically relevant features of animal social networks that provide insight at both ecological and evolutionary timescales.

Some studies have combined comparative network data with empirical epidemiological data: for example, Briard and Ezenwa (2021) used a meta-analysis to show consistent positive effects of network centrality on infection probability, with the pattern stronger for local rather than global measures of social centrality, and Poulin and

Filion (2021)) demonstrated correlations between some aspects of group social network structure and parasite species richness in parasite groups. As more simultaneously collected network and epidemiological data becomes available, these types of study will provide further tests of key hypotheses in disease ecology.

Of studies to apply comparative analysis to the outputs of simulated network epidemiological models on multispecies social network datasets, a small number (e.g., Carne et al., 2013) have focused at an individual level, comparing the role of individual heterogeneity and/or the value of network-targeted vaccination between species. Many more studies have examined how different aspects of network structure impact epidemiological dynamics, for example: providing and testing new methods to quantify the vulnerability of different hosts to outbreaks (Colman et al., 2021; Fountain-Jones et al., 2022), linking them to key epidemiological concepts such as density-dependence in transmission (Colman et al., 2021) and offering insight into how network structure for different interaction types could influence pathogen evolution (Collier et al., 2022). An area of particular interest has been the role of modular social structures (Griffin & Nunn, 2012; Nunn et al., 2015; Sah et al., 2017), providing insight into how group living shapes disease risk. One study extended these insights to other contagions (Romano et al., 2018).

## PRINCIPAL CHALLENGES FOR COMPARATIVE NETWORK ANALYSIS

Based on our methodological synthesis, we identified key challenges facing comparative analyses of social network structure and classified them into three main groups: meta-analytical choices, between-study comparability, and network features. We generated a framework to help researchers with the principal decisions at each stage of a comparative social network analysis (Figure 4), and provide a number of solutions, many of which address several interrelated issues (Figure 5). Addressing these methodological issues will be critical to tackling research questions across the themes identified in our biological synthesis, in particular by enabling comparisons that incorporate more diverse social systems, data collection approaches and social behaviours.

### Analytical choices for comparison

#### Sample sizes

In our review, the median number of networks compared was 12, and the median number of species was 4. Especially for more powerful comparative approaches (e.g., controlling for phylogeny and machine-learning approaches), this sample size substantially limits the power

to deal with confounding variables and reduces the diversity of questions can be answered. A key solution, which the field is well-placed to achieve, is the coordination and centralisation of publicly accessible databases to facilitate sufficient sample sizes. This could generate issues related to managing a large open dataset and ensuring its continuity, but social network researchers could learn from other efforts to maintain open, partially automated updating datasets (e.g., Carlson et al., 2022). Increased power could also be achieved through greater replication per species (e.g., see MacaqueNet; Box 1), which would allow quantification of within- versus between-species variation in network structure. This could arise through renewed research effort, wider data acquisition or incorporating networks at a range of temporal resolutions (e.g., weekly, monthly and yearly) where appropriate.

### Taxonomic biases

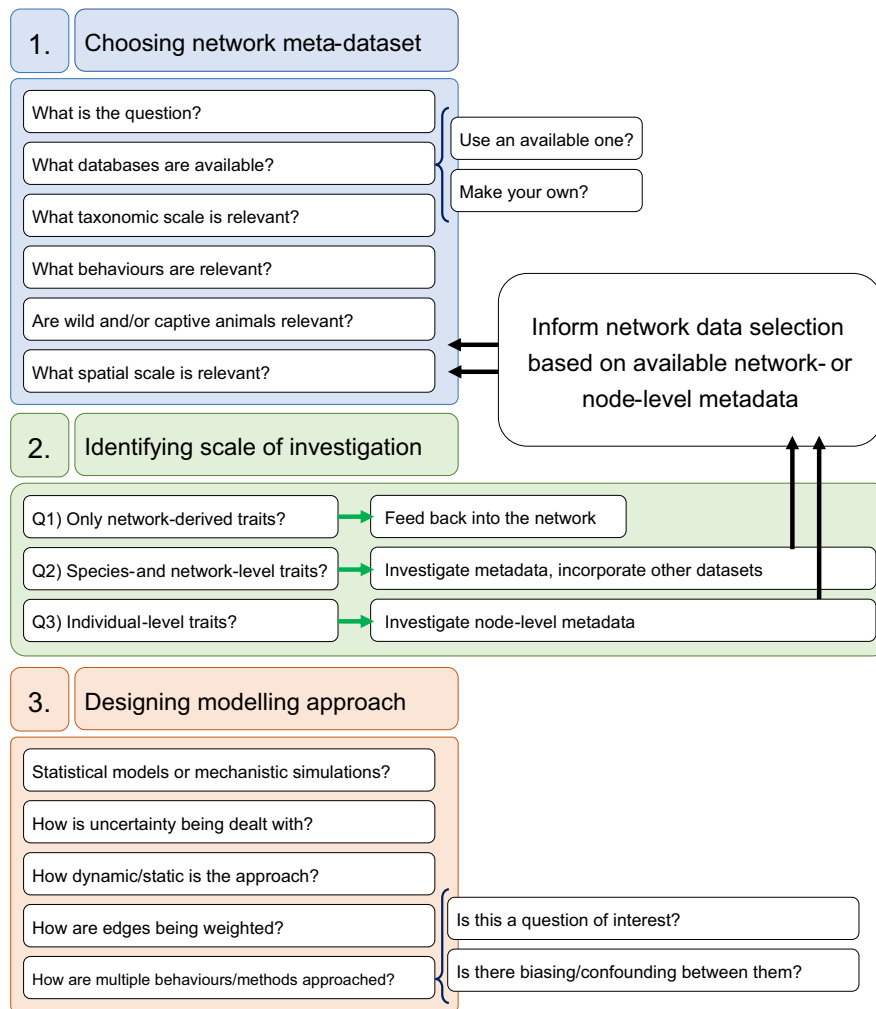
We identified an overpowering focus on non-human primates, especially macaques, across comparative studies. This was present in both the studies themselves and in aggregated datasets; with substantial overrepresentation of primates in the ASNR (e.g., Sah et al., 2019). A fear of overcoming the challenges of big taxonomic divides may have driven researchers to focus on small subsets and within-subgroup analyses rather than analysing across the animal kingdom. As such, it remains an open question how comparable these systems are, and whether generalisable rules shape social structure across these divides. This limits how general the insights provided can be across the diverse social systems present in nature.

There are other subtle biases present. For example, because ant colonies are relatively easy to replicate and observe, the ASNR contains many replicate ant networks, such that ants are overrepresented at the network level rather than at higher taxonomic level (Sah et al., 2019). Because sociality is often studied at different intensities across taxonomic groups (Sah et al., 2018), other well-studied taxa may be similarly overrepresented. Studies' findings could be swayed by these taxonomic skews. In the short term, following the lead of previous studies can help mitigate these issues, for example, by subsampling networks for overrepresented species (Collier et al., 2022) or re-analysing without them (Fountain-Jones et al., 2022). In the longer term, targeted addition of new datasets can address taxonomic biases, perhaps using innovative approaches to exploit existing social or movement data, such as approximating proximity networks using Movebank data (Kays et al., 2022).

### Choosing networks relevant to the question

Careful selection of networks from databases is required to ensure they are relevant for the question posed (Figure 4).





**FIGURE 4** Illustration of our recommended workflow for comparative network analyses, identifying key questions for researchers to consider at each of the three stages of the process: data selection, scale of investigation and model design.

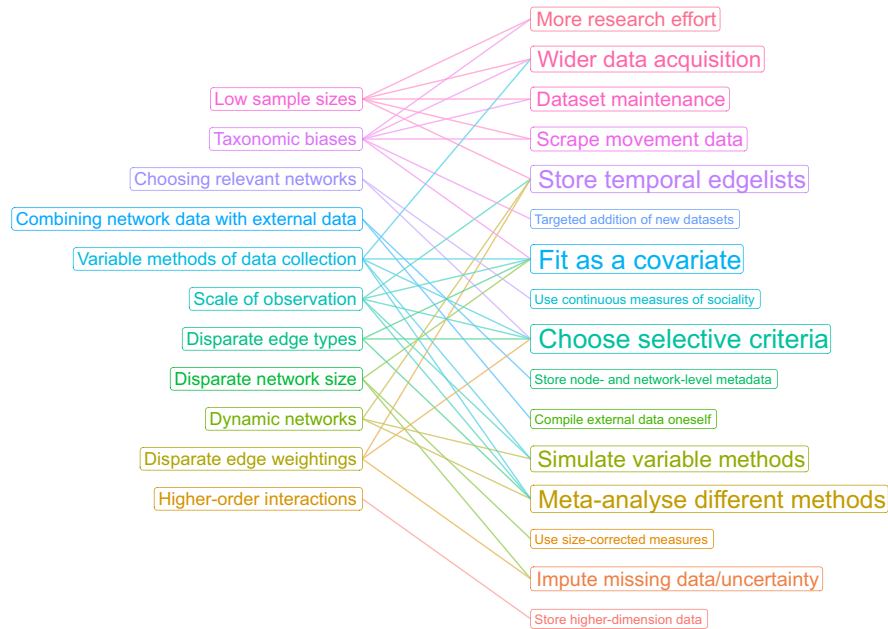
For example, there is little value in using networks based on indirect contacts to model the transmission of many contagious pathogens (Albery et al., 2021). Similarly, the relevance of wild and captive network datasets will depend on the question asked and the taxa investigated. Importantly, taxonomic biases may interact with these problems: for example, how does the effect of captivity on network structure differ between ants and macaques?

One particularly difficult incarnation of this problem lies in comparing species with qualitatively different social systems: for example, is it meaningful to compare species with well-mixed fission–fusion societies to ones that live in stable groups? A potential solution is to use existing frameworks (Prox & Farine, 2020) to inform decisions about which types of social systems to compare for any given question. These frameworks can be used to summarise networks based on multidimensional traits, employing emergent continuous variables rather than discrete a priori ‘social organisation’ categories. Also relevant here are decisions about which behaviours (and so networks) are relevant to a particular research question (see ‘Between-Study comparability’ section below).

## Combining network data with external data

Combining comparative network analyses with external data on individual-, group- or species-level traits considerably expands research scope across diverse areas. However, only rarely have studies combined network data with external data sources (Figure 2), with exceptions including cognitive traits (Pasquaretta et al., 2014) and parasite richness (Poulin & Filion, 2021). These examples illustrate how integrating comparative network data with other traits provides increased power to identify the diverse factors that shape social structure and testing hypotheses related to the variable ecological and evolutionary consequences of these structures (Figure 2). Indeed, one reason that simulations are so regularly used is because they allow approximation of epidemiological consequences of network structures without necessitating additional empirical sources of information.

One limiting factor for some comparative analyses will be the availability of other species-level traits. In general, basic life-history data will likely be available for species that have been sufficiently well-studied to



**FIGURE 5** Common problems in comparative social network analyses (left) and solutions that may help to address them (right). Links between problems and solutions are those identified in the *Principal challenges for comparative network analysis* section of the main text as an outcome of the literature review and judgement of the authors. Solutions are sized according to the number of links they have—that is, the number of problems they are likely to help solve.

collect social network data, and these types of information have been collated into existing databases such as PanTHERIA (Jones et al., 2009). However, other data types may be more limited. For example, a recent integration of the ASNR and global mammal parasite database (Sah et al., 2019; Stephens et al., 2017) resulted in a sample size of 18 primates with available infection data (Poulin & Fillion, 2021). It remains likely that comparative projects will need to compile external, non-network datasets themselves for some traits. Similarly, while existing databases (see Box 1) do contain limited individual-level data (e.g., age and sex) for some networks, this may also limit the number of networks that can be included without contacting the authors of original studies. This highlights the importance of authors providing attribute data alongside their networks to help answer individual-based questions.

## Between-study comparability

### Variable methods of data collection

Networks in multispecies datasets are collected using diverse and occasionally difficult-to-compare methodologies, and little methodological research has critically considered how this impacts comparative analyses. In some cases, there are clear issues with comparisons: for example, group-based methods of network construction will typically cause much denser social networks than other forms of data collection. However, in others, comparability can be less clear. Additionally, different data collection strategies can be confounded with taxonomy

and social system. For example, rodents may be disproportionately trapped, large mammals GPS-tracked, birds ringed or PIT-tagged, and ungulates censused. Similarly, behavioural interactions are easier to observe in species living in stable groups, while network data for less social species may typically be collected using bi-loggers (Smith & Pinter-Wollman, 2021). Further challenges will occur if sampling intensities differ across forms of data collection (e.g., more proximity interactions will be missed using focal sampling than if most individuals are carrying proximity loggers). All of these challenges create limitations that explain the taxonomic scale and narrow research focus of many existing comparative network analyses.

Dealing with the difficulties imposed by data collection methods represents a major challenge. Great care is required, especially because interactions with other study or network features are likely and effects may not be linear. The most conservative solution is to be strict with inclusion criteria (Figure 4) and avoid comparing networks collected in different ways. However, the impacts may also be mitigated by the solutions highlighted in other sections, especially when the data collection method is confounded with the type of behaviour studied or scale of interaction. In these cases, dealing with interactive effects of these confounding variables will be key. Ultimately, the best approach will be not to avoid comparing them, but to compare them explicitly—both with empirical data and simulations—with the aim of discovering such biases. This approach may be particularly powerful where multiple data collection approaches are used in a single system (e.g., Castles et al., 2014).

## Social/spatial/temporal scale of observation

Studies vary substantially in their scale, whether social (e.g., within-group vs. multigroup), spatial (study area size) or temporal. For example, studies may choose a geographic area and follow (a proportion of) a population there (Firth & Sheldon, 2016; Testard et al., 2021), or choose certain individuals across a series of groups (Papageorgiou & Farine, 2020; Silk et al., 2018), or identify a specific group and follow all its members (Kulahci et al., 2018). Terminology can exacerbate challenges here; some studies use ‘group’ and ‘network’ interchangeably, while others do not. A key challenge is identifying if and when we can compare studies focused on groups with those focused on entire populations/multiple groups. Compounding this challenge, other issues such as data collection method and network size are often confounded. Furthermore, the spatial or temporal scale of studies may also be correlated with the proportion of individuals that are tracked or identified, which can also impact topological measures (Gilbertson et al., 2021). All these differences could introduce disparities that are difficult to overcome during analysis and may either exacerbate or mask interspecific variability in social structure.

A crucial methodological development would therefore be to identify combinations of sampling approach and types of network measure that can be used more robustly in these contexts, and which should be avoided entirely. Similarly, comparing studies that occur over different timeframes represents a considerable challenge. On the one hand, network data collected over longer durations can lead to greater confidence that the observed network structure is a good representation of reality (Davis et al., 2018; Farine & Strandburg-Peshkin, 2015; Hart et al., 2023). On the other hand, observing networks for longer will lead to more densely connected networks as more infrequent or random interactions are observed. This will be a greater problem for some data types (e.g., proximity and group-based) than others (e.g., grooming). Networks aggregated over long periods also risk overlooking network dynamics (see subsequent section).

In the short term, careful screening of studies is again important in ensuring the networks used employ a relevant scale. Ensuring that metadata in databases accurately indicates this information (e.g., Sah et al., 2019) is therefore vital. Heading towards incorporating data into these databases as dynamic edge lists or at various temporal resolutions would allow researchers greater flexibility on whether to include a study or not. It will also be beneficial to apply other previously identified solutions such as (with caution) controlling for the scale of the study within the statistical model (e.g., Sah et al., 2018), or analysing separately for networks measured at different social scales (e.g., group vs. population) and integrating the results qualitatively or meta-analytically. As with data collection methods, what is most needed is a renewed effort to employ simulations using well-known

study systems to more accurately quantify when and how problems will arise when comparing networks across scales.

## Disparate edge types

There is substantial variation among networks in how edges are defined (Table 1): some use specific behavioural interactions such as grooming, while others use coarser approaches such as association within a group, or spatial proxies such as home range overlap. Frequently, these networks will not be directly comparable (Castles et al., 2014). In other cases, it is not necessarily clear to what extent different observations represent different behaviours *per se*. Some may be nested: for example, sexual contact requires spatiotemporal proximity, and so, the former network may represent a subset of the latter. Similarly, it will be challenging to work out what represents comparable behaviour types in taxa with very different ethograms. For example, DomArchive (see Box 1) only includes data on dominance networks but includes >150 different behaviours, some of which are rather distinct. Some network types will also have very different topologies: for example, fluid exchange networks are generally very sparse and skewed, exhibiting different topologies to direct contact networks (Collier et al., 2022). This issue is also confounded with differences in data collection methodologies outlined above, further reducing comparability. For example, GPS tracks might be used to detect grouping, while short-range proximity collars are used to identify direct contacts (Albery et al., 2021; Smith & Pinter-Wollman, 2021). Because these methods exhibit different sensitivities and sampling frequencies, two networks may have different topologies purely because of methodology rather than biological differences.

In the short term, careful use of selection criteria can prevent these potential issues (Figures 4 & 5). For example, questions related to within-group social stability may use data on grooming, dominance, social foraging or trophallaxis from the ASNR and combine this with relevant data from DomArchive or MacaqueNet. Researchers can also include data collection methods as fixed or random effects in comparative analyses (e.g., Albery et al., 2022). However, in many cases, it can be more effective to repeat the analysis for different data collection methodologies and then either qualitatively or quantitatively compare the results. This can be used as the strength of a study (Collier et al., 2022). One could even examine whether the results of a comparative analysis are sensitive to inclusion/exclusion of particular behavioural types. In the future, methodological research that uses the comparability of different networks from the same species can help identify interaction types that are more comparable and perhaps use advances in latent network modelling (Ross et al., 2022; Young et al., 2021) to combine insights from multiple data sources.

## Disparate network size

Network size also differs considerably between studies. Historically, differences in network size have been identified as a key problem for comparisons (Faust, 2006), by creating several overlapping issues. First and most simply, raw values of many social network measures depend on network size and how best to correct for its effect will differ between measures and is not always intuitive. For example, while degree is best normalised by dividing through by the number of possible *partners* and betweenness is best normalised by dividing by the number of possible *paths*, for other measures the choice of correction is less clear. Second, the value of using size-corrected measures can depend on both the research question and the generative process determining network structure. For example, network size in existing databases could be reflective of either sampling effort or social group size. In the latter case, it can be biologically meaningful that individuals in larger groups have more social connections. Similarly, if the number of connections an individual forms has an upper bound regardless of group size, then correcting for group size effects will remove biological signals. However, this will not universally be the case, and in some contexts failing to control for group size could drive misleading conclusions if interpreted incautiously.

Because (i) differences in network size may also be driven by variation in sampling (e.g., edge effects or the inability to identify all individuals) and (ii) how network measures covary with network size may differ between systems and approaches, great care in interpretation is necessary when network size varies considerably between studies. As such, this is an area in need of methodological research. For example, the advent of Bayesian approaches to impute missing network data (Young et al., 2021) and generate uncertainty around edge weights and network measures (Hart et al., 2023) can help mitigate issues directly related to sampling differences and allow the focus to be on analytical decisions around the biological effect of group size. One option is to fit network (or group) size as a covariate within comparative models; however, how this is done (e.g., whether it is included as a linear effect) would require careful consideration and cautious interpretation.

Differences in confounding effects of network size and sampling intensity also represent a challenge to comparative analyses assessing the relationship between conditional traits and individual network position (Box 2). In these cases, employing Bayesian methods that propagate uncertainty from this initial stage of the analysis through to the cross-system comparative analytic stage would be an ideal solution, especially by enabling studies with better-sampled or larger networks to have greater weight. This is likely to become increasingly feasible as new methods allow uncertainty around social network metric calculations in animal societies (Hart et al., 2023).

## Network features (and information loss)

Researchers must also decide what level of information loss is acceptable, especially for network dynamics, edge weights and edge sizes (Figures 4 & 5). Accepting more information loss allows for comparative analyses across more diverse species, but limits the ability to detect variation in network structure and reduces the diversity of questions one can ask.

## Dynamic networks

Social interaction patterns typically change over time and/or between ecological contexts (Shizuka & Johnson, 2020; Silk et al., 2017; Smith et al., 2018) meaning social networks are rarely static, and snapshots or aggregations captured in adjacency matrices are a simplification of reality. Currently, very few papers have considered network dynamics within a comparative framework (but see Rubenstein et al., 2015; Chase et al., 2022), in part because dynamic network data is less readily available (e.g., not in the ASNR; Sah et al., 2019). However, even when conducting comparative analyses using static networks, it is important to consider the impact of social dynamics.

Generally, researchers define data collection periods based on their research question (e.g., matching the transmission dynamics of a pathogen (White et al., 2017)) and biological knowledge. However, the duration of data collection can also be constrained by convenience factors (e.g., battery performance of biologgers and duration of presence in a study location; Gilbertson et al., 2021; Smith & Pinter-Wollman, 2021). Similar considerations and constraints also apply to the frequency of network data collection. This creates a challenge when conducting comparative analyses because the potential for variation in social dynamics between systems means it is not straightforward to control for study duration. For example, if the rate at which individuals of species A change their interaction partners is much slower than that same rate in species B, then any correction for study duration will introduce bias related to genuine biological differences, rather than achieving what is intended. The potential impact can be limited by focusing a comparative analysis on a subset of social systems (or taxonomic relatives) in which changes in network structure over time are more similar. Alternatively, if using network duration as a control variable, then allowing its effect to vary according to social system, behaviour type, method of data collection, etc. may mitigate this issue to some extent. In the longer run, another effective solution will be storing data as dynamic edge lists so that researchers can make their own decisions whether to use a dynamic or static approach, and the duration over which to aggregate static networks. However, moving

towards these higher-resolution datasets may reduce researchers' willingness to share network data, as they contain more information about their study system.

### Disparate edge weightings

Variation in edge weight definitions represents another key challenge for comparative analyses, especially when they covary with taxonomy, social system and data collection methods. For example, many studies have used association indices like the simple ratio index (Hoppitt & Farine, 2018), and the popularity of alternatives has varied over time and between research communities. In contrast, many contact-based networks use bio-logging devices to measure the duration or frequency of encounters. This creates problems for a comparative analyst because edge weights in different studies can mean very different things. Previous studies have typically used only a subset of networks that use a similar approach (limiting statistical power), extracted binary networks (losing information on connection strength) or fitted a network's weighted/unweighted status as a covariate in the comparative analyses (Collier et al., 2022). One potential alternative would be to use a simple correction to make edge weights in different networks more comparable (e.g., by dividing all edges by the maximum edge weight to generate a standardised index). However, a potentially more satisfying approach is to use statistical approaches like mixture models that can classify edges as belonging to different distributions, for example, 'weak', 'intermediate' and 'strong' (Ellis et al., 2021; Weiss et al., 2019). A key advantage would be that uncertainty in these classifications could be propagated to subsequent stages of the analysis. Additionally, as is the case with network dynamics, storing network data in raw edge list format would empower those conducting comparative analyses to make their own decisions about how to weight edges to be comparable between studies.

### Higher-order interactions

Another source of lost information in all comparative social network studies conducted so far—and existing data repositories—is that data is stored as dyadic networks, even when this is a simplification (e.g., group-based data). This loses information on interaction size that can be captured using higher-order network approaches (Silk et al., 2022). While these have only rarely been used in behavioural ecology (Musciotto et al., 2022), they are gaining popularity as a tool in network science (Battiston et al., 2021). It would be valuable to move towards also storing higher-order network data in repositories (e.g., as group-by-individual or incidence matrices) to facilitate approaches that explicitly incorporate this higher-order structure.

## FUTURE OPPORTUNITIES FOR COMPARATIVE SOCIAL NETWORK ANALYSIS

Comparative social network analysis has displayed wide informative power across diverse topics, and offers a tool to link social structure to varied ecological and evolutionary processes (Figure 2). Building on and expanding this literature, there remain numerous research areas that are as yet relatively underexplored, especially once methodological approaches facilitate effective comparisons across diverse social systems. Here, we continue to focus on disease ecology, behavioural ecology and conservation, as well as the interface between these topics. However, we encourage others to develop additional applications of these approaches (see Figure 2), especially as a tool to unify across ecological disciplines.

### Social behaviour and disease

#### Transmission and contagion processes

While transmission has been a focus of existing comparative network analyses, there remain many unanswered questions. For example, most simulation studies of transmission dynamics have examined traits of the networks themselves, rather than using the results to explain between-species differences, despite the potential added by integrating additional data (Figure 2). A prominent example of this lies in our improved understanding of modularity (Griffin & Nunn, 2012; Sah et al., 2017), which although highly informative, has largely not been related to species traits themselves. Similar studies could also extend beyond concepts such as modularity to further explore what species- and population-level traits explain important network properties revealed by existing comparative analyses (Colman et al., 2021; Fountain-Jones et al., 2022). Conducting more nuanced comparative analyses that examine differences across multiple types of social association and interaction (Collier et al., 2022) could also be extended to better quantify the expected dynamics of diverse zoonotic and agricultural diseases in their wild hosts.

Moving beyond pathogen spread, there are few explorations of how other social contagions (e.g., behaviour spread) manifest across systems. Because other contagions are often complex (e.g., non-dyadic), their spread can differ from that of pathogens (Firth, 2020), with implications for social system evolution (Evans et al., 2020). For example, Evans et al. (2021) showed that only modular networks with small sub-groups favoured conformist behavioural contagions over pathogen spread. Comparative network analyses represent an opportunity to explore the consequences of

different social systems for pathogen *and* behaviour spread, as well as to link this to species traits. A nice example of how this could be applied to multi-network comparisons is provided by Beck et al. (2023), who compared different social contagions across multiple great tit *Parus major* social networks, showing how individual network position linked to the order of behaviour acquisition. Extending these types of study to multispecies comparisons could help generalise across diverse taxa.

## Health and immunity

Applications of comparative network analyses in disease ecology could also include better quantifying cross-species social drivers of health and immunity. While the consequences of network structure for outbreak dynamics are relatively well understood (theoretically at least), an individual's social interactions can also influence their stress physiology (MacLeod et al., 2023) and health (Snyder-Mackler et al., 2020). Consequently, comparative network analyses could examine the importance of social network structure for the manifestation of individual and population-level disease (or health) itself. To provide a specific example, because mechanisms of immunity are expected to evolve in response to infection (Graham et al., 2011), species- and population-level differences in social network structure should manifest in realised differences in immunity across species via their effects on infection prevalence. Comparative network analyses offer an ideal way to test these predicted relationships that moves beyond coarse measures of sociality like group size (Côté & Poulin, 1995; Patterson & Ruckstuhl, 2013). Future work could integrate individual-level social network position with group- or population-level network structure and explicitly incorporate physiological markers of health or immunity. It should be noted that comparative studies of immunity are also difficult due to issues such as the variable sensitivity of the available eco-immunological tools (Boughton et al., 2011), but nevertheless even coarse and generalisable measures may prove informative when integrated with social networks.

## Integrative behavioural ecology

### Socio-spatial ecology and behavioural integration

Individuals' spatial and social behaviours are tightly intertwined (Webber et al., 2023), with spatial behaviour often being important in explaining social network structure (Firth & Sheldon, 2016; Mourier et al., 2012; Pinter-Wollman, 2015). Comparative network analyses offer an exciting opportunity to look at how the role of the ecological

environment and movement behaviour in explaining social structure varies among populations and species (Figure 2), testing whether variation in these relationships can be linked to species traits such as body mass, mobility and kin structure. Examining how spatial and social network types are linked across and within species could inform a wide range of empirical questions, for example, refining our ability to quantify individual variation in optimal group size and structure (Webber et al., 2023), as well as encouraging integration of spatial data types into social network workflows using spatio-temporally parameterised telemetry tracks (Robitaille et al., 2019).

## Group structure and dynamics

Existing applications of comparative social network analyses have focused on comparing group- and population-level social structure and patterns of group stability. However, typically this has involved small numbers of closely related species. Extending these approaches across diverse social systems offers the potential to tease apart the importance of the ecological environment, evolutionary history and species-level traits (e.g., life history, mode of movement, migratory tendency and mating system; Figure 2) in explaining broad patterns in animal social structure. Using a comparative network approach provides a more flexible way to capture nuanced variation in social structure and its temporal dynamics than historical approaches. Moving to finer social scales, there is considerable scope to answer novel questions as more social network datasets become available. For example, different relationships between the costs of aggression and dominance rank have been documented (Hobson, Mønster, & DeDeo, 2021; Silk et al., 2019), and comparative network analyses offer promise in finding general patterns for how this relationship varies and depends on other species traits.

## The evolution of sociality and cooperation

The evolution of cooperation is a major focus in behavioural ecology and has benefited from previous comparative analyses (Cornwallis et al., 2017; Firman et al., 2020). Despite studies in this area frequently examining the maintenance of complex sociality (e.g., Akçay, 2018), they have yet to take full advantage of comparative network approaches, either theoretically or empirically. Moving network models of the evolution of cooperation from theoretical network structures (e.g., Ohtsuki et al., 2006) to exploit multispecies data from social network repositories could help generalise findings to different real-world network structures. These approaches may also help investigate how the emergence of cooperation in different network structures is linked to species-level traits, and how

well it aligns with recorded cooperative behaviours. From an empirical perspective, comparative social network analyses can provide further metrics to help construct multidimensional projections of social complexity (Prox & Farine, 2020), as well as feeding back to inform the development of social network structures themselves (Akçay, 2018). Identifying consistent features of social networks that differ between cooperative and non-cooperative species, for example, could help quantify how the evolution of cooperation shapes wider ecological and evolutionary processes.

## Social ageing

Recent interest in social ageing has revealed age-related changes in social behaviours as older individuals become less socially connected (Siracusa et al., 2022). Because ageing itself is a complex process that needs to be demonstrated at the individual level (Nussey et al., 2008), it will greatly benefit from—if not necessitate—comparative network analyses rather than more classical approaches that look at traits such as group size and composition. Given that age data are regularly monitored in many long-term study systems and already available as a node attribute in some social network repositories, comparative network approaches can play an important role in generalising age-related changes in social interaction patterns across species and ecological contexts.

## Conservation and behaviour

### Human–wildlife interactions and conservation

Another opportunity is to test how species' social networks differ in their responses to anthropogenic disturbance. For group-living species, social networks may respond in varied ways to these anthropogenic pressures (Blumstein et al., 2023; Fisher et al., 2021). For example, endangered mountain gorillas' social networks became more cohesive when tourists were too close (Costa et al., 2023). Testing to what extent these dynamics vary according to other species traits could help inform which social species are most at risk from anthropogenic pressures and how best to protect them (Snijders et al., 2017). In a similar vein, a generalised, cross-species understanding of group social network stability or individual social integration and how it is linked to health (integrating behaviour, disease and conservation) could help inform population augmentation or reintroduction attempts if extended to endangered social species. Group stability and social integration are likely to play a key role in the initial success of such projects when social relationships strongly determine fitness.

## CONCLUDING REMARKS

By providing a tool to compare and contrast diverse social systems across species with diverse evolutionary histories and highly variable ecologies, comparative social network analyses have huge untapped potential to further our understanding of the evolutionary ecology of animal societies and to strengthen the links between different ecological sub-fields. Our synthesis reveals growing interest in comparing network structures and their ecological consequences across taxonomic divides, as well as the increasing power of approaches being used. Especially given the apparent trend of increasing data breadth, depth and availability over time, we expect that these approaches will only become more powerful for quantifying the diversity of animal social systems and explaining variability across species in the near future. Greater use of meta-analyses of within-network trends alongside these approaches will increase the reach and reliability of comparative approaches in social network analysis (Spake et al., 2022), and transform the hunt for general patterns shaping the structure of animal social systems.

## AUTHOR CONTRIBUTIONS

All authors developed the ideas for the manuscript. GFA and MJS wrote the initial draft with all authors contributing to subsequent revisions.

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## PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14345>.

## DATA AVAILABILITY STATEMENT

Studies found in the literature review are available at <https://doi.org/10.6084/m9.figshare.24552514.v1>. The dataset used to produce Figure 5 is available at <https://doi.org/10.6084/m9.figshare.24552517.v1>. Code used to produce Figures 1 and 5 is available at <https://doi.org/10.6084/m9.figshare.24552511.v1>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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