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Disease implications of animal social organization and network structure - a quantitative analysis

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Summary

1. Networks are being increasingly used to quantify interaction patterns of a broad range of social systems ranging from solitary to eusocial species. Social behavior driving the complexity of interaction networks has important consequences towards infectious disease transmission.

2. Prior studies however have been species and population specific, which highlights the need to develop a general theory towards the implications of social

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behavior on disease risk.

3. We used quantitative tools to review the commonalities and differences in the structure of 666 published interaction networks from 47 non-human species categorized into four social systems - *relatively solitary*, *fission-fusion*, *social* and *socially hierarchical* species. Additionally, we determined the disease costs of sociality due to the underlying interaction network structure.

4. We found that the interaction networks of *solitary* species have the highest variation in individual's social partners, while the interaction networks of *fission-fusion* species were the most fragmented.

5. Disease simulations show that the structure of interaction networks can alleviate the disease costs of group living for *social*, but not *socially hierarchical* species.

6. We also find clear differences between the four social systems in terms of behavioral plasticity of individuals towards increasing group size. *Socially hierarchical* species maintained network connectivity with increasing group size, whereas non-hierarchical *social* species reduced effort towards each pairwise interaction to offset the higher amount of energy invested in engaging with new social partners.

7. Our findings offer new perspective on the debate about the disease costs of group living by evaluating how social organization strategies mediate pathogen pressures.

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Keywords

animal social network, contact network, epidemiology, infectious disease dynamics, meta-analysis, social behavior, social complexity, wildlife disease

Introduction

Animal societies are increasingly being recognised as complex, including species that have traditionally been considered as solitary. Over the past 20-30 years, modern technology has enabled researchers to quantify the social structure in animal societies using tools from network analysis. Mathematically, networks describe interactions between a set of nodes by placing edges connecting the nodes. Social network approaches have been used in the literature to document animal interactions in multiple different contexts, including aggressive encounters (Casey *et al.*, 2015), affiliative contacts (e.g., grooming, Franz, Altmann & Alberts (2015), trophallaxis, Quevillon *et al.* (2015)), and spatial proximity (Reynolds *et al.*, 2015).

Social networks quantify heterogeneity in individual behaviour, and network analysis has consequently been used to examine the relationship between individual behaviour and its social network position (Aplin *et al.*, 2013; Krause *et al.*, 2016). For example, gregarious or high-ranking individuals interact with a greater proportion of individuals in a group and tend to occupy central positions in the social network (Krause *et al.*, 2014). Individual position within the social network is known to be associated with several benefits such as reproductive success (Wey *et al.*, 2013), access to mates (Oh & Badyaev, 2010), longevity (Silk *et al.*, 2010), defense against predators (Krause *et al.*, 2016), increased access to resources

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(Aplin *et al.*, 2012) and offspring survival (Silk *et al.*, 2009). Higher frequency of affiliative, agonistic and mating contacts, however, is also associated with elevated risk of pathogen transmission (Godfrey *et al.*, 2009).

The perceived difference in the costs and benefits of group living is expected to modulate individual's behavior (Kurvers *et al.*, 2014), as well as the structure of the local and global social network. However, while previous studies have focused on how the position within a social network affects an individual's fitness, few have explored the relationship between species sociality and network structure. Faust & Skvoretz (2002) compared 42 networks across human, animal and bird species and found network similarity to be dependent on the interaction type rather than the taxonomic classification. A follow-up study that compared 51 human and non-human social networks pointed out the difficulties in comparing network structures across taxa, as most of the global network properties are constrained by network size and edge density (Faust, 2006). Comparative studies of primate social networks have shown an association between neocortex size, which is linked to higher social ability, with network density, connectivity, and global network efficiency (Lehmann & Dunbar, 2009; Pasquaretta *et al.*, 2014). Lusseau & Newman (2004) compared the structure of dolphin social networks with known features of human social networks (positive degree homophily, preferential association by age), but no formal statistical comparisons were made. Other recent attempts have been limited to closely related species (e.g., comparison of grevy's zebra, *Equus grevyi* and onager, *Equus hemionus* by Sundaresan *et al.* (2007)).

Socially complex species with higher cognitive abilities are typically thought to live in larger groups (Dunbar, 1992; Lindenfors, 2005) and have elevated costs of disease transmission due to high contact rates (Loehle, 1995; Altizer *et al.*,

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2003). While social complexity is assumed to be synonymous with higher network complexity, research on the interaction patterns of less social and solitary species have suggested that this is not necessarily true. For example, the analysis of the association data in blacktip reef sharks, *Carcharhinus melanopterus* (Mourier, Vercelloni & Planes, 2012), desert tortoises, *Gopherus agassizii* (Sah *et al.*, 2016), and raccoons, *Procyon lotor* (Hirsch *et al.*, 2013) demonstrate that individuals form non-random and social preferences, even though they are typically considered as solitary species. The expectation of higher disease costs of sociality have also been weakly supported in the previous literature (Arnold & Anja, 1993; Rifkin, Nunn & Garamszegi, 2012; Patterson & Ruckstuhl, 2013). It has been argued that higher sociality might also have selected for behavioral mechanisms, life history traits, or physiology that alleviates or even confers higher disease resistance as compared to less social species (Loehle, 1995; Cremer, Armitage & Schmid-Hempel, 2007; Meunier, 2015). Recent mathematical models predict that the network structure itself, under certain conditions, can serve as a primary defense mechanism against infectious disease by lowering the risk of disease invasion and spread in socially complex species, without requiring an additional increase in physiological immunocompetence or behavioral avoidance (Hock & Fefferman, 2012). However, to our knowledge, there are no empirical evidences till date towards this prediction.

Another aspect to consider in evaluating the disease costs of social complexity is how disease transmission scales across groups (i.e., of the same species) of different sizes. This is important because group sizes can range over several orders of magnitude, even in similar environmental conditions (Sjoberg, Albrectsen & Hjalten, 2000; Griesser *et al.*, 2011). Accurate predictions of disease costs across spatially distinct groups can be made using the knowledge of how host interaction

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network scales with group size (Ferrari *et al.*, 2011). Scaling of host contacts and pathogen transmission rate is ultimately determined by the behavioral plasticity at the individual level. Change in group size can act as potent stressors to animals because it can increase the cost of group living, but on the other hand, larger group sizes may also improve group-living benefits (e.g., protection against predators and reproductive success). The social behaviour of an individual towards its group members, therefore, changes depending on the perceived trade-off between the costs and the benefits of larger group size (Vander Wal, Yip & Mclaughlin, 2012; Cross *et al.*, 2013; Gogarten *et al.*, 2014; Hubbard & Blumstein, 2015). The behavioral plasticity associated with group size has important implications towards infectious disease spread. If the costs of larger group size surpass the benefits, then animals may limit their energy invested in social interaction and restrict social partners to a smaller proportion of the total group size. This, under constant spatial area conditions, is analogous to the frequency-dependent model of disease transmission, where contact rate saturates with increasing host density. On the other hand, when there are higher perceived benefits of larger groups, then individuals may invest more energy interacting with larger proportion of group members. An increase in association rates with an increase in group-size may result in increased disease transmission from infected to susceptible host members, which is analogous to density-dependent scaling of disease transmission. Most empirical studies on the subject however have been species-specific and document specific interaction type, making it difficult to infer the relationship between group size and pathogen scaling across different social systems.

In this study, we conduct a quantitative analysis of 666 interaction networks across 47 non-human species to investigate the relationship between social organi-

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zation, network complexity, and the costs of disease transmission. This is achieved in three steps. First, we use phylogenetically-controlled Bayesian MCMC models to identify the differences in network structures associated with different social systems. Second, disease simulations are performed to determine the role of various network measures in curbing the invasion of a novel pathogen and limiting the spread of infectious diseases. Finally, we identify the relative costs of disease transmission for each social system as mediated by their network structures. Because group sizes are inherently dynamic in nature, we also compare behavioral plasticity of individuals towards increasing group size to determine how pathogen transmission scales across groups of different social systems.

It is becoming increasingly clear that the disease implications of social complexity depend on the structure of interaction networks rather than a simple dependence on group size for social groups. Network comparisons across species are however often not straightforward, especially when networks vary in size and connection density (James, Croft & Krause, 2009). This work, by broadening the scope of network analysis from being just species-specific to a meta-analytic approach, provides new insights towards how the organization of interaction patterns can mediate disease costs of sociality. A better understanding of the association between network structure and species sociality, in the future, can facilitate the development of an index that quantifies the spectrum of sociality levels observed across the taxonomic boundaries.

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Results

Structure of interaction networks associated with the social systems

We obtained 666 interaction networks spanning 47 non-human species and 18 taxonomic orders (Fig. 1). Edge connections of these networks summarized different types of interaction between individuals, including food sharing (trophallaxis), grooming, physical contact, and spatial proximity. Fig. 1 summarizes the species, their phylogenetic relationships, the number of networks available for each species and the type of interaction recorded. We classified the animal species in our database into four broad categories of sociality - relatively solitary, fission-fusion, social, and socially hierarchical. *Relatively solitary* species were defined as the species where adults infrequently interact with other adults outside the mating period. Examples of *relatively solitary* species in the database include the desert tortoise (*Gopherus agassizii*), raccoons (*Procyon lotor*), and the Australian sleepy lizard (*Tiliqua rugosa*). Species that change the composition of their groups by the means of fission and fusion of subunits were classified as *fission-fusion*. *Social* species were defined as the species where adults engage in prolonged interactions with other adults outside of breeding periods. We defined *socially hierarchical* as non fission-fusion species typically characterized by a permanent (such as ants) or temporary (e.g. baboons) social hierarchy (Grueter *et al.*, 2012; de Silva, Schmid & Wittemyer, 2016).

To determine how the structure of interaction networks is different across the social systems, we used a phylogeny-based, Bayesian generalized linear mixed

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model with the four sociality levels as the categorical response. The following network measures were included as predictors in the model (see Table S1 in the Supplementary Information for definitions): degree heterogeneity, degree homophily, clustering coefficient, weighted clustering coefficient, transitivity, betweenness centrality, weighted betweenness centrality, average group size, network fragmentation, group cohesion, relative modularity and network diameter. We found several network measures to be collinear with Variance Inflation factor (VIF) value of more than 3. These metrics were therefore removed from the analysis, and the final model consisted of five network measures - degree heterogeneity, degree homophily, betweenness centrality, group cohesion and network fragmentation (along with the number of nodes, number of edges and average edge weight to control for different sampling designs) (Table 1, Fig. 2). We found that the interaction networks of *relatively solitary* species were more likely to have the highest degree heterogeneity as compared to the other three social systems (pMCMC < 0.05, Table 1). The interaction networks of *fission-fusion* species, on the other hand, tended to be more fragmented in comparison to *solitary*, *social* and *socially hierarchical* species. In addition, social species had more fragmented interaction networks as compared to *solitary* species. No difference was detected in the average betweenness centrality measure between the *solitary* and the social systems. *Socially hierarchical* species, however, had a higher average betweenness centrality than the *fission-fusion* species, which indicates that individuals of hierarchical social systems occupy more central positions within the interaction networks. No difference was detected between the four social systems in terms of individuals' preference to associate with socially similar others (degree homophily) or preference to interact with members of own social group (group cohesion).

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Disease implications of network structure and the social systems

Comparisons of interaction networks in our database revealed differences between the network structure of relatively solitary, fission-fusion, social and socially hierarchical species. Do these differences in network measures also influence the disease costs of social organization? To answer this question, we performed Susceptible-Infected-Recovered disease simulations through the interaction networks in our database. Three measures relevant to disease management were used to summarize the simulations: (a) Proportion of individuals infected in the network (outbreak size) that estimates the total burden of mortality (or morbidity), (b) the duration of infectious disease spread (outbreak duration), which estimates how quickly the infection spreads through the network and therefore the time duration within which disease control/management interventions have to be employed, and (c) epidemic probability, that measures the likelihood of an infectious disease invasion turning into a large outbreak (viz., outbreaks that infect at least 15% of the individuals in the network).

In Fig. 3 we consider the disease costs of social organization for low, moderate and highly transmissible pathogen (see Fig. S1 in Supporting Information for the results on an extended range of pathogen transmissibility values). Disease simulations show that *socially hierarchical* species experience the largest disease outbreaks as compared to the other social systems, and have longer outbreaks of low transmissible infections. *Social* species, on the other hand, experience the lowest outbreak size from low and moderately transmissible pathogens, although the outbreak sizes were not significantly smaller than the outbreaks in *fission-*

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fusion species. The risk of disease outbreaks turning into epidemics was lowest in *relatively solitary* and *social* species for moderately transmissible infections. For highly transmissible infections, however, only *solitary* species demonstrate a low epidemic probability as compared to the other social systems.

The differences in the disease costs observed across the four social systems can be explained in terms of the organization of their underlying network structure, and its role in influencing disease transmission (Fig. 4, Fig. S2). Interaction networks of *socially hierarchical* species have lower degree heterogeneity as compared to solitary species, and lower fragmentation as compared to fission-fusion species (Table 1). Our disease simulations show that low degree heterogeneity and less subdivided networks cause larger outbreaks for most levels of pathogen contagiousness (Fig. 4). Highly fragmented networks of *fission-fusion* species, and highly degree-heterogeneous interaction networks of *solitary* species, therefore, tend to experience smaller outbreaks than *socially hierarchical* species. Interaction networks of *social* species are more subdivided than *solitary* species; disease outbreaks in these species, therefore, tend to be smaller as compared to *socially hierarchical* species. Interestingly, outbreaks of highly transmissible infection in highly fragmented networks are more likely to turn into epidemics (Fig. 4). This, along with the negative association between degree heterogeneity and epidemic probability explains why outbreaks of highly transmissible pathogen in networks of *solitary* species (that are less fragmented than *social* and *fission-fusion* species, and are highly degree heterogeneous) are less likely to turn into epidemics as compared to the other social systems.

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Behavioral plasticity of individuals in different social systems towards increasing group size

Since interaction networks are inherently dynamic in nature and pathogen transmission rate can vary with group size, we next examined how individuals of different social groups modulate their interactions with increasing group size. We identified social groups within each interaction network using the community detection algorithm as described by Blondel *et al.* (2008). Only those interaction networks in our database that showed strong modular subdivisions (relative modularity, Q_{rel}>0.3) were considered for the analysis. For each network, we calculated the four following measures of behavioral response towards increasing group size - average individual degree, average individual strength, average pairwise strength and group connectivity (see Table S1 for definitions).

Social plasticity of individuals towards increasing group size showed clear differences between the four social systems (Fig. 5). Individuals of all social systems interacted with more group members as the group size increased, but the largest increase in the number of social partners was observed in *socially hierarchical* species (Average individual degree, Figure 5). *Solitary* species, on the other hand, demonstrated the largest increase in average individual strength with larger group sizes, followed by *fission-fusion* and *socially hierarchical* species (Average individual strength, Figure 5B), which indicates that solitary individuals invest a higher amount of energy towards social interaction with members of larger groups as compared to other social systems. On a dyadic level, pairwise interaction strength decreased for *social* species, suggesting that the individuals reduce effort towards each pairwise interactions in order to offset the increase in energy spent engaging

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with new social partners in larger groups. In contrast, the amount of energy invested on pairwise interactions in *solitary*, *fission species* and *socially hierarchical* species did not change with increasing group size. Overall, group connectivity of *socially hierarchical* species remained unchanged in larger groups (Group connectivity, Figure 5). Larger group sizes, however, led to a decrease in connectivity for *solitary*, *fission-fusion* and *social* species.

Discussion

Comparative studies are a powerful approach for testing ecological and evolutionary hypotheses. Network comparisons, however, are not straight-forward, as several topological measures depend on network size and edge density (James, Croft & Krause, 2009). Different data-collection methodology, sampling scheme, and edge weighting criteria can also create biases while comparing social networks (Castles *et al.*, 2014). Beyond the differences in data sampling method and network size, comparing local network features is challenging as several metrics are correlated to each other (Farine & Whitehead, 2015). It is therefore not surprising that few studies have attempted to compare networks across different taxonomic groups and sampling schemes. This study, to our knowledge, is the first attempt to utilize an extensive database of non-human social networks to understand the disease costs of species sociality due to the underlying network structure. We demonstrate how comparative studies can be performed by accounting for variation in group sizes, network connectivity and edge weighting criteria.

Social systems and the structure of the interaction networks. Social organization of species can be highly variable, ranging from solitary to highly

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structured social societies. Species are generally categorized into social systems based on qualitative observations of life history traits (but see Aviles & Harwood (2012); Silk, Cheney & Seyfarth (2013)). The degree of social complexity of many species has, however been recently debated based on the structure of their interaction networks (Mourier, Vercelloni & Planes, 2012; Sah *et al.*, 2016). Since interaction patterns are key to assessing the social complexity, can the structure of interaction networks be used to quantify the differences among the different social systems? To answer this question, we compared the structural characteristics associated with the interaction networks of species typically characterized as *solitary*, *fission-fusion*, *social* and *socially hierarchical*. The evidence that we present here suggests that, at the least, solitary, fission-fusion, and higher social organizations can be distinguished from each other based on (a) degree of variation among social partners, (b) the extent to which the interaction network is divided into cohesive social groups (i.e., the level of network fragmentation) and (c) the proportion of individuals that occupy socially central positions in the interaction networks (i.e, the average betweenness centrality of the network). Remarkably, these differences exist between the social systems in spite of differences in the data collection methodology, type of interaction recorded and the interaction weighting criterion.

Social and *fission-fusion* species are typically considered to have large degree heterogeneity (e.g. bottlenose dolphins Lusseau *et al.* (2003), wire-tailed manakins Ryder *et al.* (2008)). Our results, however, show that the degree heterogeneity in *relatively solitary* species is much higher than the other social systems. Large variation in the nodal degree in solitary species indicates that a small proportion of individuals interact with a large number of conspecifics, which could arise simply

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due to a high variation in spatial behavior as compared to other social species (Pinter-Wollman, 2015; Sah *et al.*, 2016). Our results also show that the interaction networks of *fission-fusion* species are the most fragmented followed by *social* species. Networks of *relatively solitary* and *socially hierarchical* species, on the other hand, were the least subdivided. Interaction networks of animal societies are ubiquitously divided into socially-cohesive groups (Sah *et al.*, 2014; Griffin & Nunn, 2011). Presence of many small, socially cohesive groups within interaction networks of *fission-fusion* species can be explained based on the behavioral tendency to frequently switch affiliative partners; as a result, individuals form consistent social bonds with a small number of individuals (Rubenstein *et al.*, 2015). Social species often form groups based on sex/age class, kinship and functional roles (Kanngiesser *et al.*, 2011), and modular subdivisions has been shown in theoretical models to promote behavioural diversity and cooperation (Whitehead & Lusseau, 2012; Gianetto & Heydari, 2015). Social species may therefore limit group size to maximize benefits of cooperation, making their interaction networks fragmented (Marcoux & Lusseau, 2013).

Disease implications of network structure and the social systems

Social complexity is expected to have major implications towards infectious disease spread, and social species living in large groups are assumed to experience larger disease costs than other social systems (Altizer *et al.*, 2003). However, our study demonstrates that the disease implications of social organization extend beyond a simple dependence on group size, and organization of interactions within groups

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has important implications towards the disease costs of social complexity. Our results demonstrate that species with temporary or permanent hierarchical social organization experience larger outbreaks, and are vulnerable to outbreaks turning into epidemics as compared to other social systems. This is because interaction networks of *socially hierarchical* species are less fragmented, and individuals tend to have a similar number of social partners (i.e., low degree heterogeneity). In contrast, non-hierarchical *social* species and *fission-fusion* species experience lower disease costs because their interaction networks are highly fragmented. Disease burden in *relatively solitary* species is also lower than *socially hierarchical* species owing to the high variation in the number of social partners among individuals.

Our analysis of the role of network structure in disease transmission revealed that the networks with high degree heterogeneity have lower outbreak sizes, shorter outbreak duration and have a lower risk of turning into epidemics (Figure 4). This is because heterogeneous degree networks have a larger proportion of low degree individuals as compared to homogeneous networks, and have a minority of large-degree superspreaders. As the proportion of higher degree individuals is rare, an infectious disease outbreak rapidly depletes these super-spreaders and must infect lower-degree individuals in order to propagate through the entire network, where the risk of stochastic extinction is higher. Typical disease outbreaks therefore die sooner in degree heterogeneous networks after infecting a small proportion of individuals. In contrast, homogeneous networks with the same edge density have a higher proportion high degree nodes, and therefore local depletion of highly connected nodes occurs more slowly, leading to larger and longer disease outbreaks (Meyers *et al.*, 2005; Kiss, Green & Kao, 2006). Our disease simulations also show that network fragmentation lowers the duration of disease outbreaks and epidemic

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probability of low, but not of moderately and highly transmissible infectious diseases. A recent study has shown that network fragmentation is one of the two mechanistic features that drive modular subdivisions in animal social networks (Sah, P, unpublished data). High network fragmentation limits the global spread of infectious diseases by localizing infections to a small portion within the interaction networks (structural trapping), but can also enhance local transmission and cause structural delay of infection spread (Sah, P, unpublished data). Our results suggest that the infectious diseases from low transmissible pathogens experience strong structural trapping in fragmented networks, and therefore experience rapid extinction after infecting a local pocket of individuals in the network. In contrast, pathogens that are at least moderately transmissible avoid stochastic extinction by reaching the "bridge" nodes within the subdivided network, but experience delay in transmission due to the presence of structural bottlenecks.

Behavioral plasticity of individuals in different social systems towards increasing group size

Although living in groups confers several benefits to group members, change in group size can act as a potent stressor. Increase in group size, on one hand, can elevate the cost of group living, including higher resource competition, but on the other may also increase group-living benefits (e.g., better protection against predators and improved chances of winning between-group competition). Our study demonstrates that all species, irrespective of social complexity, can adjust their social behavior in response to the changes in their social environment. This behavioral plasticity is expected to depend on perceived costs and benefits of group living and species sociality (Gogarten *et al.*, 2014; Hubbard & Blumstein, 2015; Maldonado-Chaparro, Hubbard & Blumstein, 2015). Our results show that

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individuals in *socially hierarchical* societies increase the number of social partners proportionate to the group size in order to maintain the overall group connectivity, probably due to higher perceived benefits of group living. *Solitary* and *fission-fusion* species, on the other hand, may perceive higher costs with larger groups and therefore reduce group connectivity with increasing group size. Interestingly, group connectivity of *social* species also reduces in larger groups, which suggests that many social species experience constraints on sociality (Maldonado-Chaparro, Hubbard & Blumstein, 2015).

The knowledge of how group connectivity scales with group size is critical to make valid predictions about pathogen transmission rates across different populations. In theory, density- and frequency-dependent models of infectious disease spread have been popularly based on two distinct assumptions about how transmission scales with the host group size (McCallum, Barlow & Hone, 2001). Frequency-dependent model of disease transmission assumes that the connectivity of hosts is constant across group sizes, and therefore *per capita* transmission rate declines with increasing host group size. In contrast, density-dependent transmission models assume linear scaling of group connectivity with group size and constant per capita transmission rate across host groups (Ferrari *et al.*, 2011). Density-dependent transmission is typically assumed as a valid model for social hosts (Anderson & May, 1978), although species specific empirical evidences have been conflicted (Vander Wal, Yip & Mclaughlin, 2012; Cross *et al.*, 2013). Our results demonstrate that the density-dependent transmission model may be valid for *socially hierarchical* irrespective of pathogen transmission mode, but not for other social or solitary species. We did not find evidence for frequency-dependent transmission, as individual in all the social systems did increase their social partners

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with increasing group size.

Conclusions

Despite the current challenges of comparing networks, our study revealed striking differences in the interaction networks of species categorized into four broad social systems - relatively solitary, fission-fusion, social and socially hierarchical. At the least, the social organization of these social systems differs in terms of (a) degree heterogeneity among social partners, (b) extent of network fragmentation and (c) the tendency of individuals to occupy central positions within the interaction network. Disease simulations show that, contrary to the expectation of higher disease costs of group living for social species, the organization of interaction networks can act as a first-line of defense for *social* and *fission-fusion* species. We also show that the individual's behavioral response to larger groups can be different depending on the social organization of the species, probably due to the perceived trade-off between benefits and costs of living in larger groups. These findings shed new light on the association between group living and disease transmission, and evolution of social strategies to alleviate the disease costs of group living. In conclusion, we note that there is an enormous potential of adopting a comparative approach to study the commonalities and differences in the interaction networks across a wide range of across taxonomic groups and social systems. Although we limit our discussion to the disease implications of animal sociality and social network structure, comparative network approaches can be used to quantitatively test several other evolutionary and ecological hypotheses, including the ones on group living, social complexity, information transfer, and resilience to population stressors.

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Materials and methods

Dataset

We first conducted electronic searches in *Google Scholar* and popular data repositories, including *Dryad Digital Repository* and *figshare* for relevant network dataset associated with peer-reviewed publications. We used the following terms to perform our search: social network, social structure, contact network, interaction network, network behavior, animal network, behavior heterogeneity and social organization. Only studies on non-human species were considered in our primary search. Studies reporting non-interaction networks (such as biological networks, food-web networks) were excluded. By reviewing the quality of published networks datasets, we selected 666 social networks spanning 47 animal species and 18 taxonomic order. Edge connections of these networks summarized several different types of interaction between animals, including dominance, grooming, physical contact, spatial proximity, food-sharing (trophallaxis), foraging, and interactions based on the asynchronous use of a shared resource. Fig. 1 summarizes the species, the number of networks and the reported interaction types contributed by each taxonomic order represented in the study.

Structure of interaction networks associated with the social systems

To examine the structure of networks associated with the four social systems, we used a Bayesian mixed-model approach using the *MCMCglmm* package in R (Hadfield, 2010), with four response sociality levels - *relatively solitary*, *fission-*

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fusion, *social* and *socially hierarchical*. As fixed effects within our model we included the following network measures (Table S1): degree heterogeneity, degree homophily, clustering coefficient, weighted clustering coefficient, transitivity, betweenness centrality, weighted betweenness centrality, average group size, network fragmentation, group cohesion, relative modularity and network diameter. Community structure, or the number and composition of groups within each animal interaction network was estimated using the Louvain method (Blondel *et al.*, 2008). We also included the number of nodes and edges in the network to provide a statistical control for any variability in the sampling effort, and average edge weight was included to control for different edge weighting criteria. All continuous fixed-effects were centered (by subtracting their averages) and scaled to unit variances (by dividing by their standard deviation) to assign each continuous predictor with the same prior importance in the analysis (Schielzeth, 2010).

Traditional random-effect models assume that each data-point is independent. However, in meta-analysis involving multiple taxonomic groups, it is necessary to control for non-independence arising from shared evolutionary histories of species. We therefore controlled for phylogenetic relationships in the analyses by including a correlation matrix derived from phylogeny as a random factor. The phylogenetic relationship of all species in the database was estimated from the NCBI taxonomy database using phyloT (http://phylot.biobyte.de). We also controlled for repeated measurements within groups and the type of interaction recorded by including *group* and *interaction type* as random effects in the analysis.

We avoid model selection and present the results of the full model, so that the fitted estimates are conditional on the values of all predictors and the estimated confidence interval are more robust (Harrell, 2002). A potential drawback

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of including all predictors in the model is the presence of multicollinearity between different network measures. We therefore estimated Variance inflation factor (VIF) for each covariate in the fitted model, and covariates with VIF greater than 3 were sequentially removed to obtain the final model formulation. We used a weakly informative Gelman prior for fixed effects and parameter-expanded priors for the random effects to improve mixing and decrease the autocorrelation among iterations (Gelman, 2006). Specifically, a χ^2 distribution with 1 degree of freedom was used as suggested by Hadfield (2014). We ran three MCMC chains for 15 million iterations, with a thinning interval of 1000 after burn-in of 50,000. Convergence of chains was assessed using the Gelman-Rubin diagnostic statistic (Gelman & Rubin, 1992) in the *coda* package (Plummer *et al.*, 2006).

Disease implications of network structure and the social systems

Disease simulations

We performed Monte-Carlo simulations of discrete-time susceptible-infected-recovered (SIR) model of disease spread through each network in our database. For disease simulations, we ignored the weights assigned to social interactions between individuals, because the impact of weight (whether they represent contact duration, frequency or intensity) is generally unclear and is usually context-dependent. Transmissiblity of the simulated pathogen was defined as the probability of infection transmission from an infected to susceptible host during the infectious period of the host. Assuming the individual's recovery and infection transmission to be a Poisson process, pathogen transmissiblity can be calculated as $T = \frac{\beta}{\beta+\gamma}$, where

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β and γ is the infection and recovery probability parameter, respectively. Each disease simulation was initiated by infecting a randomly chosen individual in the social group. At subsequent time steps every infected individual(s) in the population could either transmit infection to a susceptible neighbor with probability parameter β or recover with probability γ. The disease simulation were terminated when there were no remaining infected individuals in the network. We performed disease simulations of pathogens with a wide range of trasmissibility (0.001 to 0.5). Disease simulations for each value of pathogen transmissibility and social network were summarized using three measures: (a) Epidemic probability, measured as the proportion of simulations that ended up infecting at least 15% of individuals present in the interaction network, (b) outbreak size, or the average proportion of individuals infected and (c) outbreak duration, measured as the time interval between the beginning of an outbreak and the time the last infected individual in the interaction network recovers.

Statistical analysis

We used multivariate Bayesian-MCMC framework to establish disease costs of network measures and species sociality. Epidemic probabilities across different pathogen transmissibility were entered as the (multivariate) response variables. To evaluate the role of network structure on the probability of large outbreaks, network measures identified in the final model of the previous analysis were included as predictors. We repeated the analysis with species sociality as predictor to directly estimate the vulnerability of different social systems towards disease transmission. In both the models, number of nodes and number of edges were included as predictors to control for variability in sampling effort and edge weighting

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criteria. (Average edge weights were not included because disease simulations were performed over unweighted networks). Phylogenetic correlations, group identification and the interaction type were included as the random effects in the analysis. Similar models were used to estimate the implications of network structure and social system towards the size and duration of outbreaks by replacing epidemic probability with outbreak size and duration as (multivariate) response terms, respectively.

Behavioral plasticity of individuals in different social systems towards increasing group size

We first identified group size and composition within each interaction network in the database using the Louvain algorithm (Blondel *et al.*, 2008) that showed strong modular subdivisions (relative modularity, Q_{rel}>0.3). For each social group, the following four network measures that are related to disease transmission were estimated - average individual degree, average individual strength, average pairwise strength and group connectivity (Table S1). To assess how individuals of different social systems respond to increase in group size we used a linear mixed model implemented in the *lme4* package in R (version 3.2.3; R Development Core Team 2015). Four separate models were run, each with one of the four network measures as the response variable, and group size interacted with species sociality (relatively solitary, fission-fusion, social and socially hierarchical) as the fixed effect. The interaction network nested within species and type of interaction recorded was included as a random effect to control for repeated measurements within species and variation in data-collection methods.

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Data accessiblity

The data for all animal interaction network measures used in the study, and references where the actual network can be accessed, is available through the Bansal Lab Dataverse at (link).

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Table captions

Table 1. Effect size estimates of the generalized linear mixed models (by MCMCglmm) examining the characteristics of interaction network structure for different social systems. Shown are the posterior means of the expected change in log-odds of being in focal social system (column headers), as compared to the base social system (row headers), with one-unit increase in the network measure. The 95% confidence intervals are included in brackets. Significant terms with pMCMC $<$ 0.05 are indicated in bold, where pMCMC is the proportion of MCMC samples that cross zero.

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Figure captions

Figure 1. Phylogenetic distribution of non-human species represented in the interaction network dataset used in this study. Numbers next to the inner ring denote the total networks available for the particular species. The inner and the middle ring is color coded according to the taxonomic class and the social system of the species. The colors in the outer ring indicates the type of interaction represented in the network

Figure 2. A stylized illustration of the network measures used (in the final model) to characterize the differences in the interaction networks species categorized into four social-systems: *relatively solitary*, *fission-fusion*, *social* and *socially hierarchical*. (A) Degree heterogeneity, measured as the coefficient of variation (CV) of the degree distribution. Shown is the frequency distribution of nodal degrees for a network with homogeneous degree distribution (CV $\ll 1$), and a network with an exponential degree distribution (CV $= 1$). (B) Degree homophily (ρ), or the tendency of social partners to have a similar degree. Shown is an example of a disassortative network, where high degree individuals tend to associate with low degree individuals ($\rho < 0$), and assortative degree networks, where high degree individuals tend to form social bonds with each other ($\rho > 0$). (C) Average betweenness centrality, that measures the tendency of nodes to occupy central position within the interaction network. Shown is an example of a network with low average betweenness centrality and a network with high average betweenness centrality. Node colors represent the betweenness centrality values - nodes with darker colors occupy more central positions within the network. (D) Group cohe-

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sion measures the tendency of individuals to interact with members of own group. The network to the left has three low cohesive social groups, while the network to the right has highly cohesive social groups where most of the interactions occur within (rather than between) groups. (E) Network fragmentation, measured as the log-number of the social groups (modules) present within an interaction network. Shown is an example of low (left) and highly (right) fragmented network

Figure 3. Disease costs of social organization due to interaction network structure. Disease cost has been quantified in terms of outbreak size (proportion of individuals infected in the interaction network), outbreak duration (time to disease extinction) and epidemic probability (likelihood of large outbreaks infecting at least 15% of individuals in the network) for low (=0.1), moderate (=0.25) and highly (=0.5) transmissible pathogen. Error bars represent standard errors, and different letters above the bars denote a significant difference between the means ($P < 0.05$)

Figure 4. Role of network structures in influencing disease transmission. The three network measures shown are the ones that were found to differ between the four social systems (Table 1). Error bars represent 95% confidence intervals. Confidence intervals that do not include zero suggest significant association with disease transmission (red = significant effect, black = non-significant effect)

Figure 5. Change in individual social behavior and group connectivity with change in social group size across the four social systems. Group size and composition was determined using the community detection algorithm described in

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Blondel *et al.* (2008). Only those interaction networks that showed strong modular subdivisions ($Q_{rel} > 0.3$) were included in this analysis. Error bars represent 95% confidence intervals, and different letters above the points denote a significant difference between the means ($P < 0.05$). Confidence intervals that do not include zero suggest significant association with group size (red = significant effect, black = non-significant effect)

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Table 1:

Degree heterogeneity	Focal / Base	Solitary	Fission-fusion	Social	Socially hierarchical
	Solitary		**-4.15 [-7.97, -0.34]**	**-4.37 [-8.03, -1.22]**	**-4.47 [-8.74, -0.50]**
	Fission-fusion			-0.4 [-4.04, 3.38]	-0.81 [-4.54, 2.79]
	Social				-0.99 [-4.57, 2.63]
Degree homophily	**Focal / Base**	**Solitary**	**Fission-fusion**	**Social**	**Socially hierarchical**
	Solitary		-0.29 [-1.91, 1.32]	-0.54 [-1.90, 0.87]	-0.71 [-2.36, 0.96]
	Fission-fusion			-0.23 [-1.80, 1.39]	-0.44 [-2.06, 1.17]
	Social				-0.43 [-1.88, 1.02]
Betweenness centrality	**Focal / Base**	**Solitary**	**Fission-fusion**	**Social**	**Socially hierarchical**
	Solitary		-3.95 [-8.88, 0.59]	0.41 [-2.29, 3.32]	1.80 [-1.31, 4.87]
	Fission-fusion			2.87 [-0.84, 7.09]	**4.67 [0.87, 8.94]**
	Social				1.58 [-0.73, 4.04]
Group cohesion	**Focal / Base**	**Solitary**	**Fission-fusion**	**Social**	**Socially hierarchical**
	Solitary		-1.42 [-3.77, 0.79]	0.32 [-2.27, 1.64]	-0.79 [-3.15, 1.55]
	Fission-fusion			1.04 [-0.83, 2.90]	0.38 [-1.80, 2.48]
	Social				-0.21 [-2.08, 1.53]
Network fragmentation	**Focal / Base**	**Solitary**	**Fission-fusion**	**Social**	**Socially hierarchical**
	Solitary		**6.41 [2.86, 10.00]**	**2.62 [-0.13, 5.52]**	0.51 [-2.94, 3.78]
	Fission-fusion			**-2.96 [-5.69, -0.25]**	**-4.79[-7.82, -1.84]**
	Social				-1.50 [-3.95, 1.02]

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Figure 1: Phylogenetic distribution of non-human species represented in the interaction network dataset used in this study. Numbers next to the inner ring denote the total networks available for the particular species. The inner and the middle ring is color coded according to the taxonomic class and the social system of the species. The colors in the outer ring indicates the type of interaction represented in the network

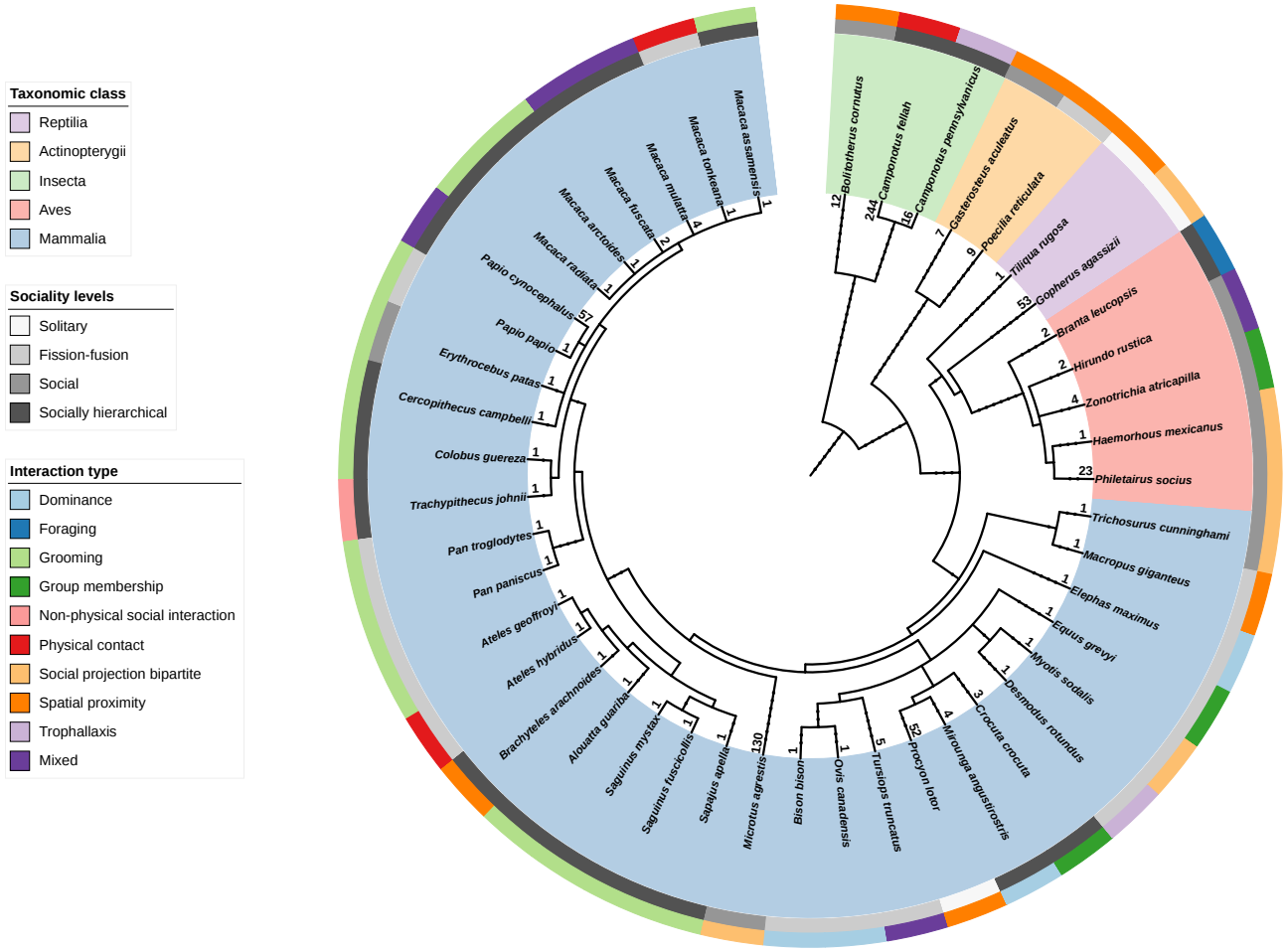

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Figure 2:

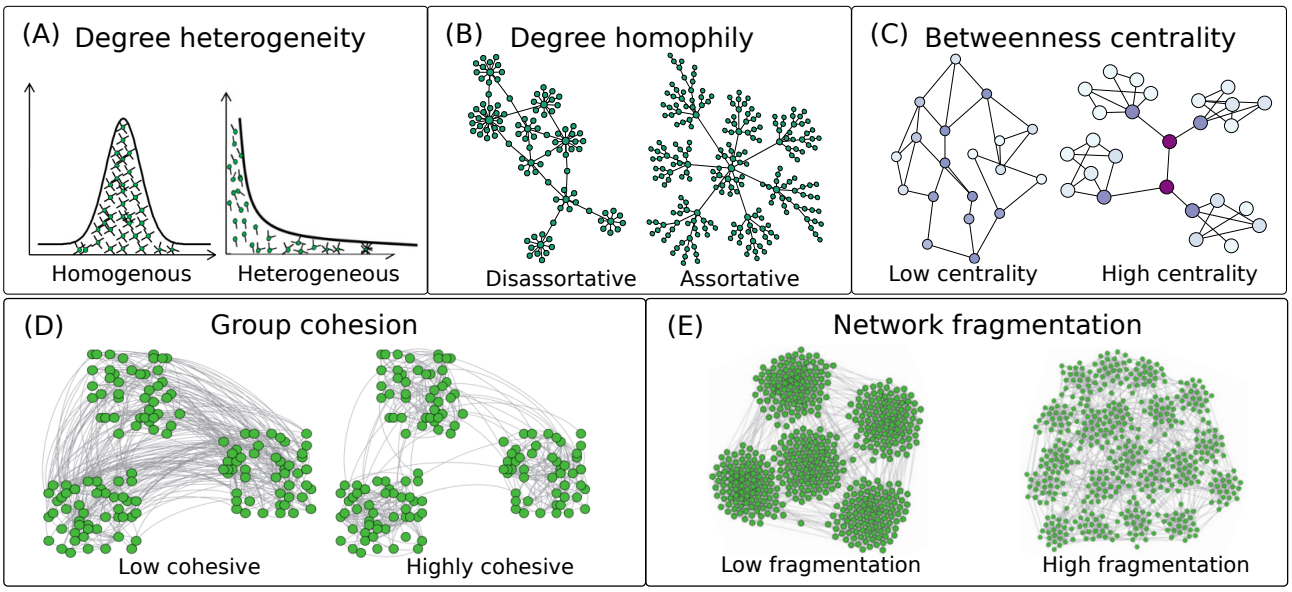

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Figure 3:

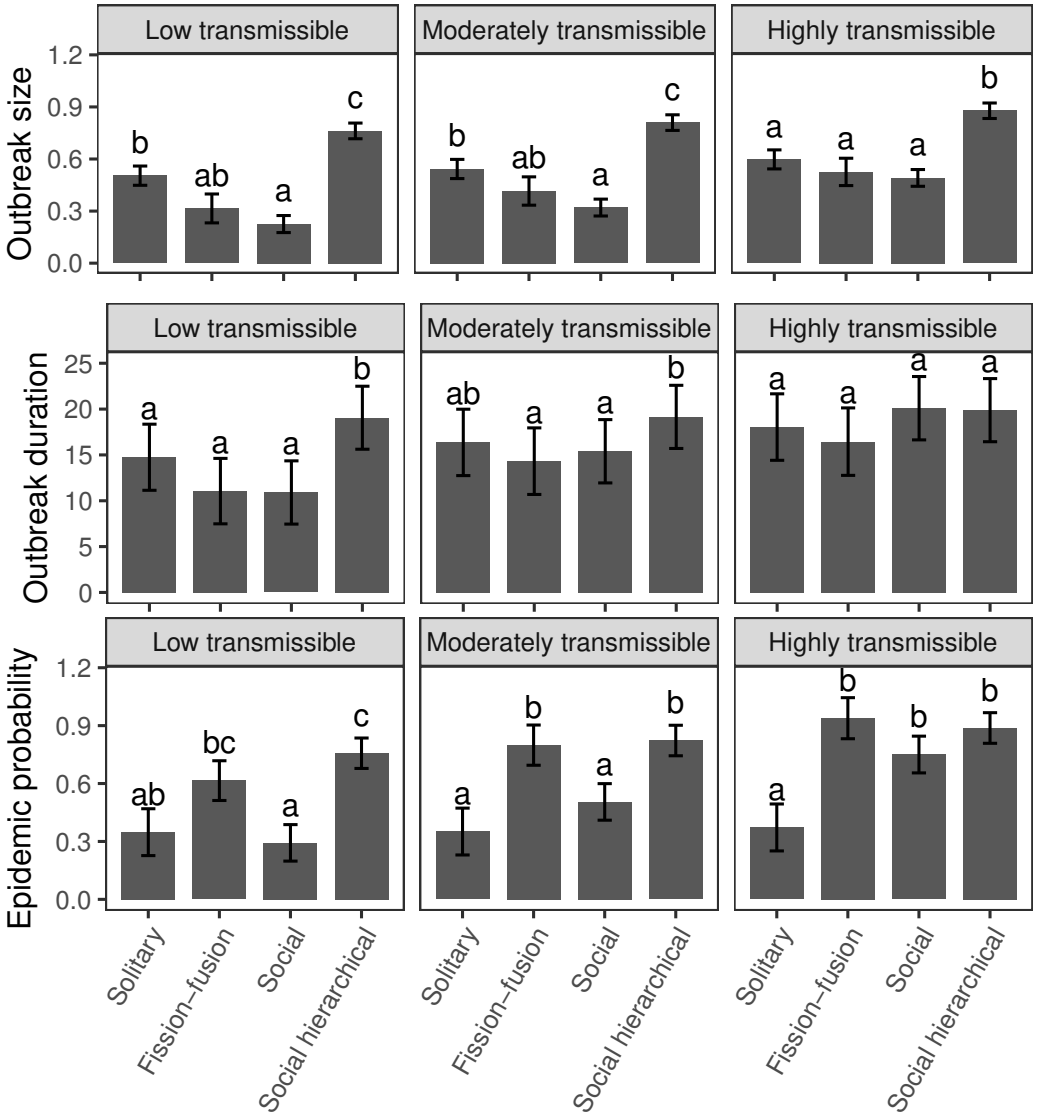

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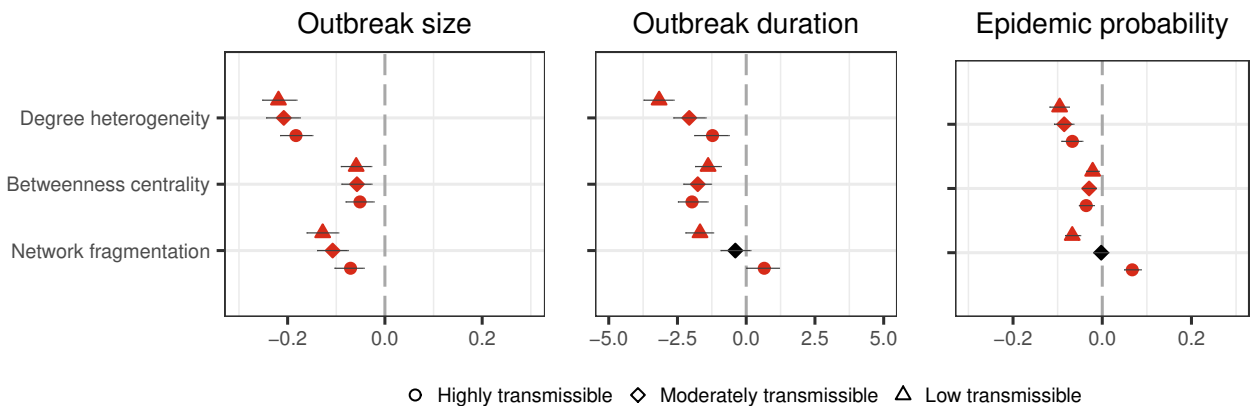
Figure 4:



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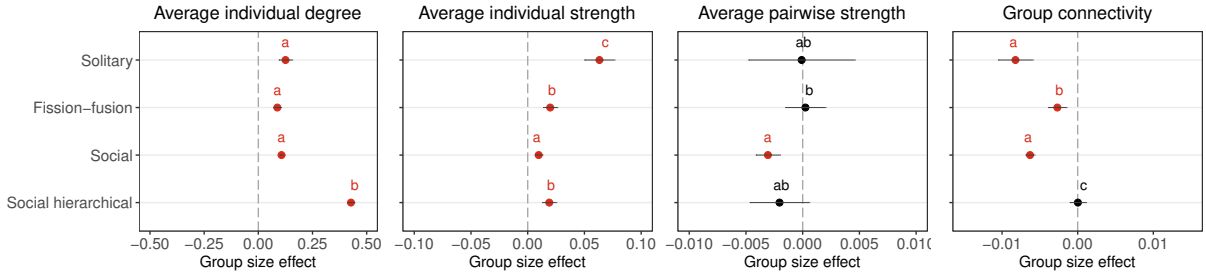
Figure 5: