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

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Summary

1. Previous studies examining the disease costs of sociality have largely focused on the link between group size and transmission. However, infectious disease spread is driven by the structure of infection-spreading interactions between individuals.

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2. We used statistical tools to review the organization of the interaction networks of 47 species, including mammals, birds, reptiles, fish and insects by categorizing each species into one of four social systems, *relatively solitary*, *fission-fusion*, *gregarious* and *socially hierarchical*. Additionally, using computational experiments of infection spread, we determined the disease costs of each social system.

3. Our analysis predicts consistent structural differences across social systems, regardless of species or interaction type. We find that solitary species have large variation in numbers of interactions, that socially hierarchical species are the least clustered in their interactions, and that fission-fusion species tend to be the most fragmented. However, these structural differences are primarily driven by low weighted edges, which suggests that different social systems have evolved unique strategies to organize weak ties.

4. Disease simulations show that the organization of interaction networks can mitigate the disease costs of group living for certain social systems under certain conditions. In particular, the low clustered and fragmented interactions networks of socially hierarchical species are expected to cause frequent outbreaks of lowly transmissible pathogens, but a reduced risk of epidemic outbreaks of fast spreading infections. In contrast, the network structure of fission-fusion and gregarious species predict frequent and prolonged epidemic outbreaks of highly transmissible pathogens.

5. By evaluating the implications of network organization across social systems, our finding offers new perspective on the debate about the disease costs of group living. Additionally, this study demonstrates the scope of meta-

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analytic methods in social network analysis, which in future could be used to test ecological and evolutionary hypotheses on cooperation, group-living, communication, and resilience to extrinsic pressures.

Keywords

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

Introduction

Host social behaviour plays an important role in the spread of infectious diseases. Socially complex species from honeybees to primates live in large groups and are considered to have elevated costs of pathogen transmission due to high contact rates (Loehle, 1995; Altizer *et al.*, 2003). Previous studies, therefore, have tested hypotheses on the disease costs of sociality by associating group size with infection transmission (Rifkin, Nunn & Garamszegi, 2012; Patterson & Ruckstuhl, 2013). Beyond a simple dependence on group size, however, recent work in the field of network epidemiology has shown that infectious disease spread largely depends on the organization of infection-spreading interactions between individuals (Godfrey *et al.*, 2009; White, Forester & Craft, 2015; Craft, 2015; VanderWaal & Ezenwa, 2016). Indeed, when interactions between individuals are assumed to be homogeneous, the expectation of higher disease costs of group-living has been mixed (Arnold & Anja, 1993; Rifkin, Nunn & Garamszegi, 2012; Patterson & Ruckstuhl, 2013).

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The advantage of social network analysis is that it integrates heterogeneity in interaction patterns at individual, local and population scales to model global level processes, including the spread of social behaviour and infectious diseases. A fundamental individual-level characteristic relevant to the spread of social or biological contagion in networks is the number of direct social partners, associates or contacts, capturing the interaction necessary for transmission. In recent years, network analysis tools have allowed for rapid advances in our understanding of how individual interaction rates are related to the risk of infection. For example, Otterstatter & Thomson (2007) demonstrated that the contact rate of a bumble bee is a significant predictor of *Crithidia bombi* infection risk from an infected nestmate. Leu, Kappeler & Bull (2010) showed that lizards that frequently visited neighbouring refuges had higher tick loads. While much attention has been focused on disease implications of individual sociality, the implications of species' social system (henceforth also referred to as *species sociality*), ranging from solitary to ones with stable and hierarchical group composition, remains unclear.

By quantifying group-level metrics that describe global structures in interaction patterns, the network approach provides a unique opportunity to examine the disease costs of species sociality. The role of higher-order network structures such as degree heterogeneity, network fragmentation, modularity and global clustering coefficient on infectious disease spread is complex, but is relatively well understood (Keeling, 2005; Meyers *et al.*, 2005; Sah *et al.*, 2017). For example, as degree heterogeneity in a network increases, the epidemic threshold (i.e., the minimum pathogen transmissibility that can cause large outbreaks) approaches zero. However, outbreaks are less likely to reach epidemic proportions in highly degree heterogeneous network than in the other networks (Meyers *et al.*, 2005).

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Network clustering and modularity measures the tendency of nodes to form cliques and subgroups, respectively (Fig. 1). Although the dynamics of infectious disease spread remain largely unaffected in networks with moderate levels of clustering and modularity, extreme levels of these metrics in networks reduce outbreak size and prolong epidemic outbreaks (Keeling, 2005; Sah *et al.*, 2017).

Recent mathematical models predict that the network structure of socially complex species can serve as a primary defence mechanism against infectious disease by lowering the risk of disease invasion and spread, without requiring an additional increase in physiological immunocompetence or behavioural avoidance (Hock & Fefferman, 2012). It remains unproven, however, whether the structure of interaction networks naturally observed in less-complex social systems mediates infectious disease risk and transmission. A systematic examination of the disease costs associated with species sociality requires a comparative approach that isolates unique structural characteristics of interaction patterns, while controlling for population size, data collection methodology and type of interaction recorded. However, comparing networks across different taxonomic groups has proven to be a difficult task, with only a few cross-species network comparisons (Faust & Skvoretz, 2002; Faust, 2006).

In this study, we conduct a quantitative analysis across 47 species based on 666 interaction networks to investigate the relationship between network complexity and the disease costs for different species sociality. This is achieved in three steps. First, we use phylogenetically-controlled Bayesian MCMC models to identify network structures which are predictive of species sociality. Second, we perform computational model-based disease experiments to determine the role of various global network metrics in curbing the invasion of a novel pathogen and

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limiting the spread of infectious diseases. Finally, we identify the relative costs of disease transmission for each social system as mediated by their network structure. We hypothesized that social species organize their network structure to mitigate pathogen transmission associated with group living. However, we expected the presence of alternate disease defence mechanisms in socially complex species to also play an important role: social insects, for example, could rely on social immunity as a primary strategy to minimize disease transmission risk, allowing these species to organize their interactions to maximize information transfer.

Our analysis, by broadening the scope of network analysis from species-specific analysis to meta-analytic approach, offers new perspective on how social structure strategies mediate the disease costs of group living. A better understanding of the association between network structure and different social systems, in the future, can facilitate investigations on other evolutionary and ecological hypotheses, including the ones on group living, social complexity, communication, population robustness and resilience to extrinsic population stressors.

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 datasets associated with peer-reviewed publications. We used the following terms to perform our search: "social network", "social structure", "contact network", "interaction network", "network behaviour", "animal network", "behaviour heterogeneity"

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and "social organization". Only studies on non-human species were considered in our primary search. Network studies not reporting interactions (such as biological networks, food-web networks) were excluded. By reviewing the quality (i.e., whether enough information was provided to accurately reconstruct networks) of published networks datasets, we selected 666 social networks spanning 47 animal species and 18 taxonomic orders. Edge connections in these networks represented several types of interactions between individuals, including dominance, grooming, physical contact, spatial proximity, direct food-sharing (i.e. trophallaxis), foraging, and interactions based on the asynchronous use of a shared resource. Fig. 2 summarizes the species, the number of networks and the reported interaction types contributed by each taxonomic order represented in the study.

Classifying species sociality

Developing a definition of sociality that encompasses the spectrum of social systems across diverse taxonomic groups is challenging. Consequently, we followed Slater & Halliday (1994) to classify species into four broad categories of sociality based on the degree of association between adults during activities such as foraging, travelling, sleeping/resting and rearing offspring. *Relatively solitary* species were defined by infrequent aggregation or association between adults outside of the breeding period. Examples of *relatively solitary* species in the database include the desert tortoise (*Gopherus agassizii*), wild raccoons (*Procyon lotor*), and the Australian sleepy lizard (*Tiliqua rugosa*). Recent studies suggest that the social structure of a species traditionally considered as solitary can be complex (Sah *et al.*, 2016; Prange *et al.*, 2011). We therefore categorized the three species as *rel-*

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atively solitary and not solitary. Species that aggregate for one or more activities, but have unstable group composition and do not have a hierarchical social organization were classified as *fission-fusion*. Examples of fission-fusion species in our database include bottlenose dolphins (*Tursiops truncatus*), bison (*Bison bison*), Indiana bats (*Myotis sodalis*), Asian elephants (*Elephas maximus*), and guppies (*Poecilia reticulata*). Species characterized by a permanent or temporary social hierarchy where individuals form stable associations were classified as *socially hierarchical*. Examples of socially hierarchical species include carpenter ants (*Camponotus fellah*), yellow baboons (*Papio cynocephalus*), elephant seals (*Mirounga angustirostris*) and spotted hyenas (*Crocuta crocuta*). Finally, all species that demonstrated behavior of colonial breeding, communal roosting or aggregating behavior during foraging that were not classified as *socially hierarchical* or *fission-fussion* were categorized as *gregarious*. Examples of gregarious species represented in our database include field voles (*Microtus agrestis*), sociable weavers (*Philetairus socius*) and golden-crowned sparrows (*Zonotrichia atricapilla*).

Identifying unique network structures of species sociality

To examine the structure of interaction networks associated with our four classified social systems, we used a Bayesian mixed-model approach using the *MCMCglmm* package in R (Hadfield, 2010), with species sociality as the 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, global clustering coefficient, weighted clustering coefficient, transitivity, average betweenness centrality, weighted betweenness centrality, average group

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size, network fragmentation, group cohesion, relative modularity and network diameter. Network fragmentation (i.e., the number of groups within the largest connected component of the interaction network) and Newman modularity was estimated using the Louvain method (Blondel *et al.*, 2008). Relative modularity was then calculated by normalizing Newman modularity with the maximum modularity that can be realized in the given interaction network (Sah *et al.*, 2014, 2017). We included the number of nodes and edges in the network to provide a statistical control for dependence of global network metrics on network size and density, and average edge weight was included to control for data sampling design. To control for phylogenetic relationships between species, a correlation matrix derived from a phylogeny was included as a random factor. The phylogenetic relationship between species was estimated based on NCBI taxonomy using phyloT (http://phylot.biobyte.de). We also controlled for repeated measurements within groups, animal species, the type of interaction recorded, and edge weighting criteria by including *group*, *taxa*, *interaction type* and *edge weight type* as random effects in the analysis. The random effect of *interaction type* consisted of 10 levels, including: dominance, foraging, grooming, group membership, non-physical social, physical contact, non coincident resource use, spatial proximity, trophallaxis, and mixed interactions (Fig. 2). The *edge weight type* random effect was categorized into 6 levels: frequency, duration, half weight index, simple ratio index, twice weight index, and unweighted.

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). Since network measures can be highly correlated to each other, variance

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inflation factor (VIF) was estimated for each covariate in the fitted model, and covariates with VIF greater than 5 were removed to avoid multicollinearity. 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).

Groups of certain species in our database were represented with multiple networks, each summarizing a set of interactions occurring in a discrete time period. To ensure that such animal groups were not over-represented in the original analysis, we performed a cross-validation of our analysis by random sub-sampling. Specifically, we repeated the analysis 100 times with a random subset of the data composed of (randomly selected) single networks of each unique animal group in our database. An average of coefficient estimates across the multiple subsamples was then calculated and compared to the coefficient estimate of the full dataset.

Evaluating the role of weak ties in driving structural differences in species sociality

The analysis described in the previous section assumes equal importance of all edges recorded in an interaction network. To examine the role of weak ties in driving the structural differences between the four social systems, we removed edges with weights lower that a specified threshold. Three thresholds were examined in detail: 5%, 10% and 20% of highest edge weight. In particular, all edges

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with weights below the specified cut-off point were removed to obtain filtered interaction networks. Next, the phylogenetically controlled Bayesian mixed model analysis was performed to determine the structural difference between the filtered interaction networks of the four social systems. We ran three separate models, each with one of the three specified cutoff points.

Disease implications of structure and species sociality

We consider the disease costs of species sociality with synthetic experiments based on a computational disease model, and follow up with statistical analyis of the results.

Disease simulations

We performed Monte-Carlo simulations of the discrete-time susceptible-infected-recovered (SIR) model of infection 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) on infection transmission 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 infection transmission to be a Poisson process and a constant recovery probability, the pathogen transmissiblity can be calculated as $T = \frac{\beta}{\beta+\gamma}$, where 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

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every infected individual(s) in the population could either transmit infection to a susceptible neighbour 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 simulations of pathogens with a wide range of trasmissibility values (0.025 to 0.5). Disease simulations for each value of pathogen transmissibility and social network were summarized using three measures: (a) epidemic probability, the likelihood of an infectious disease invasion turning into a large epidemic (i.e., outbreaks that infect at least 15% of the individuals in the population), (b) epidemic size, the number of individuals infected in the population, and (c) epidemic duration, the duration of infectious disease spread.

Evaluating disease outcomes of structure and sociality

Three separate multivariate Bayesian-MCMC models, one corresponding to each outbreak measure (epidemic probability, epidemic size and epidemic probability), were fit to establish disease costs of network measures associated with species sociality. Outbreak measures across different pathogen transmissibility were entered as multivariate response variables. To evaluate the role of network structure on the probability of large outbreaks, network measures investigated in the final model of the previous analysis were included as predictors (Table1). 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, the effective number of nodes (i.e., the number of individuals with degree greater than zero), network density and the size of the largest connected component of the network were also included as predictors. (Average edge weights were not in-

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cluded because disease simulations were performed over unweighted networks). As before, phylogenetic correlations, group identification, animal species, interaction type and edge weight type were included as random effects in the analysis. To make posthoc comparisons within the models, we performed pairwise comparisons between the four social systems with a Tukey adjustment of p values, using the *lsmeans* R package (Lenth, 2016).

Results

Unique network structures of species sociality

The final model (after removing collinear predictors) consisted of seven global network measures - degree heterogeneity, degree homophily, global betweenness centrality, global clustering coefficient, group cohesion, network fragmentation and network diameter (Fig. 1, Table 1). Of the four social systems (relatively solitary, fission-fusion, gregarious and socially hierarchical), the interaction networks of solitary species demonstrated high degree heterogeneity, or large variation in the number of individual social partners (Table 1). On the contrary, variation in individual degree was much lower in socially hierarchical species as compared to other social systems. In addition, socially hierarchical species experience a local social environment that is not as well inter-connected; this is evident by the low global clustering coefficient of their interaction networks as compared to other social systems. In terms of network fragmentation (which was calculated on the largest connected component of a network), the interaction networks of fission-fusion species were the most subdivided into socially cohesive groups. The

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interaction networks of solitary species were less fragemented, or had fewer socially cohesive groups as compared to gregarious species (Table1). No statistically significant differences were observed between the social systems with respect to degree homophily, betweenness centrality, group cohesion and network diameter. Table S2 reports the average coefficient estimates of all seven global network metrics from the cross-validation analysis; all estimates were within the 95% confidence interval of the effect sizes reported in the full model (Table 1).

Role of weak ties in driving structural differences in species sociality

When the weakest 5% edges were removed from all weighted networks, the structural differences between the four social systems were observed mainly in two network metrics - degree heterogeneity and network fragmentation. Similar to the unfiltered networks (Table 1), the 5% filtered interaction networks of solitary species had the highest variation in individual degree as compared to other social systems; and 5% filtered networks of fission-fusion species were more fragmented compared to solitary and socially hierarchical species (Table S3). When the weakest 10% and 20% edges were removed, the global network measures across all social systems were similar to each other, except for one important difference. Both 10% and 20% filtered networks of social species (fission-fusion, gregarious and socially hierarchical) demonstrated a statistically significant higher global betweenness centrality, or higher global connectivity than solitary species (Table S4, S5). This difference was not observed in unfiltered or 5% filtered networks.

The reason behind why filtering out 10% and 20% weak edges removed most structural differences lies in the organization of weak edges within the four social systems. In solitary species, the weakest edges are disproportionately distributed

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between individuals in a network. Removal of lowest 5% edges therefore increased the degree heterogeneity and reduced the local and global connectivity in these species as compared to the unfiltered networks (Fig. S1).

In contrast to solitary species, large structural changes were observed in other social systems (fission-fusion, gregarious, socially hierarchical) only when 10% and 20% of the weakest edges were removed from their interaction networks (Fig. S1). In particular, the degree heterogeneity of 10% and 20% filtered networks were comparable across all social systems. The decrease in global betweenness centrality in social species, however, was minor as compared to solitary species. Consequently, the global connectivity of social species in 10%-20% filtered networks was significantly higher than solitary species.

Disease costs of interaction structure and species sociality

Our previous analysis revealed important differences in the structure of interaction networks in relatively solitary, fission-fusion, gregarious and socially hierarchical species. Do these topological differences then mediate differential disease costs of sociality among the four social systems? To answer this question, we first examined how degree heterogeneity, clustering coefficient and network fragmentation influence outbreak risk and transmission of low, moderate and highly transmissible pathogens (Fig. 3; see Fig. S2 in Supporting Information for the results on an extended range of pathogen transmissibility values). High variation in individual sociality (i.e., high degree heterogeneity) in interaction networks was predictive of a reduced risk of frequent epidemic outbreaks; outbreaks that did reach epidemic proportion were shorter and infected a lower proportion of the population

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(Fig. 3). The presence of cliques in interaction networks (high global clustering coefficient), and the subdivision of networks into socially cohesive groups (high fragmentation) was associated with a reduced risk of lowly transmissible infections becoming large epidemics. Conversely, highly contagious pathogens caused frequent epidemic outbreaks in networks with higher global clustering coefficient and network fragmentation. In terms of disease transmission, network clustering and fragmentation was associated with smaller but prolonged epidemic outbreaks, but the effect was more prominent at low pathogen transmissibility (Fig. S2).

Consequently, the risk of epidemic outbreaks due to low transmissible pathogen was higher in socially hierarchical species than fission-fusion and gregarious social systems. This effect reversed for highly transmissible infections: socially hierarchical species experienced significantly fewer epidemic outbreaks from highly contagious pathogens as compared to other social (fission-fusion and gregarious) species. The reason behind this can be explained in terms of how network fragmentation and clustering influence epidemic risk. Interaction networks of socially hierarchical species are less clustered than the networks of gregarious and fission-fusion species, and are less subdivided than gregarious species (Table 1). For low transmissible pathogens, network fragmentation and clustering reduce the probability of large outbreaks, but for highly transmissible pathogen both network metrics are associated with higher epidemic probability (Fig. 3).

Low clustered networks of socially hierarchical species also experienced large epidemic outbreaks of moderately transmissible pathogens as compared to gregarious species (epidemic size; Fig. 4). No statistical difference was observed in terms of outbreak size of low and highly transmissible pathogens, probably due to high variation between networks within each social systems. However, moderately

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contagious infections persisted longer in gregarious species than in solitary species, and highly transmissible outbreaks died out quickly in solitary species than both fission-fusion and gregarious social systems (epidemic duration; Fig. 4). This is because interaction networks of fission-fusion and gregarious are highly subdivided as compared to solitary species (Fig. 1), and fragmentation of interaction networks prolongs disease spread (Fig. 3).

Discussion

Disease has long been proposed as a major cost to social living, though few studies have explicitly examined how the structure of social systems may affect vulnerability to disease transmission. It is also becoming increasingly clear that the impact of an infectious disease on a population depends on the structure of interaction networks, not just group size. This has critical implications for understanding evolutionary tradeoffs between social systems and disease dynamics. However, network comparisons are not straightforward, making it difficult to perform meta-analysis across taxonomic groups and sampling schemes (James, Croft & Krause, 2009; Castles *et al.*, 2014; Farine & Whitehead, 2015). By employing phylogenetically-controlled Bayesian mixed effects models, we demonstrate how comparative methods can be applied to social network analysis. This study, to our knowledge, is the first attempt to utilize an extensive database of animal social networks to understand the disease costs of species sociality mediated by the structure of their interaction networks.

Our analysis compared global structural features associated with interaction networks of species classified into four social systems: relatively solitary, fission-

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fusion, gregarious 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 *(i)* degree of variation among social partners (i.e. degree heterogeneity), *(ii)* local connectivity, as indicated by the presence of cliques within the interaction networks (i.e, global clustering coefficient), and *(iii)* the extent to which the interaction network is divided into cohesive social groups (i.e., fragmentation). Remarkably, these differences exist between social systems in spite of differences in network size, number of interactions recorded, data collection methodology, type of interaction recorded and the interaction weighting criterion. Other global network metrics analysed (degree assortativity, global betweenness centrality, group cohesion and network diameter) could be dependent on data collection methods, and therefore no difference was observed between the social systems after controlling for sampling designs (Fisher, Silk & Franks, 2017).

Social species are typically assumed to have a skewed degree distribution (for e.g. bottlenose dolphins Lusseau *et al.* (2003), wire-tailed manakins Ryder *et al.* (2008)), which implies that a small proportion of individuals have a large number of social partners. Our results, however, show that degree heterogeneity in relatively solitary species can be much higher than social species. Large variation in the number of social connections in solitary species may simply arise due to a high variation in spatial behavior as compared to social species (Pinter-Wollman, 2015; Sah *et al.*, 2016). Conversely, interaction networks of socially hierarchical species, such as ants and savanna baboons demonstrated the least variation in individual sociality, and the lowest global clustering coefficient. A homogeneous network structure as observed in these species allows for efficient and equitable

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information transfer to all individuals, while low global clustering coefficient increases network resilience and stability in dealing with crisis, including removal or death of individuals (Krause *et al.*, 2014).

Our results also show that the interaction networks of fission-fusion species are the most subdivided into cohesive social groups followed by gregarious species. The presence of many but small, socially cohesive groups within interaction networks of fission-fusion species can be explained based on the behavioural tendency to frequently switch affiliative partners; as a result, individuals form consistent social bonds with a small number of individuals (Rubenstein *et al.*, 2015). Many social species form groups based on sex or 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). Gregarious and fission-fusion species may therefore limit group size to maximize benefits of cooperation, making their interaction networks subdivided (Marcoux & Lusseau, 2013).

Previous studies have typically focused on group size as the key parameter impacting disease transmission and group living costs. While this might be an easy parameter to measure, it does not capture the complex spatio-temporal dynamics of most animal societies. Our analysis shows that the unique strategy of how interactions are organized across different social systems has important impact on disease transmission patterns. We find that socially complex species with temporary or permanent hierarchical social organization experience frequent epidemics of lowly contagious pathogens, and larger epidemic size of moderately transmissible infections, as compared to non-hierarchical gregarious species. This is because socially hierarchical species have low variation in the number of interactions and

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low local connectivity as compared to other social and solitary species.

Networks with high degree heterogeneity have a larger proportion of low degree individuals compared to homogeneous networks, and have a minority of high degree nodes. As the proportion of high degree individuals is rare, an infectious disease outbreak rapidly depletes these superspreaders and must infect low degree individuals in order to propagate through the entire network, where the risk of stochastic extinction is higher. It follows that typical disease outbreaks dissipate sooner in degree heterogeneous. 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 more persistent disease outbreaks (Meyers *et al.*, 2005; Kiss, Green & Kao, 2006). High global clustering coefficient in an interaction network creates redundant paths between individuals which makes it harder for infections to encounter new susceptible individuals and percolate throughout the network (Newman, 2003). In contrast to frequent and larger epidemics of low and moderately contagious infection, socially hierarchical species experience reduced disease burden from highly contagious pathogens than other social species. We postulate that the conflicting efficiency of interaction networks towards infection spread in socially hierarchical species reflects the trade-off between maximizing information flow and minimizing pathogen spread. Social insects, for instance, have sophisticated group-level defences (including sanitary behaviors, allogrooming and the use of antimicrobials) that may serve as primary defence mechanism against low to moderately spreading infections. The organization of interaction networks in these species, therefore, may have evolved to maximize information flow, while relying on social immunity to reduce the spread of low to moderately spreading infections.

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Challenges and opportunities

Sociality of animal species has been traditionally classified based on qualitative phenotypes and life history traits, and the classification typically differs between the taxonomic groups. While this categorization scheme is convenient, it does not capture the true continuum of social behavior. As a step forward, recent studies have proposed quantitative indices of sociality (Silk, Altmann & Alberts, 2006; Aviles & Harwood, 2012). Our study provides insights towards the potential use of network structure as a means of quantitatively defining social complexity across taxonomic boundaries. However, we need to overcome several challenges before robust comparative analysis can be performed on interaction networks to address such issues. First, comparing network structure across taxonomic groups where data is aggregated over different spatio-temporal scales is challenging. Aggregating interactions over small time-periods may omit important transient interactions, whereas aggregating data over long time-periods may lead to a saturated network where distinguishing social organization may be difficult. In addition, spatial constraints and environmental heterogeneity can impose a considerable influence on the interaction network structure (Davis *et al.*, 2015; Leu *et al.*, 2016). Future comparative studies should therefore consider standardizing data over time and spatial scales. The second challenge lies in defining a social group that is consistent across species and social systems. This is difficult because the general rules of defining groups in social species (including definitions of spatial and temporal coherence) do not hold true for solitary and fission-fusion species. Network size correlates to sampling intensity in many cases, and is therefore a poor proxy to group size. In this study, we use community detection algorithm that utilizes the organization

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of network structure to infer the number and composition of social groups (modules) within the interaction network. The third challenge for comparative studies of networks lies in utilizing data-sources published in inconsistent formats. At minimum the network datasets should be accompanied with the following details to facilitate data-reuse: location of the data collection, type of population monitored (captive, semi-captive, free-ranging), edge definition, edge weighting criteria, node attributes (such as demography), temporal resolution of data, temporal and spatial aggregation of the data, proportion of animals sampled in the area, and population density.

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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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 Bayesian generalized linear mixed models (by MCMCglmm) examining the characteristics of interaction network structure among the four social systems: *relatively solitary*, *fission-fusion*, *social* and *socially hierarchical*. 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. A stylized illustration of the global network measures used (in the final model) to identify the structural differences in the interaction networks among different social systems. (A) Degree heterogeneity, measured as the coefficient of variation (CV) of the frequency distribution of the number of social partners (known as the *degree distribution*). Shown is the degree distribution of a homogenous network (CV $\ll 1$), and an exponential degree distribution of a network with large variation in individual degrees (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) Global 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 global betweenness centrality and a network with high global betweenness centrality. Node colors represent the betweenness centrality values - nodes with darker colors occupy more central positions within the network. (D) Group cohesion 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 the largest connected component of an interaction network. Shown is an example of low (left) and highly (right) fragmented network. (F) The global clustering coefficient measures the ratio of

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(closed) triplets in versus the total number of all possible triplets in the networks. (G) Network diameter is the longest of all shortest paths between pairs of nodes in a network. Shown is an example of a network with low network diameter (longest of shortest paths = 3) and a similar network with network diameter of 5, indicated by coloured edges.

Figure 2. Phylogenetic distribution of animal 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. The tree was constructed in the Interactive Tree Of Life (http://itol.embl.de/) from the NCBI taxonomy database (http://www.ncbi.nlm.nih.gov/Taxonomy/).

Figure 3. Role of network structures in influencing disease transmission summarized as epidemic probability (likelihood of large outbreaks infecting at least 15% of individuals in the network), average outbreak size (proportion of individuals infected in the interaction network), average outbreak duration (time to disease extinction) for low (=0.05), moderate (=0.15) and highly (=0.45) transmissible pathogen. The three global network measures shown are the ones that were found to differ among the four social systems (Table 1). DH, degree heterogeneity; CC, average clustering coefficient; NF, network fragmentation. Error bars represent 95% confidence intervals. Confidence intervals that do not include zero suggest significant association with disease transmission (red = significant effect, black =

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non-significant effect)

Figure 4. Disease costs of social systems due to interaction network structure. Disease cost has been quantified in terms of epidemic probability, average epidemic size and average epidemic duration for low (=0.05), moderate (=0.15) and highly (=0.45) transmissible pathogen. Error bars represent standard errors, and different letters above the bars denote a significant difference between the means ($P < 0.05$)

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Table 1:

Degree heterogeneity	Focal / Base	Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Solitary		**-6.45 [-11.79, -1.32]**	**-6.36 [-11.58, -1.52]**	**-12.76 [-19.48, -5.79]**
	Fission-fusion			-0.50 [-5.17, 4.11]	**-6.27 [-11.76, -0.80]**
	Gregarious				**-6.23 [-11.94, -0.69]**
Degree homophily	**Focal / Base**	**Solitary**	**Fission-fusion**	**Gregarious**	**Socially hierarchical**
	Solitary		0.37 [-1.48, 2.19]	-0.344 [-1.93, 1.15]	-1.82 [-4.21, 0.49]
	Fission-fusion			-0.74 [-2.56, 1.22]	-1.93 [-4.37, 0.38]
	Gregarious				-1.34 [-3.37, 0.76]
Global betweenness centrality	**Focal / Base**	**Solitary**	**Fission-fusion**	**Gregarious**	**Socially hierarchical**
	Solitary		-3.38 [-8.87, 1.97]	1.27 [-2.24, 4.91]	1.37 [-2.67, 5.48]
	Fission-fusion			3.12 [-1.56, 7.88]	3.39 [-1.32, 8.12]
	Gregarious				1.12 [-1.83, 4.63]
Global clustering coefficient	**Focal / Base**	**Solitary**	**Fission-fusion**	**Gregarious**	**Socially hierarchical**
	Solitary		-0.57 [-3.68, 2.20]	-0.08 [-2.81, 2.61]	**-4.21 [-8.10, -0.76]**
	Fission-fusion			0.02 [-2.55, 2.65]	**-3.23[-6.98, -0.25]**
	Gregarious				**-3.39 [-6.30, -0.54]**
Group cohesion	**Focal / Base**	**Solitary**	**Fission-fusion**	**Gregarious**	**Socially hierarchical**
	Solitary		-0.82 [-3.89, 2.44]	-0.58 [-3.22, 1.79]	-1.25 [-4.46, 1.82]
	Fission-fusion			0.48 [-1.75, 2.72]	0.04 [-2.77, 2.83]
	Gregarious				-0.06 [-2.46, 2.30]
Network fragmentation	**Focal / Base**	**Solitary**	**Fission-fusion**	**Gregarious**	**Socially hierarchical**
	Solitary		**8.12 [3.67, 12.73]**	**3.43 [0.22, 6.79]**	0.28 [-3.74, 4.44]
	Fission-fusion			**-3.38 [-6.50, -0.26]**	**-6.19[-9.94, -2.51]**
	Gregarious				-2.40 [-5.71, 0.81]
Network diameter	**Focal / Base**	**Solitary**	**Fission-fusion**	**Gregarious**	**Socially hierarchical**
	Solitary		-3.85 [-9.08, 1.31]	-1.34 [-4.73, 1.89]	0.73 [-4.22, 5.91]
	Fission-fusion			1.95 [-1.72, 5.95]	4.06[-0.58, 8.87]
	Gregarious				0.99 [-2.69, 4.57]

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Figure 1:

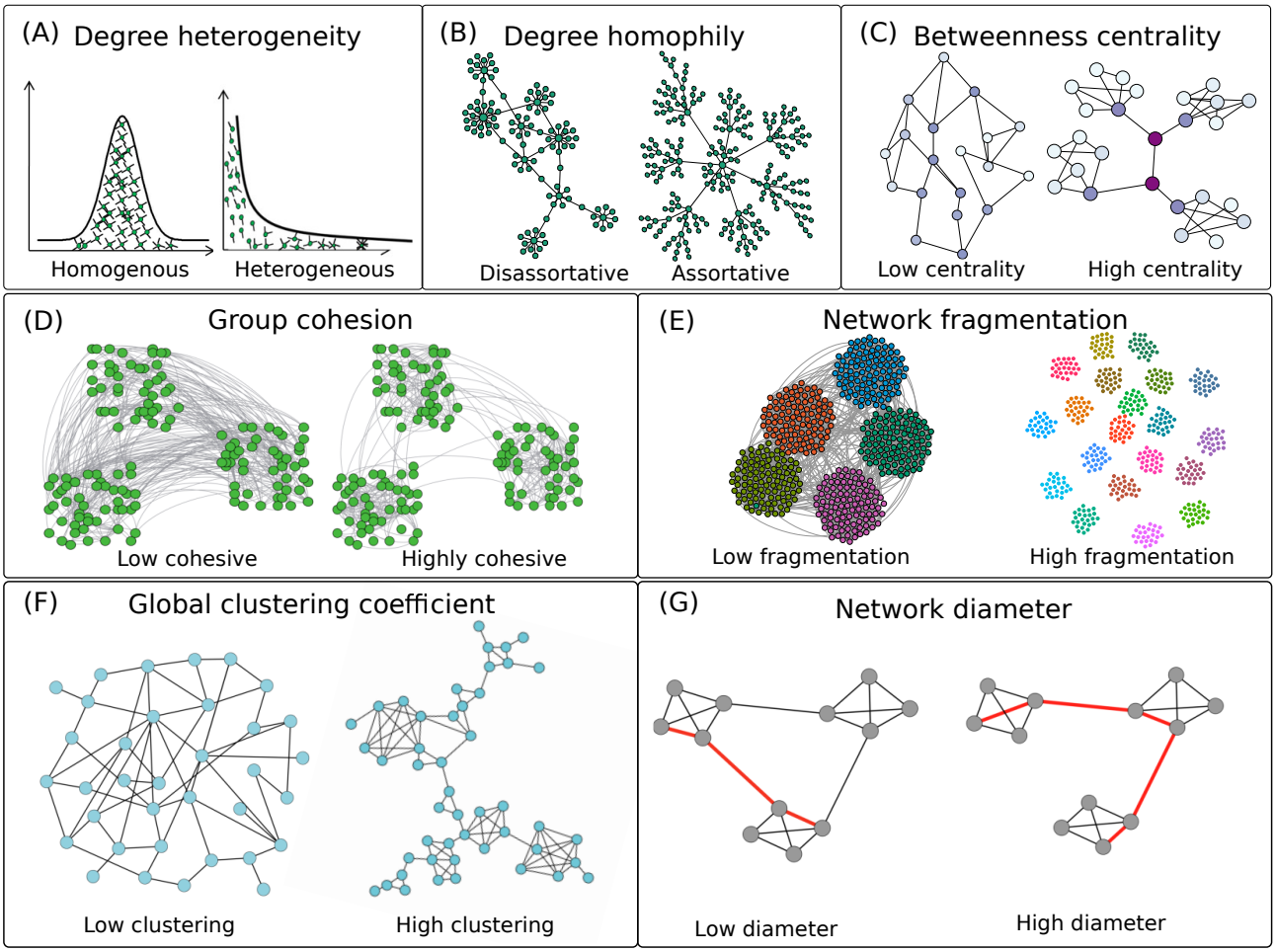

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Figure 2:

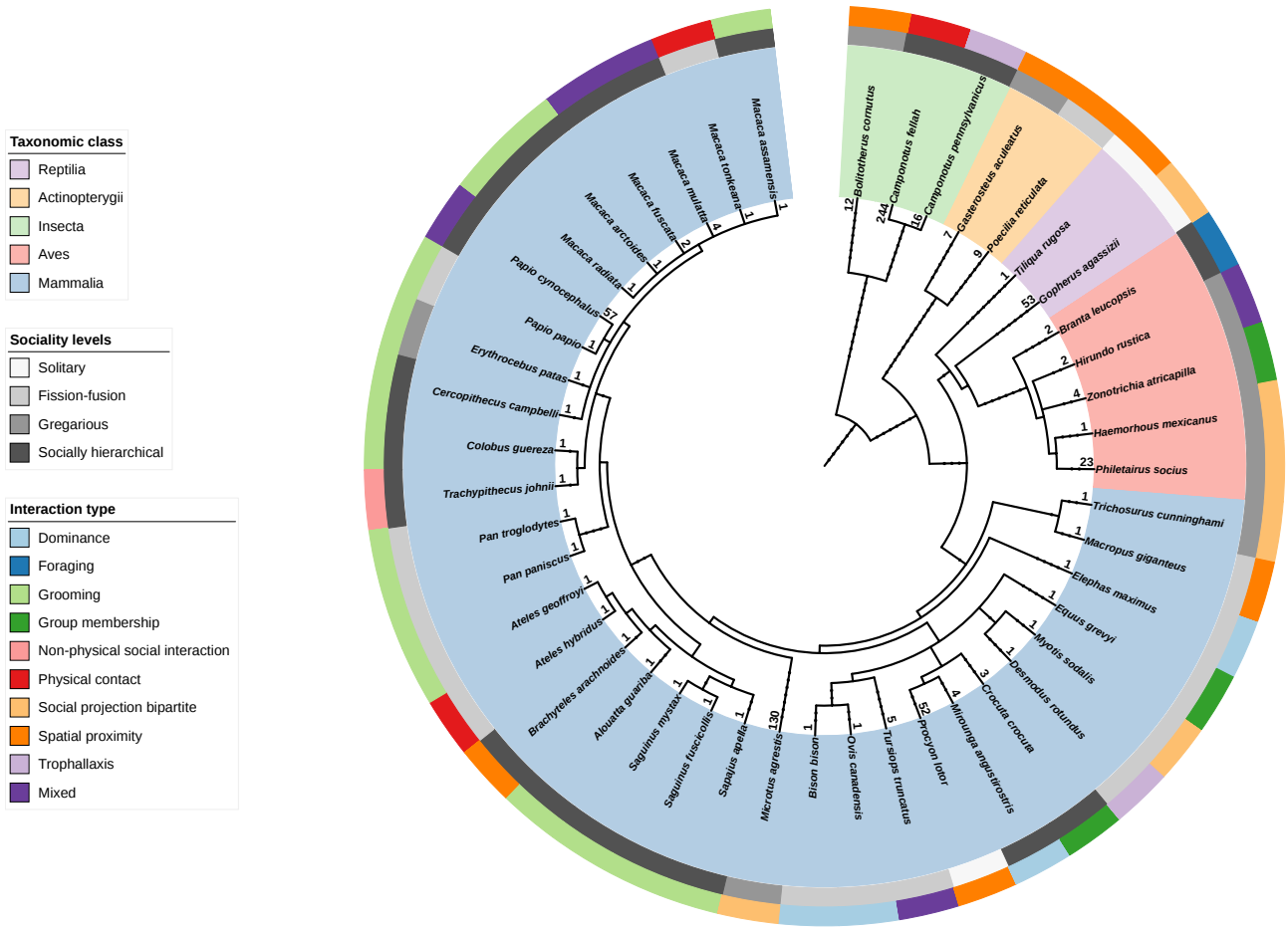

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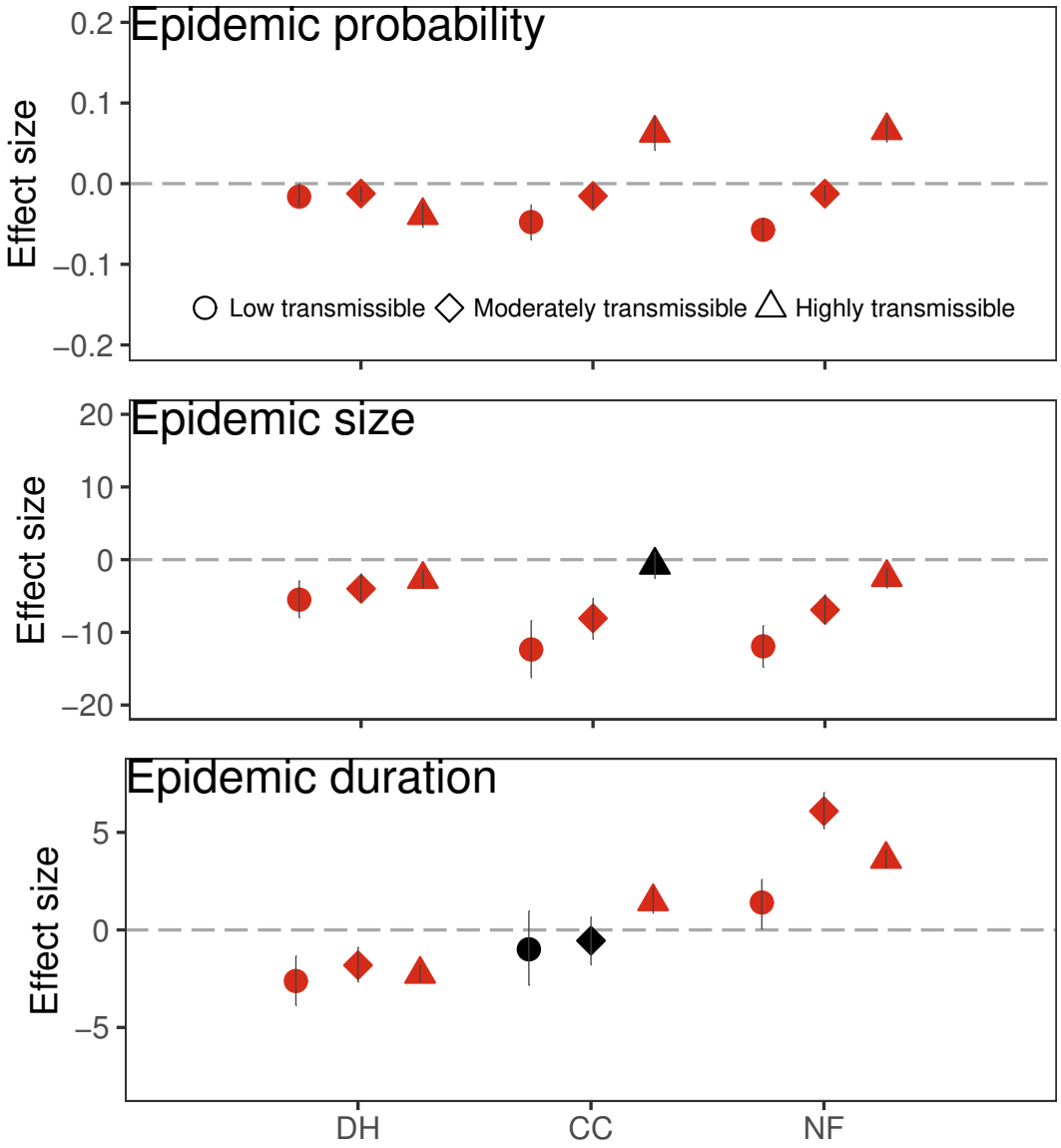
Figure 3:



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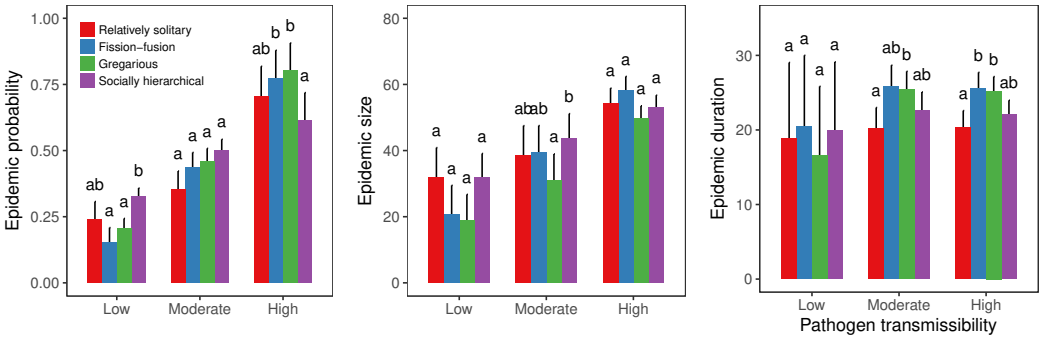
Figure 4: