PROCEEDINGS OF
THE ROYAL SOCIETY B
BIOLOGICAL SCIENCES

Indirectly connected: simple social differences can explain the causes and apparent consequences of complex social network positions

Journal:	*Proceedings B*
Manuscript ID	RSPB-2017-1939.R1
Article Type:	Research
Date Submitted by the Author:	18-Oct-2017

Complete List of Authors:	Firth, Josh; University of Oxford, Department of Zoology Sheldon, Ben; University of Oxford, Deaprtment of Zoology; Brent, Lauren; Roehampton University, Centre for Research in Evolutionary Anthropology

Subject:	Behaviour < BIOLOGY, Ecology < BIOLOGY, Evolution < BIOLOGY
Keywords:	Sociality, Network Structure, Complex Behaviour, Individual Variation, Social Cognition, Simulation Models
Proceedings B category:	Behaviour

Indirectly connected: simple social differences can explain the causes and apparent consequences of complex social network positions

Josh A. Firth[1], Ben C. Sheldon[1] and Lauren J. N. Brent[2]

[1]Edward Grey Institute, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK
[2]Centre for Research in Animal Behaviour, School of Psychology, University of Exeter, Exeter, UK

Correspondence: joshua.firth@zoo.ox.ac.uk; l.j.n.brent@exeter.ac.uk

ABSTRACT

Animal societies are often structurally complex. How individuals are positioned within the wider social network (i.e. their indirect social connections) has been shown to be repeatable, heritable, and related to key life history variables. Yet, there remains a general lack of understanding surrounding how complex network positions arise, whether they indicate active multifaceted social decisions by individuals, and how natural selection could act on this variation. We use simulations to assess how variation in simple social association rules between individuals can determine their positions within emerging social networks. Our results show that metrics of individuals' indirect connections can be more strongly related to underlying simple social differences than metrics of their dyadic connections. External influences causing network noise (typical of animal social networks) generally inflated these differences. The findings demonstrate that relationships between complex network positions and other behaviours or fitness components do not provide sufficient evidence for the presence, or importance, of complex social behaviours, even if direct network metrics provide less explanatory power than indirect ones. Interestingly however, a plausible and straightforward heritable basis for complex network positions can arise from simple social differences, which in turn creates potential for selection to act on indirect connections.

INTRODUCTION

Societies across the animal kingdom, ranging from humans to insects, are often characterized by complex organisation [1, 2]. It is the social behaviour of individuals within the population that gives rise to the intricate structure of social systems [3-5]. Indeed, within such systems, individuals differ in the manners in which they interact with others and in the strength and extent of social relationships [6-9]. Much of the study of animal social behaviour aims to understand these differences between individuals, including the selective pressures that have shaped and maintained them, their implications for our understanding of divergent social strategies, and their physiological and genetic underpinnings [5, 10, 11].

One of the major complexities in the study of individual variation in social behaviour results from the fact that the social environment almost always consists of a polyadic network of non-independent social ties [12, 13]. Animals are connected to the individuals with whom they associate with directly (direct connections), but are also tied indirectly to the partners of their social partners (indirect connections) [8, 13-15]. Social network analysis has become a popular tool for animal social behaviour research [14, 16] as it allows researchers to look beyond how individuals differ at the level of direct, dyadic, associations and to explore how animals are positioned in the wider social environment [13]. The many different measures of individuals' general social centrality or integration within a social network allows their indirect connections and network positions to be quantified in various ways. For example, commonly considered metrics include: 'eigenvector centrality', which sums their associates' associations; 'betweenness', which calculates how many of the shortest social paths between others in the network pass through them; and 'closeness' which measures their social distance to every other individual [13].

Currently, many questions remain surrounding the importance of indirect network connections to our understanding of animal social behaviour [13, 48]. Indirect connections are, by definition, an emergent feature of associations between pairs of individuals. Yet the extent of information regarding polyadic connections that individuals possess, and whether they can use this to influence their social environment, is largely unknown. Whether the relationships between indirect network positions and wider traits (e.g. fitness) are evidence of the importance of indirect connections, or whether simpler, and perhaps more parsimonious, explanations underpin such findings also needs to be established. Further, how complex network positions, which intrinsically depend upon the direct social associations among pairs of others, can be repeatable, heritable or the target of selection at the individual-level remains uncertain.

Despite the lack of clarity surrounding these fundamental issues regarding indirect connections, recent findings have shown that an individual's tendency to be indirectly connected to others can be consistent [9, 17, 18], even following disturbance [19-21], heritable [9, 22, 23], and strongly related to other variables of interest, including the likelihood of contracting disease [24-27], obtaining new information [28, 29], or of leading group movements [30]. Indirect connections have even been associated with proxies of fitness, with studies reporting positive associations between indirect network metrics and an individual's future social status [31-33], survival [34] and reproductive output [9, 33, 35-37]. Within this body of research, a growing number of studies have found effects of indirect connections even after controlling for dyadic associations, and an even greater relative importance of these complex metrics than direct dyadic ones (reviewed in Brent (2015) [13] and more recent studies thereafter [36, 37]), leading to various conclusions regarding the importance of indirect connections within societies.

Extended interpretations surrounding complex network positions have suggested that the consequences of indirect connections stem from individuals actively undertaking complex social manoeuvers and making decisions based on their understanding of the wider network structure and relationships between third parties [36, 37]. These suggestions certainly fit well with evidence suggesting that some species have the ability to obtain social information in an indirect manner. For example, cichlids may infer the relative dominance status of pairs of males using information on the pairs' relative status with other fish [38]; primates and corvids appear to eavesdrop on the relationships between pairs of third parties [39, 40], and to shape their behaviour around others' social bonds [41-44]. Further, it has recently been reported that the human brain may be capable of spontaneously encoding the indirect network positions of others [45-47]. These results, combined with the fitness correlates of indirect metrics described above, may even suggest that selection is acting directly to shape not just the dyadic, but also the polyadic social world.

Identifying how simple differences between individuals generate differences in their complex indirect network positions not only helps avoid misleading conclusions about social structure, but is also important for understanding how both simple social behaviours and complex social network structure can evolve. In this study, we use a simulation approach to assess how direct social network metrics (quantified using social associations at a dyadic-level) and indirect network metrics (intended for quantifying higher-level structure) emerge from simple differences in individuals' association patterns. By creating different social scenarios, we determine how basic sources of individual variation in terms of social associations can actually be more strongly predictive of indirect network metrics than direct network metrics. Further, we examine how external processes that shape the network itself (or how we measure it), can affect the relationship between simple social differences and variation in social network metrics. We highlight the importance of understanding the relationships between simple association patterns and network positions for drawing conclusions in relation to the causes of variation, and how such relationships allow the repeatability, heritability, and the selection of complex social positions to result from relatively simple mechanisms.

METHODS

General framework

In research on empirical social networks, the data are based upon the social association patterns observed within the inferred social network. Therefore, underlying social differences between individuals are deduced from their positions within the social network ('social network metrics'). These measures of individuals' social network positions are then often used in analyses relating to various other traits/processes, from which conclusions are drawn about the causes and consequences of individuals' social behaviour [1, 14]

For example, if a metric measuring the sum of individuals' indirect social associations (i.e. their associates' social associations – 'eigenvector centrality') held a stronger relationship to their fitness than a metric measuring the sum of their direct social associations (i.e. how often they associate with others - 'weighted degree' or 'strength'), it might be concluded that individuals' propensity to indirectly associate with others (e.g. by associating with others who themselves have lots of associations) is more important to fitness than simply their propensity to associate with others [36, 37]. Therefore, drawing conclusions related to underlying differences in social behaviour often relies on the assumption that the network metric used as a proxy of the underlying social differences is accurate, and more related to this social behaviour than the other network metrics it is been compared to. However, within the field of animal social networks, it has been notoriously difficult to assess how social network metrics actually effectively relate to underlying social differences, and the consequences of this. Therefore, we use a computational approach that allows us to vary individuals' underlying social association patterns, simulate the arising social network, and subsequently assess how the initially specified variation can be recovered using social network metrics. In particular, we aim to determine how direct social network metrics and indirect social network metrics (see below) are generated from simple social differences between individuals.

We separately considered three simple scenarios, each with its own specified process underlying social differences between individuals (see above, and see *Supplementary Methods* for details). For each of these three scenarios, we carried out simulations where social associations occurred at random apart from the specified scenario to generate the arising social networks. Within the simulations, each individual was randomly assigned a trait value from a standard uniform distribution on which their social differences were conditioned (*see Supplementary Methods* for details). Each simulation consisted of 1000 individuals with, on average, 100 associations assigned to each individual (but see *supplementary information* for variations of this).

First, we considered individuals' general sociability' ('GS') as the number of individuals that a focal individual generally associates with (which is also analogous to gregariousness or average group size). In this simulation scenario, we assigned individuals to 'grouping events' based on their trait value, whereby those with high GS had a higher probability of occurring in larger grouping events than those with a low GS. Grouping events ranged in size from 1-10 individuals (but see *supplementary information* for variations). All individuals within a grouping event were classed as holding an association to one another. This is similar to the commonly-used 'gambit of the group' approach whereby spatio-temporally clustered individuals are considered associated [49, 50]. This process was carried out until, on average, each individual had engaged in 100 associations (see *supplementary methods*).

In a second scenario, individuals were set to vary in their 'reassociation tendency' ('RT'), which was defined as their propensity to reassociate with individuals they had associated with before. Each association was assigned one-by-one by selecting an individual within a random step-wise process (see *supplementary methods*). The probability that the association was then directed towards either a random previous associate of the selected individual, or to a random new associate of the selected individual, was directly proportional to the selected individual's trait value. Therefore, those with lower RT had a lower social stability and were more likely to associate with others they hadn't associated with previously.

Finally, we varied individuals' 'within-group association' ('WGA') i.e. their likelihood of associating with their own group members over non-group members. The 'groups' defined here could be analogous to any predetermined social groups, such as cliques, animals who share the same home-range, or even a shared phenotype. Individuals were randomly assigned to equally sized 'groups' at the beginning of each simulation (100 separate groups of 10 individuals in the primary analysis, but see *supplementary information* for variations). Associations were then assigned between dyads on the basis of both of the individual's trait values and whether or not they were in the same preset 'group' (see *supplementary methods*). In this way, higher WGA values increased an individual's propensity to direct more of their associations towards those categorized as being in the same 'group' as themselves, whilst lower WGA increased the likelihood of engaging in associations with different individuals.

Variation in social network positions

Upon generating the social networks under the three scenarios, we then examined how the initially specified social differences (i.e. trait values) related to variation in social network metrics (or 'social network positions'). Therefore, for each of the scenarios, we first calculated the relationship between the trait value and the relevant simple metric usually used for measuring such differences directly (see below). Then we calculated the relationship between the trait value and a relevant complex metric that incorporates information on indirect connections [13, 37]. Such metrics are usually used to infer more complex processes than single-dimension variation in dyadic social associations. However, by incorporating information on the wider social structure as well as the individual's own associations, this may provide a better description of simple social behaviours in emerging networks (see *Network error and noise* and *Discussion: Individual variation and network structure* for further details).

Specifically, when simulating General Sociability (GS) variation, we used 'weighted degree' as the simple direct metric. This measure represents the sum of an individual's dyadic associations to others and is thus often used with the intention that it is a direct measure of the general sociability of an individual. We used 'eigenvector centrality' as the indirect metric, which is derived from the sum of each individual's associates' associations (i.e. their 'second-order associations'). This complex metric is usually used with the intention to describe individuals' propensity to form connections with highly connected individuals. However, eigenvector centrality may relate to initial GS due to incorporating information on individuals' associates' associations when assortment by degree can arise due to passive processes [51, 52].

In the Reassociation Tendency (RT) variation simulations we used 'average edge weight' (or 'mean non-zero edge weight') as the intuitive direct metric, which is an individual's mean dyadic association strength to each of their associates. Thus, this may be viewed as a direct measure of reassociation tendency (or social stability), with those possessing the strongest bonds (i.e. high average edge weights) having the highest reassociation tendency. As a relevant, but more complicated metric, we used 'betweenness centrality', calculated as the number of shortest paths between all individuals in the network that pass through the focal individual. This is commonly used to infer the extent to which individuals act as a 'bridge' within the network, and therefore those that may be particularly important to information and disease spread [14]. In this case, betweenness may be expected to correlate with RT as differences in stability of associations could give rise to variation in the amount of mixing individuals engage in within the resultant network.

Finally, when simulating variation in Within-Group Association ('WGA'), we calculated individuals' 'EI index' that is used as a direct measure of within-group associations in relation to out-group associations (ranging from -1 to +1, where -1 = all associations directed to non-group members and +1 = all associations held are with group members, and 0 = equal number of associations with group and non-group members). As the indirect complex metric, we used 'closeness', which assesses the path length of the focal individual to every other individual within the network. As segregation arises when distinct classes/groups exist, those which are most likely to focus their associations towards their own class/group may be expected to be relatively distant from the majority of others within the wider network, whilst those with more equal mixing will experience higher general 'closeness' within the network.

Network noise

Together with consistent social differences between individuals, the structure of empirically derived social networks are likely to be subject to noise, such as due to external processes or imperfect observation and inference due to the wide variety of sampling intensities and accuracies across studies [53, 54]. It is therefore important to gain insight into how such noise may influence the strength of, and our quantification of, the relationship that specified sources of individual variation holds with direct dyadic network metrics and complex indirect metrics.

We examined four types of noise processes separately: (i) Link removal is the deletion of social associations between dyads (Figure 1a) and (ii) node removal is the deletion of individuals and their social associations to others (Figure 1b). Either of these deletion processes may arise from incomplete observation or limited sampling of a population. Therefore, carrying out these removal processes at different intensities on generated networks mimic the effect of different levels of sampling intensities of individuals or associations between individuals. Alternatively, the deletion processes could also be viewed as similar to external factors that put limitations on which individuals can interact or are consistently present in the system. (iii) Link rewiring refers to reassignment of social associations between random triads, whereby the value of the social association between individual 'A' and individual 'B' would be swapped with the social association between individual 'A' and individual 'C', thus the strengths of the social associations between dyads are randomised (even if was previously zero) (Figure 1c). (iv) Node rewiring is randomising the identity (and all associated information) of a subset of individuals (Figure 1d). Either of these rewiring processes may arise from imperfect inference of associations or individual identification (which again may be related to sampling intensities), or external influences and other factors determining which interactions actually take place. We generated each noise processes (i.e. removal and rewiring of links or nodes) ranging from 10% to 90% of links or nodes selected for removal or rewiring. This was carried out in intervals of 10% on final versions of the simulated networks arising from each scenario. We carried out 1000 simulations of each noise process (n=4) for networks generated from each scenario described above (n=3) at each different level (0% to 90%) resulting in 120 different types of simulated network (360 including *supplementary information* variations) and a total of 1,200,000 networks (3,600,000 including *supplementary information*). In each case, we examined the relationship between the initially specified simple trait values of individuals and their relevant direct and indirect metrics calculated from the simulated network.

RESULTS

As expected, the simulations gave rise to fully connected networks of different structures (Figure 2). The differences in structures were maintained when various types of noise/error (Figure 1) were inputted even at relatively high levels (Figure S1).

The ranked correlation of the simple initial trait with the direct metrics and with the indirect metrics provides an intuitive measure of which type of metric is most related to the social differences between individuals. First, when considering simulation scenario (1) individuals' general sociability ('GS') correlated more with their complex indirect social network position (eigenvector centrality) than the simple direct measure (weighted degree), even before any simulated noise (i.e. the start point in Figure 3a). With increasing levels of link removal (randomly deleting associations), the strength of the relationship between the initially specified social differences and both direct and indirect social network metrics decreased (particularly for >50% noise) but eigenvector centrality always remained the stronger predictor of GS.

A similar pattern was also found for the second simulation scenario, as individuals' reassociation tendency ('RT') was more strongly related to their betweenness centrality (the indirect metric) than their average bond strength (direct metric). In this scenario, this difference was exaggerated with increasing link removal, as the correlation between re-association tendency and average bond strength declined more than its correlation with the indirect network metric of betweenness (Figure 3b).

Finally, the direct measure of in-group out-group ties (the EI index) was a slightly better predictor of variation in individuals' within-group association ('WGA') before any noise was introduced. But, increasing the proportion of nodes removed rapidly resulted in the indirect metric (closeness) being more strongly correlated to WGA than the direct metric. This was due to the EI index suffering a greater reduction in prediction ability with increased error (Figure 3c). For all three scenarios, removing nodes appeared to differ slightly from removing links in how it affected overall network structure (Figure S1). However, the extent to which indirect metrics were more strongly related than direct metrics to the underlying social differences under increased node removal generally mimicked that of increased link removal (as described above) over all three scenarios (Figure 3d-f).

We also considered how rewiring aspects of the network (links and nodes), rather than removing them, influenced the relationship between the specified social differences and the direct and indirect metrics across the three different scenarios (Figure 4). Increased link rewiring reduced the difference between the indirect metric and the direct metric, as eigenvector centrality and weighted degree were similarly correlated to GS when >50% of links were rewired (Figure 4a). Under the RT and WGA scenarios however, link rewiring increased the difference between the direct (average edge weight and EI-index respectively) and the indirect metrics' (betweenness and closeness respectively) correlations to the initial social differences (RT and WGA respectively) (Figure 4b-c). This resulted in the indirect metrics being even more strongly related to the initial social differences than the direct metrics. In both cases, although the correlation remained highest for the indirect metrics across all levels of rewiring, the raw differences (but not proportional differences) in predictive ability decreased as >60% of links were randomized (Figure 4b-c).

Rewiring nodes (i.e. randomly swapping individuals' positions) caused a similar linear decrease in the correlations between social differences in the GS and RT scenarios and both direct and indirect metrics (Figure 4d-e). Although the raw difference in the correlations decreased slightly (Figure 4d-e), it should be noted that the proportional difference between these correlations remained the same with increasing node rewiring, thus the initial slight advantage of the indirect metrics was maintained. Although the correlation between WGA and the indirect metric (closeness) again decreased linearly, the direct metric (EI-index) suffered a larger decrease in predictive power under increased node rewiring (Figure 4f). Intuitively, the decreasing relationship between WGA and the EI-index under node rewiring is driven by assigning individuals to positions unrelated to their actual group.

Overall, indirect metrics generally provided a much more robust representation of the specified source of individual variation – even within these rather simple scenarios (Figure 3;4). However, to further verify the conclusions from these simulations, we carried out supplementary analyses considering networks of different sizes and variations (see *Supplementary Methods*). We found that all the same patterns as described above were replicated when considering smaller networks (Figure S2-3), larger networks (Figure S4-5) as well as when altering the core aspects of the scenario specifications (Figure S6-7) i.e. varying co-occurrence sizes in scenario 1 (GS), stability level in scenario 2 (RT) and number of pre-set groups for scenario 3 (WGA). Thus, the results found within the primary setting were generalizable to the different circumstances and variations of the analysis.

DISCUSSION

We use simulations to show that individual variation based on simple, dyadic-based, social rules can be more strongly related to indirect metrics of social network position than direct measures. We show that this difference can be further exaggerated under random noise that frequently characterises social network data in animal populations. These findings echo previous research showing that complex collective and group-level patterns can be explained by simple rules [30, 55, 56]. In this case, our results show how simple social differences can explain the causes of variation in complex network metrics. The results have direct implications for: (i) interpreting social network positions, (ii) understanding how selection may act on social systems through simple means, and (iii) considering how individual variation gives rise to overall network structure.

Interpreting social network positions

Our findings contribute to the debate regarding the complexity of individual-level behaviour needed to generate complex patterns within a system [13, 55, 57, 58]. For example, we show that simple differences in the number of associates with which individuals occur can ultimately govern whether they associate with highly central individuals or with peripheral individuals (i.e. variation in eigenvector centrality). Importantly, the initial source of variation holds a stronger relationship to a complex network metric than it does to a measure that directly considers associations with others (weighted degree). Individuals need not, therefore, actively shape this complex network position - for instance by preferentially engaging in associations with high centrality individuals – for a correlation between eigenvector centrality and individual-level traits to arise. In the same sense, any trait of interest with a stronger relationship to a complex measure need not necessarily be linked to an individuals' innate propensity to engage in complex social behaviour, but rather could be generated by a simpler mechanism.

Along with the clear implications for interpreting results within animal systems, our findings have some relevance for understanding human behaviour. For instance, recent studies monitoring brain activity suggested that humans are able to spontaneously identify the complex (indirect) network positions of others [46, 47, 59]. However, if unmeasured simple behaviours or traits hold relatively strong relationships to indirect metrics, humans may simply use these traits as a general cue of indirect social connections. Indeed, modeling and empirical research has demonstrated that individuals can infer the complex network position of others in terms of their propensity to spread information using simple dyadic-level cues with no knowledge of overall structure [29, 60]. Thus, even if humans within networks have little knowledge of its structure [61, 62], the relationship between simple traits and complex metrics may produce patterns which imply the opposite. Nevertheless, across all systems, even if indirect social metrics do not provide evidence of complex social mechanics at the individual level, we also point out that the demonstrated resilience to noise (Figure 3;4; S2-S7) may mean that they do offer a robust indication of social differences between individuals (whether or not this is complex).

Although previous research reporting relationships between indirect metrics and other processes does not necessarily imply complex behavioural processes, equally, we do not suggest that such phenomena can be ruled out. Future work using novel approaches to clearly assess whether, and how, certain animals (including humans) infer the network positions of others and shape their indirect associations would be of great interest. For such conclusions to be drawn, methodological approaches which allow the separation of simple dyadic level behaviour and complex social behaviour from observed social network data would be valuable. For instance, future work trying to separate the effects of indirect network positions over and above simple behaviours on other variables (such as fitness) will likely require appropriate null models that are conditioned on the simple behaviours themselves, rather than on the network i.e. permutations of the raw behavioural data [53, 63] or simulation models parameterized on the system itself. Simply controlling for other network properties (i.e. direct metrics) will not adequately rule out the influence of simple social differences on arising indirect metrics. Further, novel experiments that manipulate simple behaviours and examine the resultant consequences for social networks [20, 64], and the consequences of this for social processes [65], would be particularly useful in elucidating the relationship between simple behaviours and arising network metrics, and their causal relationships with other variables.

In light of our findings, we advise that studies demonstrating a relationship between an aspect of interest (e.g. a particular trait, process, or measure) and indirect social network metrics do not necessarily indicate that indirect, or complex, social behavioural differences are present or hold any particular importance (even if direct metrics provide less explanation). This is particularly relevant to animal social networks, when the factors driving underlying behavioural differences usually are unknown and social network metrics are instead used as a proxy for those factors [14].

Selection on social network positions

Our findings also have implications for understanding how selection may act on social network positions of individuals. Although previous research has reported links between individual fitness and complex social network positions [9, 31-37], the mechanisms driving such relationships, as well as the heritable basis of such complex differences, remains less intuitive. Indeed, how complex indirect network positions, which essentially rely upon the connections between third parties, could be heritable (or even repeatable) appears puzzling – particularly when it is to a greater extent than direct network measures [9]. The strong causal relationship between simple underlying social differences and indirect connections within arising networks demonstrated here allows the heritability of these complex traits through much simpler mechanisms. For example, if disease spread caused those with highest betweenness to suffer fitness costs, then a strong link between a simple trait which could intuitively have a heritable basis (e.g. tendency to reassociate) and betweenness could allow selection to act on individuals with the highest betweenness to an even greater extent than on simpler association metrics. These phenomena would then result in higher apparent heritability of the complex metrics than simple dyadic network metrics [9]. Secondly, the relationship between simple behaviours and indirect metrics could also allow selection to act on complex network positions indirectly (i.e. as a by-product of selection on a simple correlated trait). Again, this could be to an even greater extent than the indirect selection on more simple association metrics. For example, our simulations suggest if variation in individuals' propensity to occur in larger groups was linked to fitness (whereby the most sociable individuals have higher fitness), this would concurrently cause strong indirect selection on eigenvector centrality, and this would be stronger than the selection on individuals' number of associates.

Thus, the relationship between individual social differences and indirect metrics creates the potential for selection to act even more strongly on complex network positions than simple network metrics, through allowing the heritability of complex positions subject directly to selection (as in the first example) or by indirectly selecting for complex positions through their association with simple underlying traits (as in the second example). Both explanations offer convincing and plausible explanations for how selection can sculpt the entire network structure more so than would be expected under selection on simple dyadic network positions. Further work using selection and quantitative genetic models to intricately assess this, along with examining how changes in overall network architecture across generations that result, may interact with this, would be of great interest to understanding how wider social structure evolves.

Individual variation and network structure

The complexity of actual animal societies [53] is likely to be much greater than considered within the simulations within this work. Within our study, we only consider social systems arising from simple social differences, and each are only subjected to one type of random noise process. Natural networks are likely to be shaped by various processes simultaneously, and contain combinations of noise processes dependent on sampling protocol and intensity, and such error may even be non-random [53, 66]. Our findings suggest that increased levels and types of external network-shaping processes may cause simple social differences to be relatively more strongly related to indirect network positions compared to more direct measures. Thus, the simulations employed here represent a conservative test of how indirect metrics may be strongly correlated to simple underlying variation, even in the absence of complex social behaviour. However, we caution that we do not suggest that indirect metrics will always universally be better measures of underlying social variation that direct metrics. Rather, we aim to emphasize that consideration should be given to the potential factors shaping network structure, and that appropriate metrics should be chosen and conclusions should be drawn carefully.

Mathematical, simulation-based, or empirical data that address precisely how social differences give rise to variation in complex indirect network positions would now also be of interest. For instance, positive assortativity is a common feature of many social networks [51], particularly when networks are created using the gambit-of-the-group approach [49, 50, 52]. Our simulations show that simple differences in general sociability (or group size preference), cause this positive assortativity (scenario 1 – assortativity generally ranging from r=0.15-0.40 depending on noise/error type) which results in individuals having associates with similar numbers of associates as themselves. Therefore, as eigenvector centrality also includes information about an individual's associates' associates, this then provides an even more robust measure of an individual's underlying behaviour than simply considering their own associations i.e. considering an individual's wider position within the network enables more accurate estimation of their dyadic-level behaviour than just considering their dyadic associations due to the complex patterns that arise even within simple scenarios. In the same sense, differences in the stability of individuals' social ties (i.e. their reassociation tendency) causes those engaging in higher levels of mixing to act as bridges within the network and experience higher betweenness. Additionally, when distinct classes/groups exist (WGS scenario), segregation within the network arises and individuals who are most likely to focus their associations towards their own class/group will be removed from the other classes, whilst those with more equal mixing will experience higher 'social closeness' within the network. Gaining a broader and more general understanding of how social positions arise from generative sources of individual behavioural variation, and the correlation between these metrics, will further advance our knowledge of how overall network structure arises [67-69].

Conclusion

We show that simple social differences can be more related to individuals' indirect connections than to their direct connections within social networks. Therefore, while indirect network metrics need not illustrate the presence of complex social decisions, or their importance for apparent social or biological processes, the relationship that indirect social positions hold with simple underlying individual variation allows for their heritability and for selection to act on them (and therefore wider network structure) through this. We suggest that future research should now focus on assessing how natural selection acts on complex network positions, and on developing new analytical and experimental methods to assess whether certain species actively shape their indirect connections and how social structure develops from underlying individual variation.

Data accessibility

The code required for generating the simulated data is provided in the supplementary material

Authors' contributions

J.A.F. conceived the study, carried out the analysis and wrote the initial draft. All authors contributed towards designing the study, interpreting the results and revising the manuscript.

Competing interests

We declare we have no competing interests.

Funding

The work was funded by a Research Fellowship from the EGI, and a Junior Research Fellowship from Merton College, Oxford University, to J.A.F. and a BBSRC grant (BB/L006081/1) to B.C.S.

Acknowledgments

We thank Alex Thornton and two anonymous reviewers for helpful feedback on this manuscript.

References

1. Krause J., James R., Franks D.W., Croft D.P. 2015 *Animal Social Networks*. Oxford, UK, Oxford University Press.
2. Ward A.J.W., Webster M.M. 2016 *Sociality: the behaviour of group-living animals*. Switzerland, Springer International Publishing.
3. Wilson E.O. 1975 *Sociobiology: the new synthesis*. Cambridge, MA, Harvard University Press.
4. Hinde R.A. 1976 Interactions, relationships and social structure. *Man* **11**, 17. (doi:10.2307/2800384).
5. Krause J., Ruxton G.D. 2002 *Living in groups*. Oxford, Oxford University Press.
6. Reale D., Reader S.M., Sol D., McDougall P.T., Dingemanse N.J. 2007 Integrating animal temperament within ecology and evolution. *Biol Rev* **82**(2), 291-318. (doi:10.1111/j.1469-185X.2007.00010.x).
7. Sih A., Cote J., Evans M., Fogarty S., Pruitt J. 2012 Ecological implications of behavioural syndromes. *Ecol Lett* **15**(3), 278-289. (doi:10.1111/j.1461-0248.2011.01731.x).
8. Krause J., James R., Croft D.P. 2010 Personality in the context of social networks. *Philos T R Soc B* **365**(1560), 4099-4106. (doi:10.1098/rstb.2010.0216).
9. Brent L.J.N., Heilbronner S.R., Horvath J.E., Gonzalez-Martinez J., Ruiz-Lambides A., Robinson A.G., Skene J.H.P., Platt M.L. 2013 Genetic origins of social networks in rhesus macaques. *Sci Rep* **3**. (doi:10.1038/srep01042).
10. Alexander R.D. 1974 The evolution of social behavior. *Annu Rev Ecol Syst* **5**, 325-383. (doi:10.1146/annurev.es.05.110174.001545).
11. Maynard Smith J. 1982 *Evolution and the theory of games*. Cambridge, UK, Cambridge University Press.
12. Madden J.R., Drewe J.A., Pearce G.P., Clutton-Brock T.H. 2011 The social network structure of a wild meerkat population: 3. Position of individuals within

networks. *Behav Ecol Sociobiol* **65**(10), 1857-1871. (doi:Doi 10.1007/S00265-011-1194-2).
13. Brent L.J.N. 2015 Friends of friends: are indirect connections in social networks important to animal behaviour? *Anim Behav* **103**, 211-222. (doi:10.1016/j.anbehav.2015.01.020).
14. Croft D.P., James R., Krause J. 2008 *Exploring animal social networks*. Princeton, Princeton University Press.
15. Wey T., Blumstein D.T., Shen W., Jordan F. 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim Behav* **75**, 333-344. (doi:10.1016/j.anbehav.2007.06.020).
16. Hasenjager M.J., Dugatkin L.A. 2015 Social Network Analysis in Behavioral Ecology. In *Adv Study Behav* (eds. Naguib M., Brockmann H.J., Mitani J.C., Simmons L.W., Barrett L., Healy S., Slater P.J.B.), pp. 39-114, Elsevier.
17. Blumstein D.T., Petelle M.B., Wey T.W. 2013 Defensive and social aggression: repeatable but independent. *Behav Ecol* **24**(2), 457-461. (doi:10.1093/beheco/ars183).
18. Aplin L.M., Firth J.A., Farine D.R., Voelkl B., Crates R.A., Culina A., Garroway C.J., Hinde C.A., Kidd L.R., Psorakis I., et al. 2015 Consistent individual differences in the social phenotypes of wild great tits, Parus major. *Anim Behav* **108**, 117-127. (doi:10.1016/j.anbehav.2015.07.016).
19. Formica V.A., Wood C., Phoebe C.s., Brodie III E. 2016 Consistency of animal social networks after disturbance. *Behav Ecol*. (doi:10.1093/beheco/arw128).
20. Firth J.A., Voelkl B., Crates R.A., Aplin L.M., Biro D., Croft D.P., Sheldon B.C. 2017 Wild birds respond to flockmate loss by increasing their social network associations to others. *P Roy Soc B-Biol Sci*. (doi:10.1098/rspb.2017.0299).
21. Krause S., Wilson A.D.M., Ramnarine I.W., Herbert-Read J.E., Clement R.J.G., Krause J. 2017 Guppies occupy consistent positions in social networks: mechanisms and consequences. *Behav Ecol* **28**(2), 429-438. (doi:10.1093/beheco/arw177).
22. Fowler J.H., Dawes C.T., Christakis N.A. 2009 Model of genetic variation in human social networks. *Proc Natl Acad Sci USA* **106**(6), 1720-1724. (doi:10.1073/pnas.0806746106).
23. Lea A.J., Blumstein D.T., Wey T.W., Martin J.G.A. 2010 Heritable victimization and the benefits of agonistic relationships. *Proc Natl Acad Sci USA* **107**(50), 21587-21592. (doi:10.1073/pnas.1009882107).
24. Corner L.A.L., Pfeiffer D.U., Morris R.S. 2003 Social-network analysis of Mycobacterium bovis transmission among captive brushtail possums (Trichosurus vulpecula). *Prev Vet Med* **59**(3), 147-167. (doi:10.1016/S0167-5877(03)00075-8).
25. Hamede R.K., Bashford J., McCallum H., Jones M. 2009 Contact networks in a wild Tasmanian devil (Sarcophilus harrisii) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecol Lett* **12**(11), 1147-1157. (doi:10.1111/j.1461-0248.2009.01370.x).
26. Weber N., Carter S.P., Dall S.R.X., Delahay R.J., McDonald J.L., Bearhop S., McDonald R.A. 2013 Badger social networks correlate with tuberculosis infection. *Curr Biol* **23**(20), R915-R916. (doi:10.1016/J.Cub.2013.09.011).

27. Drewe J.A. 2010 Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *P Roy Soc B-Biol Sci* **277**(1681), 633-642. (doi:10.1098/rspb.2009.1775).

28. Aplin L.M., Farine D.R., Morand-Ferron J., Sheldon B.C. 2012 Social networks predict patch discovery in a wild population of songbirds. *P Roy Soc B-Biol Sci* **279**(1745), 4199-4205. (doi:10.1098/rspb.2012.1591).

29. Banerjee A., Chandrasekhar A.G., Duflo E., Jackson M.O. 2017 Using Gossips to Spread Information: Theory and Evidence from a Randomized Controlled Trial. *arXiv - Physics and Society*, Pre-Print. (doi:arXiv:1406.2293v6).

30. King A.J., Sueur C., Huchard E., Cowlishaw G. 2011 A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Anim Behav* **82**(6), 1337-1345. (doi:10.1016/j.anbehav.2011.09.017).

31. McDonald D.B. 2007 Predicting fate from early connectivity in a social network. *Proc Natl Acad Sci USA* **104**(26), 10910-10914. (doi:10.1073/pnas.0701159104).

32. Ryder T.B., McDonald D.B., Blake J.G., Parker P.G., Loiselle B.A. 2008 Social networks in the lek-mating wire-tailed manakin (Pipra filicauda). *P Roy Soc B-Biol Sci* **275**(1641), 1367-1374. (doi:10.1098/rspb.2008.0205).

33. Gilby I.C., Brent L.J.N., Wroblewski E.E., Rudicell R.S., Hahn B.H., Goodall J., Pusey A.E. 2013 Fitness benefits of coalitionary aggression in male chimpanzees. *Behav Ecol Sociobiol* **67**(3), 373-381. (doi:10.1007/s00265-012-1457-6).

34. Stanton M.A., Mann J. 2012 Early Social Networks Predict Survival in Wild Bottlenose Dolphins. *PLoS ONE* **7**(10). (doi:ARTN e47508
10.1371/journal.pone.0047508).

35. Lehmann J., Majolo B., McFarland R. 2016 The effects of social network position on the survival of wild Barbary macaques, Macaca sylvanus. *Behav Ecol* **27**(1), 20-28. (doi:10.1093/beheco/arv169).

36. Cheney D.L., Silk J.B., Seyfarth R.M. 2016 Network connections, dyadic bonds and fitness in wild female baboons. *Roy Soc Open Sci* **3**(7). (doi:UNSP
160255
10.1098/rsos.160255).

37. Page A.E., Chaudhary N., Viguier S., Dyble M., Thompson J., Smith D., Salali G.D., Mace R., Migliano A.B. 2017 Hunter-Gatherer Social Networks and Reproductive Success. *Sci Rep* **7**. (doi:ARTN 1153
10.1038/s41598-017-01310-5).

38. Grosenick L., Clement T.S., Fernald R.D. 2007 Fish can infer social rank by observation alone (vol 445, pg 429, 2007). *Nature* **446**(7131), 102-102. (doi:10.1038/nature05646).

39. Crockford C., Wittig R.M., Seyfarth R.M., Cheney D.L. 2007 Baboons eavesdrop to deduce mating opportunities. *Anim Behav* **73**, 885-890. (doi:10.1016/j.anbehav.2006.10.016).

40. Massen J.J.M., Pasukonis A., Schmidt J., Bugnyar T. 2014 Ravens notice dominance reversals among conspecifics within and outside their social group. *Nat Commun* **5**. (doi:ARTN 3679
10.1038/ncomms4679).

41. Bergman T.J., Beehner J.C., Cheney D.L., Seyfarth R.M. 2003 Hierarchical classification by rank and kinship in baboons. *Science* **302**(5648), 1234-1236. (doi:DOI 10.1126/science.1087513).

42. Emery N.J., Seed A.M., von Bayern A.M.P., Clayton N.S. 2007 Cognitive adaptations of social bonding in birds. *Philos T R Soc B* **362**(1480), 489-505. (doi:10.1098/rstb.2006.1991).

43. Slocombe K.E., Zuberbuhler K. 2007 Chimpanzees modify recruitment screams as a function of audience composition. *Proc Natl Acad Sci USA* **104**(43), 17228-17233. (doi:DOI 10.1073/pnas.0706741104).

44. Massen J.J.M., Szipl G., Spreafico M., Bugnyar T. 2014 Ravens Intervene in Others' Bonding Attempts. *Curr Biol* **24**(22), 2733-2736. (doi:10.1016/j.cub.2014.09.073).

45. Parkinson N.J., Buechner-Maxwell V.A., Witonsky S.G., Pleasant R.S., Werre S.R., Ahmed S.A. 2017 Characterization of basal and lipopolysaccharide-induced microRNA expression in equine peripheral blood mononuclear cells using Next-Generation Sequencing. *PLoS ONE* **12**(5). (doi:ARTN e0177664 10.1371/journal.pone.0177664).

46. O'Donnell M.B., Bayer J.B., Cascio C.N., Falk E.B. 2017 Neural bases of recommendations differ according to social network structure. *Soc Cogn Affect Neurosci* **12**(1), 61-69. (doi:10.1093/scan/nsw158).

47. Curley J.P., Ochsner K.N. 2017 Neuroscience: Social networks in the brain. *Nature Human Behaviour* **1**. (doi:10.1038/s41562-017-0104).

48. Rankin R.W., Mann J., Singh L., Patterson E.M., Krzyszczyk E., Bejder L. 2016 The role of weighted and topological network information to understand animal social networks: a null model approach. *Anim Behav* **113**, 215-228. (doi:10.1016/j.anbehav.2015.12.015).

49. Whitehead H., Dufault S. 1999 Techniques for analyzing vertebrate social structure using identified individuals: Review and recommendations. *Advances in the Study of Behavior, Vol 28* **28**, 33-74. (doi:Doi 10.1016/S0065-3454(08)60215-6).

50. Franks D.W., Ruxton G.D., James R. 2010 Sampling animal association networks with the gambit of the group. *Behav Ecol Sociobiol* **64**(3), 493-503. (doi:Doi 10.1007/S00265-009-0865-8).

51. Newman M.E.J. 2002 Assortative mixing in networks. *Phys Rev Lett* **89**(20). (doi:10.1103/PhysRevLett.89.208701).

52. Fisher D.N., Silk M.J., Franks D.W. 2017 The Perceived Assortativity of Social Networks: Methodological Problems and Solutions. *Trends in Social Network Analysis* **23**(1), 1-19.

53. Whitehead H. 2008 *Analyzing animal societies*. Chicago, University of Chicago Press.

54. James R., Croft D.P., Krause J. 2009 Potential banana skins in animal social network analysis. *Behav Ecol Sociobiol* **63**(7), 989-997. (doi:10.1007/s00265-009-0742-5).

55. Couzin I. 2007 Collective minds. *Nature* **445**(7129), 715-715. (doi:10.1038/445715a).

56. Strandburg-Peshkin A., Farine D.R., Couzin I.D., Crofoot M.C. 2015 Shared decision-making drives collective movement in wild baboons. *Science* **348**(6241), 1358-1361. (doi:10.1126/science.aaa5099).

57. Shettleworth S.J. 2010 Clever animals and killjoy explanations in comparative psychology. *Trends Cogn Sci* **14**(11), 477-481. (doi:10.1016/j.tics.2010.07.002).

58. Hemelrijk C.K., Bolhuis J.J. 2011 A minimalist approach to comparative psychology. *Trends Cogn Sci* **15**(5), 185-186. (doi:10.1016/j.tics.2011.02.007).
59. Parkinson C., Kleinbaum A.M., Wheatley T. 2017 Spontaneous neural encoding of social network position. *Nature Human Behaviour* **1**. (doi:10.1038/s41562-017-0072).
60. Banerjee A., Chandrasekhar A.G., Duflo E., Jackson M.O. 2013 The Diffusion of Microfinance. *Science* **341**(6144), 363-+. (doi:ARTN 1236498 10.1126/science.1236498).
61. Friedkin N.E. 1983 Horizons of Observability and Limits of Informal Control in Organizations. *Soc Forces* **62**(1), 54-77. (doi:Doi 10.2307/2578347).
62. Krackhardt D. 1987 Cognitive Social-Structures. *Social Netwks* **9**(2), 109-134. (doi:Doi 10.1016/0378-8733(87)90009-8).
63. Farine D.R., Firth J.A., Aplin L.M., Crates R.A., Culina A., Garroway C.J., Hinde C.A., Kidd L.R., Milligan N.D., Psorakis I., et al. 2015 The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. *Roy Soc Open Sci* **2**(4), 150057. (doi:10.1098/rsos.150057).
64. Firth J.A., Sheldon B.C. 2015 Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *P Roy Soc B-Biol Sci* **282**(1802), 20142350. (doi:10.1098/Rspb.2014.2350).
65. Firth J.A., Sheldon B.C., Farine D.R. 2016 Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biol Lett* **12**(6), 20160144. (doi:10.1098/rsbl.2016.0144).
66. Silk M.J., Jackson A.L., Croft D.P., Colhoun K., Bearhop S. 2015 The consequences of unidentifiable individuals for the analysis of an animal social network. *Anim Behav* **104**, 1-11. (doi:Doi 10.1016/J.Anbehav.2015.03.005).
67. Schoch D., Valente T.W., Brandes U. 2017 Correlations among centrality indices and a class of uniquely ranked graphs. *Social Netwks* **50**, 46-54. (doi:10.1016/j.socnet.2017.03.010).
68. Cantor M., Shoemaker L.G., Cabral R.B., Flores C.O., Varga M., Whitehead H. 2015 Multilevel animal societies can emerge from cultural transmission. *Nat Commun* **6**. (doi:ARTN 8091 10.1038/ncomms9091).
69. Ilany A., Akcay E. 2016 Social inheritance can explain the structure of animal social networks. *Nat Commun* **7**. (doi:ARTN 12084 10.1038/ncomms12084).

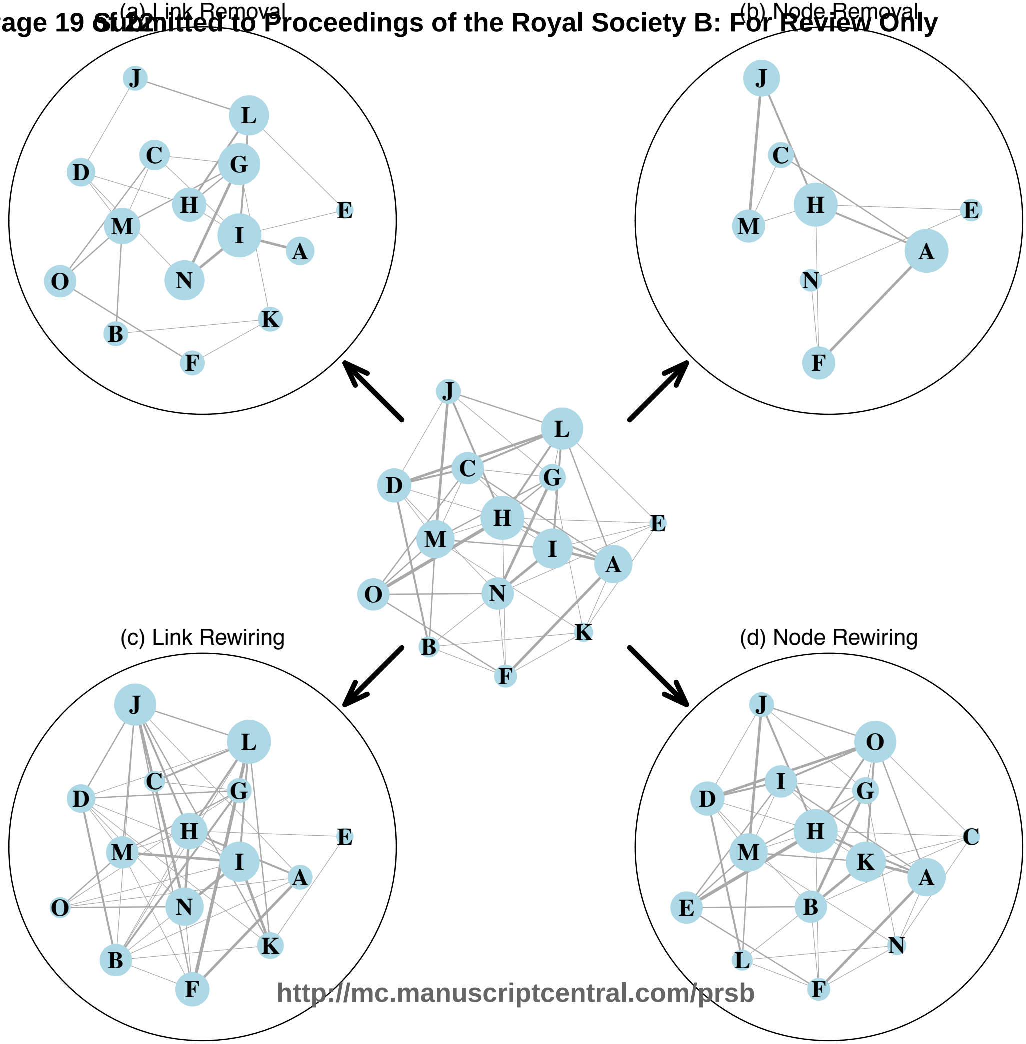
Figure Legends

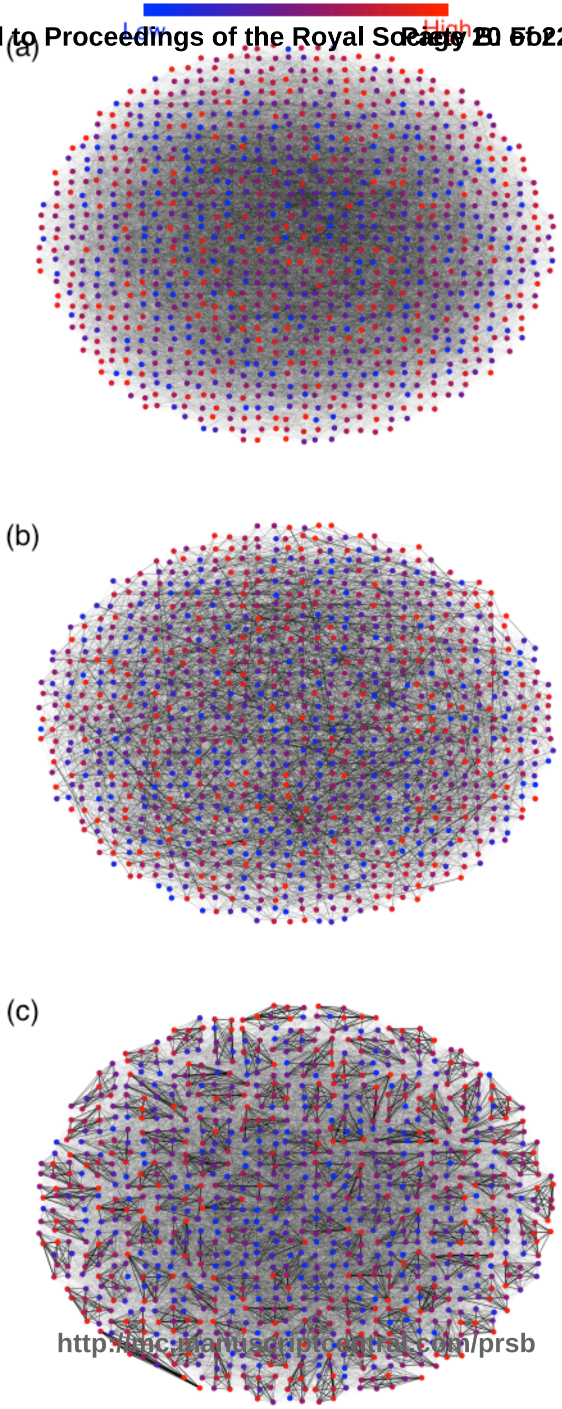
Figure 1. Illustrative examples of the different kinds of network noise input. In this example, the initial network contains 15 individuals with 50 random associations between them (central network). The surrounding networks show (a) link removal, (b) node removal, (c) link rewiring and (d) node rewiring. Each of the noise/error processes is carried out at the 50% level. The size of nodes shows the sum of their associations, the thickness of the lines indicates the strength of each dyadic association, and nodes are positioned using a spring layout of the initial (central) network.

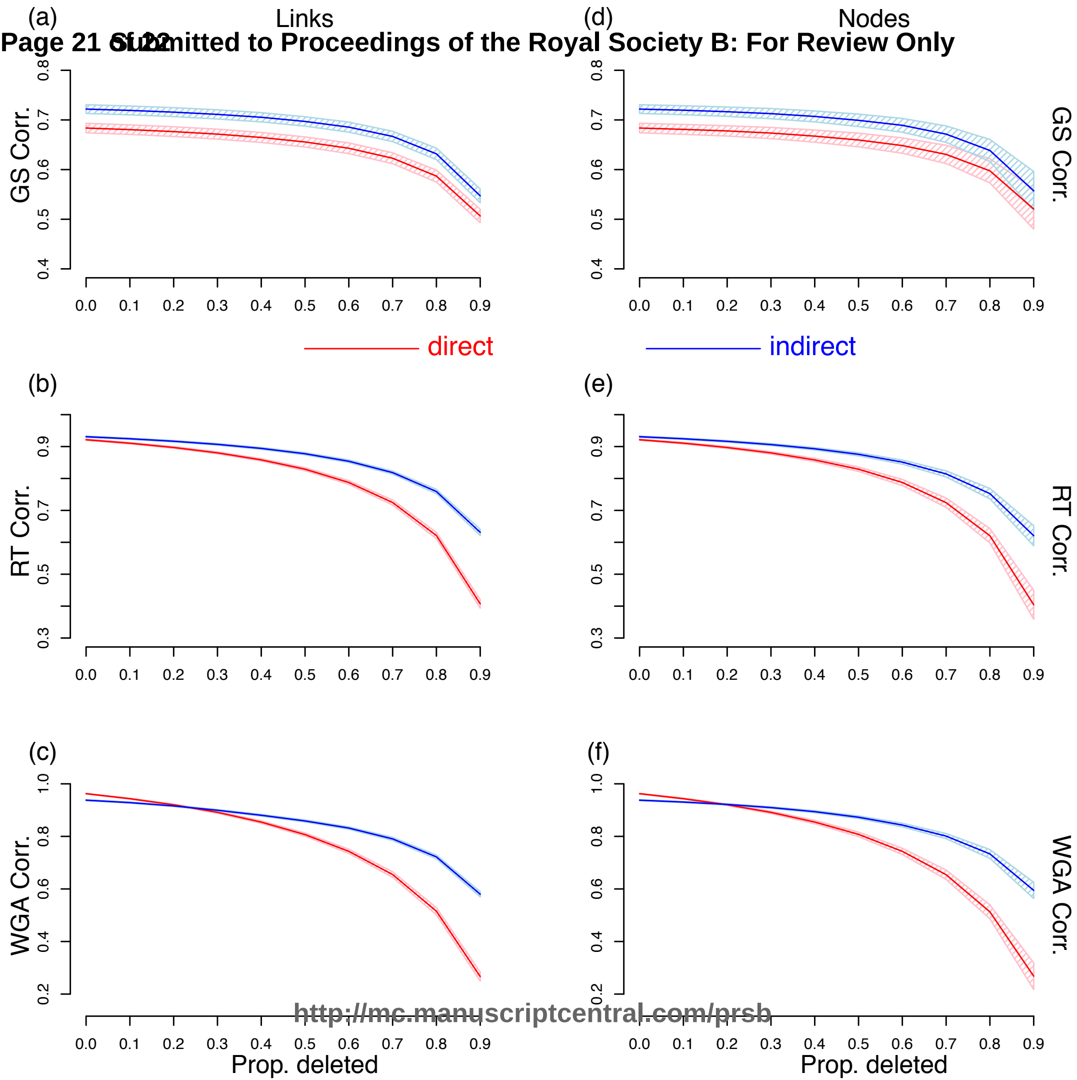
Figure 2. Example networks from each of the three simple scenarios of individual variation in (a) general sociability, (b) reassociation tendency, and (c) within-group association. All three panels show the networks using the baseline specifications (1000 individuals, an average of 100 associations per individual) before any noise/error. (a) Points show individuals and colour denotes their initial trait value (blue = low, red = high). Lines show social links between individuals, and line thickness shows strength of the social link (number of associations). Points are laid out in a circular format that minimizes overlap between links. See Figure S1 for example networks with noise.

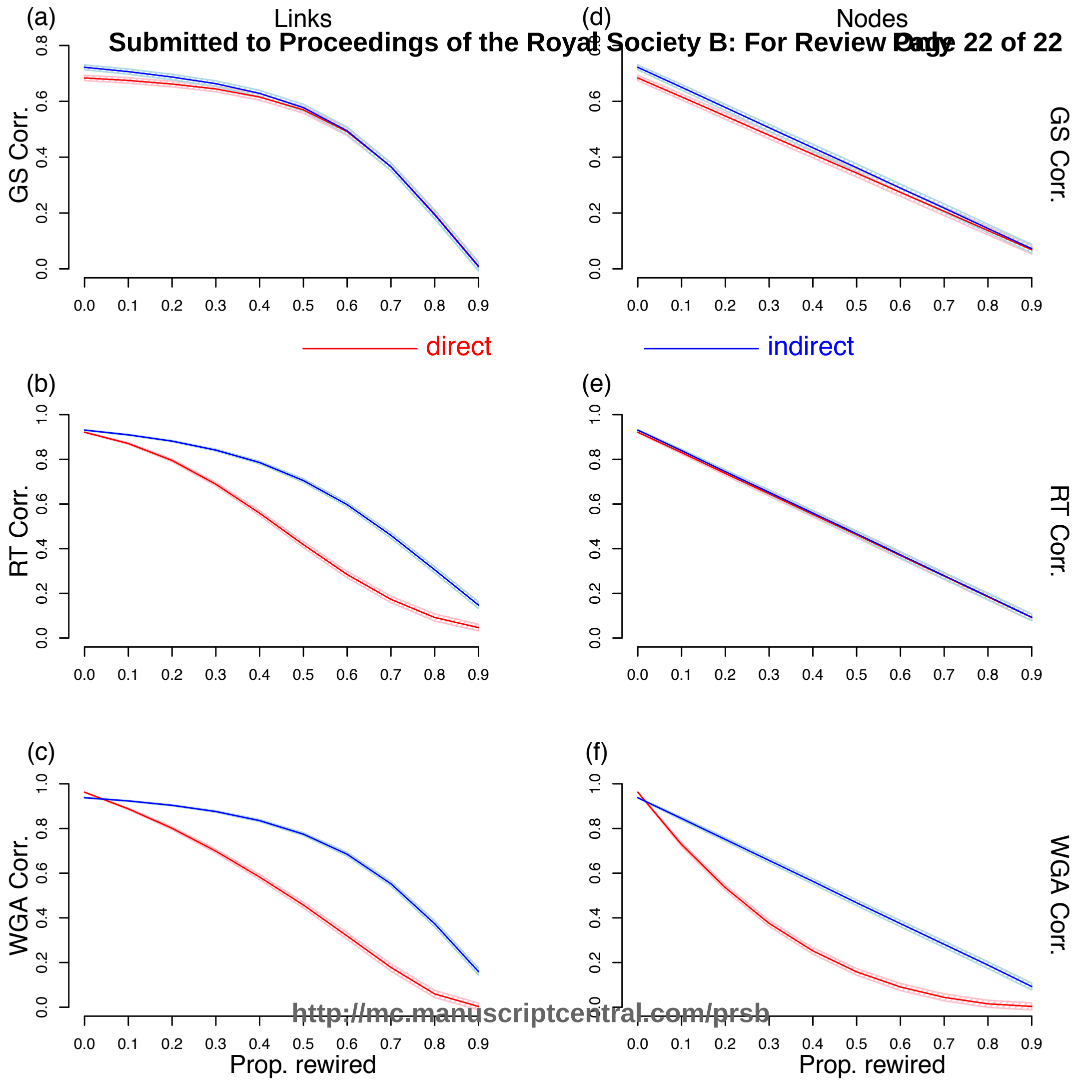
Figure 3. The relationship between simple social differences and direct (red lines) and indirect metrics (blue lines) in three simulation scenarios (rows) over different levels of missing links (a-c; left hand panels) and nodes (d-f; right hand panels). Each row shows the different social scenarios as denoted by y-axis whereby GS = 'General Sociability' (a & d; top row; scenario 1), 'RT' = 'Reassociation Tendency' (b & e; mid row; scenario 2), and 'WGA' = 'Within-Group Association'. The value of the y-axis denotes the correlation between individuals' initial traits and the direct/indirect metric of interest (scenario 1: direct = weighted degree, indirect = eigenvector centrality; scenario 2: direct = average edge weight, indirect = betweenness, scenario 3: direct = EI-index, indirect = closeness). 1000 simulations of each level of the considered proportion of nodes/links removed (x axis) were carried out: mid-lines report the mean r and shaded surrounding area denotes 1 standard deviation around this.

Figure 4. The relationship between simple social differences and direct (red lines) and indirect metrics (blue lines) in three simulation scenarios (rows) over different levels of rewiring of links (a-c; left hand panels) and nodes (d-f; right hand panels). Each row shows the different social scenarios as denoted by y-axis whereby GS = 'General Sociability' (a & d; top row; scenario 1), 'RT' = 'Reassociation Tendency' (b & e; mid row; scenario 2), and 'WGA' = 'Within-Group Association'. The value of the y-axis denotes the correlation between individuals' initial traits and the direct/indirect metric of interest (scenario 1: direct = weighted degree, indirect = eigenvector centrality; scenario 2: direct = average edge weight, indirect = betweenness, scenario 3: direct = EI-index, indirect = closeness). 1000 simulations of each level of the considered proportion of nodes/links rewired (x axis) were carried out: mid-lines report the mean r and shaded surrounding area denotes 1 standard deviation around this.


(a) Link Removal
J
L
C
G
D
H
E
M
I
A
O
N
K
B
F
(b) Node Removal
J
C
H
E
M
A
N
F
J
L
C
G
D
H
E
M
I
A
O
N
K
B
F
(c) Link Rewiring
J
L
C
G
D
H
E
M
I
A
O
N
K
B
F
(d) Node Rewiring
J
O
I
G
D
H
C
M
K
A
E
B
N
L
F


Low
High
(a)
(b)
(c)


(a)
Links
(d)
Nodes
GS Corr.
GS Corr.
direct
indirect
(b)
(e)
RT Corr.
RT Corr.
(c)
(f)
WGA Corr.
WGA Corr.
Prop. deleted
Prop. deleted


(a)
Links
(d)
Nodes
GS Corr.
RT Corr.
WGA Corr.
(b)
(e)
(c)
(f)
direct
indirect
0.0
0.2
0.4
0.6
0.8
1.0
0.1
0.3
0.5
0.7
0.9
Prop. rewired
Prop. rewired