The influence of phylogeny, social style, and sociodemographic factors on variation in macaque social networks

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Abstract:

In group-living animals, social network approaches capture group-level characteristics of social structure that emerge from interactions between individuals. Despite their recent application in animal behavioral research, the evolutionary underpinnings of social network variation in primates remain debated. Here we assess whether interspecific variation in aspects of female macaque (genus: *Macaca*) social network structure derived from dominance and grooming relationships show phylogenetic signals, and co-vary with each other and/or hypothetical species-typical social style grades. We also examine whether social networks co-varied with sociodemographic characteristics, specifically group size, sex-ratio, and current living condition. We assembled 38 datasets of female-female dyadic aggression and allogrooming among captive and free-living macaques representing 10 species. We calculated dominance (transitivity, certainty) and grooming (centralization of dominants, density, clustering coefficient) network metrics. Computations of K statistics on multiple phylogenies extracted from the *10ktrees* website revealed strong phylogenetic signals in dominance metrics, but weak signals in grooming metrics. GLMMs showed that grooming metrics strongly co-varied neither with dominance metrics, nor with species' social style grade. On the other hand, grooming density and clustering coefficient, but not centralization of dominants, were strongly predicted by group size independent of their living condition, with larger groups showing more clustered, sparser networks than smaller groups. These findings reveal that across female macaques, dominance networks may be phylogenetically conserved, whereas grooming networks may be more labile to one or more sociodemographic/ecological factors. They narrow down the evolutionary processes that may have independently produced the observed interspecific variation in two core aspects of macaque social structure. Future directions include using phylogeographic approaches, and addressing the challenges in comparing the effects of socioecological factors on primate social network structures.

Key words:

Social networks, phylogenetic signals, social style, group size, macaques

Introduction:

In group-living animals, diversity in sociality may be characterized by variation in social structure, i.e. the patterning and distribution of different types of interactions (e.g. competitive, affiliative, cooperative) and relationships among group members (Hinde, 1976). Variance in social structure thus emerges from individual-level preferences for interacting with (or avoiding) specific partners such as kin, age peers, and alliance partners (Kappeler & Van Schaik, 2002). Lately, Social Network Analysis (hereafter SNA: (Farine & Whitehead, 2015; Sueur, Jacobs, et al., 2011) has provided novel approaches to quantitatively describing variation in social structure. Yet our ability to understand the evolution and ecological factors producing diverse social structures remains limited. Specifically, the extent to which such sociality and network structure may have been influenced by species' ancestral relationships, or alternatively may be more labile to variation in current conditions, remains debated (Clutton-Brock & Janson, 2012; Kasper & Voelkl, 2009; Koenig et al., 2013; Thierry, 2004). Here we assess whether variation in aspects of social networks among multiple species of macaques (genus: *Macaca*) is influenced by species-typical intrinsic characteristics, specifically by their phylogenetic relatedness (Balasubramaniam et al., 2012a; Blomberg et al., 2003;

Thierry, 2007; Thierry et al., 2008), and by tendencies for behavioral traits to co-evolve in suites or packages that are consistent with their social styles (de Waal & Luttrell, 1989). We also investigate the extent to which two sociodemographic characteristics, group size and sex-ratio, may influence this co-variation (Kasper & Voelkl, 2009; Sueur, Petit, et al., 2011).

Across a wide range of animal taxa (e.g. bottlenose dolphins, elephants, bats, and primates), SNA has enabled the detection of higher order aspects of group- or species-typical social structure that emerge from the patterning of both direct and (more pertinently) indirect connections among individuals that are not just based on direct interactions (reviewed in (Farine & Whitehead, 2015; Kasper & Voelkl, 2009)). In other words, SNA expands the description of social structure to beyond simple outcomes of dyadic relationships, by recognizing inter-individual and inter-dyadic dependencies not as obstacles but rather as key factors contributing to group-level social structure. This is particularly evident for core aspects of primate social structure that emerge from agonistic encounters (dominance: (Bernstein, 1976)), and from the patterning of affiliative relationships (allogrooming: (Henzi & Barrett, 1999)). For instance, dyadic wins and losses in agonistic encounters have traditionally been used to compute group-level outcomes of dominance relationships, specifically dominance gradient (hierarchical steepness: (de Vries et al., 2006; Gammell et al., 2003)) and dominance asymmetry (Directional Consistency Index: DCI: (de Vries, 1998)). However, a recently developed network approach, dominance certainty, considers dyadic interactions as well as direct and indirect pathways of dominance, thereby (1) reducing the potential errors due to chance-interactions by individuals that avoid one another, and (2) incorporating the roles of both interacting and non-interacting dyads ((Fujii et al., 2013; Fushing et al., 2011); see Methods)). Similarly, social networks of allogrooming relationships, in addition to characterizing well-developed, consistent dyadic interactions, also capture the formation of subgroups of individuals that interact preferentially with one another, such as close kin and/or coalitionary supporters (e.g. clustering coefficient, community modularity: (Griffin & Nunn, 2012; Kasper & Voelkl, 2009; Sueur, Petit, et al., 2011)). Finally, SNA techniques that combine information from dominance and grooming relationships may be better able to describe the roles of both peripheral and central individuals in group social structure (e.g. degree and eigenvector centrality coefficient: (Sueur, Jacobs, et al., 2011)) (see also Methods and Supplementary Table 1). For these reasons, the most recent comparative studies of nonhuman primate social structure have used SNA to compare various types of societies (Griffin & Nunn, 2012; Kasper & Voelkl, 2009; Pasquaretta et al., 2014; Sueur, Petit, et al., 2011). Here we also use SNA methods to assess interspecific variation in macaque dominance and grooming networks (de Waal & Luttrell, 1989; Thierry, 2007).

A major explanatory framework for the evolution of variation in primate social networks is related to species' ancestry or phylogenetic closeness (Blomberg et al., 2003). According to this framework, aspects of sociality may be expected to show phylogenetic signals, i.e. exhibit greater similarity among more closely related compared to more distantly related species (Blomberg et al., 2003). Ecological adaptation is not ruled out but rather hypothesized to occur minimally, or in response to novel, drastic environmental changes (Chan, 1996; Matsumura, 1999). In the past, proponents of phylogenetic signals have often referred to them as outcomes of phylogenetic constraints or phylogenetic inertia (Blomberg & Garland, 2002). However, more recent theory recognizes that phylogenetic signals may be the observed pattern of trait similarity, rather than one or more evolutionary processes, including Brownian motion or random genetic drift, stabilizing selection, pleiotropy, or low rates of evolution, via which such patterns may arise (reviewed in (Kamilar & Cooper, 2015)). Rather than attempt to distinguish between possible processes or the rates at which they occur, here we simply aim to identify strong and weak phylogenetic signals in order to determine the extent to which social network structure co-varies with macaques' phylogenetic closeness.

Across animal societies, behavioral traits are more labile to evolutionary change in comparison to morphological and/or physiological characteristics (Blomberg et al., 2003). Primates are no exception, with traits like brain size, body mass and canine dimorphism exhibiting stronger phylogenetic signals than those such as social organization and activity budgets (Kamilar & Cooper, 2015). As such, phylogenetic signals for aspects of primate social network traits have been hard to identify. Kasper and Voelkl (2009) established that several aspects of affiliative social networks, including community modularity or the tendency for sub-group formation, mean centrality in the connectedness of individuals, and density of network connections all showed greater variation between closely related than between distantly related species, indicating weak phylogenetic signals and a greater effect of ecological or demographic factors. Similarly, (Pasquaretta et al., 2014) found no effect of phylogenetic signals on the efficiency of information flow through affiliative social networks of primates, including humans. Tests for phylogenetic signals in aspects of sociality within specific primate families and genera have revealed inconsistencies. In the genus *Eulemur*, group size and sex-ratio both strongly correlated with phylogenetic distances (Ossi & Kamilar, 2006). Yet among both baboons (genus: *Papio*) and squirrel monkeys (genus: *Saimiri*), interspecific variation in multiple forms of social organization seem to be strongly linked to ecological factors like food distribution, predation pressure, and intergroup feeding competition (Barton et al., 1996; Boinski, 1999; Henzi & Barrett, 2003).

Nevertheless, among all primate genera, phylogenetic signals in social traits have been most consistently detected within the genus *Macaca*. Macaques constitutes 23 species of Old-World primates, with wide-spread geographic distributions in nature (Abegg & Thierry, 2002; Cords, 2013). Although all species show a predominantly similar social organization, living in multi-male, multi-female social groups in which females are philopatric and males disperse (Thierry, 2007), they show broad inter- and intraspecific variation in several aspects of female social structure (Thierry, 2007). Specifically, traits like post-conflict affiliation, rates of affiliative contact (Thierry et al., 2008), the steepness of dominance hierarchies (Balasubramaniam et al., 2012a), and asymmetry in aggression (Balasubramaniam et al., 2012a; Thierry et al., 2008) all showed phylogenetic signals (Blomberg et al., 2003; Kamilar & Cooper, 2015), whereas grooming kin bias showed a weak signal (Thierry et al., 2008). These finding have led some proponents of phylogenetic explanations to posit that core aspects of macaque social structure may also be structurally linked, co-varying with each other at the species level (Petit et al., 1997; Thierry et al., 2008). Thierry (2007) has characterized this tendency to co-vary by assigning macaque species to positions on a four-grade social style scale that is broadly consistent with phylogenetic lineage splits (Thierry, 2007). At one extreme, 'grade-1' species (e.g. rhesus macaques (*Macaca mulatta*), Japanese macaques (*M. fuscata*)) of the Fascicularis lineage are hypothesized to show 'despotic' social structures, characterized by steep and asymmetric dominance hierarchies, low levels of post-conflict affiliation, and intense affiliative kin-bias. At the other extreme, 'grade-4' species (e.g. Tonkean macaques (*M. tonkeana*), crested macaques (*M. nigra*)) belonging to the Sulawesi lineage are hypothesized as being more 'tolerant' or 'egalitarian', showing shallower dominance hierarchies with more frequent counter-aggression from subordinates towards dominants, high proportions of post-conflict affiliation, and more even distributions of grooming relationships across kin and non-kin (Balasubramaniam et al., 2012a; Berman & Thierry, 2010; de Waal & Luttrell, 1989; Thierry, 2007; Thierry et al., 2008). The systematic variation hypothesis posits that a species that shows a single behavioral trait associated with a particular social style will display all other traits (Castles et al., 1996; Petit et al., 1997). However, this extent of co-variation has not always been found. Rather, most work (but see (Thierry et al., 2008)) thus far has revealed marked differences between species at the extreme ends of the social style scale (grade-1 and grade-4 macaques), but inconsistencies in the positions of macaques in intermediate grades (reviewed in (Balasubramaniam et al., 2012b)). Only one study of this sort has focused on social network traits: (Sueur, Petit, et al., 2011) revealed marked differences across four species of macaques that represented grades 1 and 4 that were consistent with their social style grades. Specifically, grade-1 'despotic' species showed more clustered or modular and less dense affiliative networks in which grooming was more centralized among dominants, i.e. individuals formed sub-groups or communities with preferred partners, and rarely interacted with partners outside these communities, whereas grade-4 tolerant species showed the opposite characteristics. In the present study, we expand on the above findings by (Sueur, Petit, et al., 2011) by assessing phylogenetic signals and co-variation across 10 species of macaques representing all four social style grades, and groups from both captive and free-living conditions. Given the inclusion of free living groups, we also examine whether sociodemographic factors, specifically group size and living condition, influence social network metrics in addition to, or instead of social style or phylogenetic closeness. Broadly, theoretical socioecological models predict that among free-living primates, larger group size, on account of either heightened levels of contest competition for resources (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989) and/or increased temporal constraints (Berman & Thierry, 2010; Dunbar, 1992; Korstjens et al., 2010), may be expected to influence the evolution of more despotic social network structures characterized by steeper, asymmetric dominance hierarchies, and highly centralized, clustered grooming networks. On the other hand, smaller groups may be expected to show greater within-group social tolerance characterized by more reversals in dominance interactions and de-centralized, denser grooming networks. Such effects may also be influenced by the spatial constraints imposed by captive housing that may result in more frequent social interactions among individuals with a potentially wider range of partners (Duboscq et al., 2013; McCowan et al., 2008).

We first ask whether aspects of female dominance and grooming networks (Q1) show strong phylogenetic signals and further, whether grooming networks co-vary with (Q2) dominance networks and/or (Q3) hypothesized social style grades across macaques. Despotic species tend to show steeper dominance hierarchies with more decided, asymmetric dominance outcomes compared to tolerant macaques (Balasubramaniam et al., 2012a; Thierry, 2007). Given this, we predict that macaque species that have more transitive, decided and/or certain dominance relationships will also show despotic grooming networks, including greater tendencies for more high-ranking individuals to occupy more central positions in less dense and more clustered grooming networks, compared to those with less transitive and/or uncertain dominance relationships. Further, we predict that phylogenetic shifts from more despotic (e.g. grade-1) to more tolerant (e.g. grade-4) social styles will be correlated with systematic decreases in the centralization of grooming among dominants, as well as less clustered but denser networks. Finally, we also examine (Q4) the potential impact of sociodemographic factors on networks and patterns of co-variation. In accordance with socioecological models, we examined whether group size was positively associated with both the centralization of grooming among dominants and with clustering of grooming networks, but negatively associated with grooming density. We also tested the potentially confounding effect of living condition on such relationships. Finally, we explored the impact of a third sociodemographic characteristic, female-to-male sex ratio, on such co-variation.

Methods:

We first assembled behavioral and phylogenetic datasets from various sources – published literature, personal data, and personal donations from other researchers (Table 1). Below we describe these data, the computation of social network metrics, and statistical analyses.

Datasets – macaque social behaviors and phylogenetic trees:

To compute dominance network metrics, we assembled a total of 38 behavioral datasets on dyadic aggressive interactions among adult female macaques (individuals ≥ 3.5 - 4 years of age, depending on species-typical ages of maturity) from groups living in captive and free-living (free-ranging and wild) conditions (Table 1). These encompassed 20 populations representing 10 macaque species from all four social style grades. Except for stumptailed macaques (*M. arctoides*) and bonnet macaques (*M. radiata*), we acquired at least two datasets for each species; these were either from different social groups or from the same social group during different long-term study-periods. In the latter case, each study period represented a time period during which group composition or other sociodemographic factors (e.g. group size, age-class and/or sex ratios) were stable. To compute grooming network metrics, we obtained data from 34 (out of the 38) datasets from nine species (Table 1). We chose datasets collected using focal-animal, all-occurrences, and/or scan sampling methods (Altmann, 1974). Given differences in observation times across datasets (Table 1), we computed all grooming metrics from unweighted networks. Out of 38 datasets, the majority (27, or 71%) was from free-living groups of macaques. We found significant differences in group size (ANOVA: $F_{1,\,32} = 6.04, p = 0.02$) and sex ratios (ANOVA: $F_{1,\,32} = 12.07, p < 0.01$) between captive vs. free-living macaques. Hence, we either conducted separate assessments for only free-living groups (Q1), or directly examined the effect of living condition in our analyses (Q2 - Q4).

In order to assess and control for the effects of phylogenetic signals, we extracted and used a Bayesian consensus tree (Supplementary Figure 1) and a tree-block of 10 trees from the online resource for primate phylogeny *10KTrees* (Arnold et al., 2010). All 11 phylogenies showed proportional branch-lengths, and identical topologies that were also consistent with previously constructed macaque topologies using parametric approaches (e.g, (Chatterjee et al., 2009; Tosi et al., 2003)). We therefore report the results of tests performed using the consensus phylogeny, with those from the tree-block submitted as supplementary material (Supplementary Table 3).

SNA – Dominance and Grooming Metrics:

Supplementary Table 1 provides the definitions and details of the dominance and grooming network metrics that we computed. We computed dominance network metrics from winner-loser dominance matrices in which non-diagonal cells contained data on the frequencies of dyadic contact and non-contact aggression from animals in the rows to animals in the columns. Acts of bi-directional or counter-aggression were scored twice, once on either side of the diagonal for each interactant. We computed two metrics – triangle transitivity and dominance certainty (Fujii et al., 2013; Fushing et al., 2011) – that have not been used in previous comparative studies of primate social networks (see Supplementary Table 1 for definitions). These metrics, particularly dominance certainty, enable the detection of patterns of group-specific dominance network architecture that, unlike traditional aspects of dominance structure such as hierarchical steepness (de Vries et al., 2006) or DCI (de Vries, 1998), are based not only on both dyadic interactions but also indirect pathways. They therefore capture more global aspects of a dominance hierarchy that steepness or DCI are not likely to capture. They are also less susceptible to error due to the numbers of non-interacting dyads present in the dataset than steepness (Balasubramaniam et al., 2012a). Rather, dominance certainty specifically incorporates the presence of non-interacting dyads in its calculation (Supplementary Table 1) by weighting both the total number of direct wins by an individual 'A' against an individual 'D' (A→D), as well as imputed wins incurred via the likelihood of traversing longer paths (e.g. A→B→C→D) through the dominance network. In doing so, the certainty measure characterizes the network-level flow-structure of dominance information, thereby accounting for hidden elements in dominance structure such as avoidance between individuals (Fujii et al., 2013; Fushing et al., 2011) (Supplementary Table 1).

We constructed grooming networks (Figure 1) and calculated network metrics using the *statnet*, *sna and igraph* R packages (Csardi & Nepusz, 2006; Handcock et al., 2006). We calculated network centrality metrics from *unweighted, directed* networks (Farine & Whitehead, 2015; Sueur, Jacobs, et al., 2011), i.e. where individuals represented by *nodes* were connected by *edges* that represent the directions of interactions between initiators and recipients (Figure 1). Unweighted networks were used to account for the potential impact of differences in observation times across comparative datasets (Griffin & Nunn, 2012; Kasper & Voelkl, 2009). Specifically, we calculated standardized *degree centrality* (the number of an individual's direct grooming connections) and *eigenvector centrality* (the number of an individuals' direct *and* indirect grooming connections, indicating its access to *social capital or support* (Farine & Whitehead, 2015) for each individual in a dataset. Reviews of the utility of animal social networks agree that these metrics are among the most biologically meaningful of the centrality metrics (Farine & Whitehead, 2015; McCowan et al., 2008; Sueur, Jacobs, et al., 2011). Specifically, they are more indicative of individuals' social status than measures of *betweenness* and *closeness* among taxa such as primates that have more complete rather than sparse social network graphs (Kasper & Voelkl, 2009). From individual scores, we calculated group-level centrality distributions and coefficients that also take into consideration the dominance status of individuals (as in (Sueur, Petit, et al., 2011); see Supplementary Table 1 for definitions). We also calculated two other group-level grooming network metrics – density and clustering coefficient (a correlate of group substructuring or modularity: (VanderWaal et al., 2013)) – from *unweighted* but *undirected* networks (Supplementary Table 1 for details and definitions). Supplementary Table 2 shows the values of the various network metrics computed for each dataset.

Statistical Analyses:

To examine evidence for phylogenetic signals (Q1) in dominance and grooming network metrics at the species level, we used the Phytools R package (Revell, 2012). For each metric, we computed Blomberg's Kappa (K) coefficient (Blomberg et al., 2003) as the ratio between the Mean-Squared Errors (or MSE) of the raw, species-means of behavioral metrics over the MSEs of metrics that have been phylogenetically transformed using tree-specific branch-length information. The K coefficient therefore indicates the strength of the phylogenetic signal and further, is scaled by a similar ratio of MSEs calculated assuming a Brownian motion model of evolution (Blomberg et al., 2003). We considered $K > 1$ from the randomization test as indicative of a "strong" signal that exceeds the amount of signal expected under a Brownian motion model of evolution (Blomberg et al., 2003). Values of $0.8 < K < 1$ were considered to be indicative of a "moderate" signal, while values that are $<< 0.8$ indicate a weak signal, i.e. greater plasticity on account of adaptation to current conditions in a trait (Blomberg et al., 2003). These assignments were based on previous comparative studies of nonhuman primate behavioral traits that also examined phylogenetic signals among smaller numbers of species (Balasubramaniam et al., 2012a; Thierry et al., 2008). We avoided splitting terminal species' nodes into multiple nodes to represent groups within species. Although doing so offers the potential advantage of increased statistical power, it would also artificially inflate phylogenetic signals (Blomberg et al., 2003; Thierry et al., 2008). Blomberg's K generates identical results to Pagel's Lambda (λ : (Pagel, 1997, 1999)), an alternate indicator of phylogenetic signal. However, since K is more useful in informing about trait variation relative to Brownian evolution (Kamilar & Cooper, 2015), we chose to estimate and report this statistic. In addition, we conducted randomization tests to compare the MSE of phylogenetically transformed data to those computed from 1000 randomized datasets generated by scattering the behavioral scores randomly on a phylogeny. In addition to handling the intrinsic dependency of the data, such tests indicate whether any observed phylogenetic signal is greater than that expected by chance. We recognize that for sample sizes of 7-10 species, randomization tests yield a low statistical power of 20-35% (Blomberg et al., 2003). They have nonetheless been used in estimations of phylogenetic signals in previous studies with similarly small sample sizes (Balasubramaniam et al., 2012a; Thierry et al., 2008).

To examine whether grooming network metrics were linked to dominance metrics (Q2) or by social style scale (Q3) across species, and to assess the potential impact of sociodemographic factors and living-condition (Q4) on such co-variations, we constructed General Linear Mixed-effects Models (GLMMs: (Bates et al., 2016)). We implemented an Information-Theoretical approach (Burnham et al., 2011; Grueber et al., 2011) using the *lme4* and *MuMIn* R packages. Given the relatively small number of species, we were not able to account for interspecies phylogenetic distances via

Phylogenetic Least Squares regression (PGLS: (Nunn, 2011)). Instead, we indirectly tested for the effects of phylogeny by assessing the effect of social style, since social style and phylogeny have been shown to be strongly correlated across macaques (Thierry et al., 2000). We first generated 6 global models, one for each grooming network metric treated as the outcome variable. Centralization indices followed a Normal or Gaussian distribution (e.g. degree coefficient: Shapiro-Wilk test: $w = 0.96, p = 0.25$; eigenvector distribution: $w = 0.98, p = 0.64$), but grooming density and clustering coefficient were log-transformed to fit a Gaussian distribution (log(clustering coefficient): $w = 0.95, p = 0.16$). As recommended by I-T approaches (Burnham et al., 2011; Grueber et al., 2011), our global models were constructed by the inclusion of just those co-variates that catered to testing our specific predictions (Q2-Q4), with species set as a random effect to avoid pseudoreplication issues. They were defined as:

Grooming metric (e.g. log(density)) ~ transitivity + dominance certainty + factor(social style) + group size + factor(living condition) + group size*living condition + sex ratio + (1|Species)

We next used the *arm* package in R to z standardize (μ = 0, SD = 1) the predictors in the global model, which is essential for interpreting parameter estimates after model averaging (Gelman et al., 2009). We next used the automated 'dredge' function in the *MuMIn* R package to generate a 'complete' set of 80 models from multiple possible combinations of predictors from the global models (Grueber et al., 2011) (Supplementary Tables 4-9). This included a 'null' or an intercept-only model with just species as a random effect for the sake of comparison. For models with multiple predictors, we performed collinearity diagnostics by (a) checking correlation matrices and (b) assessing variance inflation using the. Models with multiple predictors met diagnostic criteria that ruled out multicollinearity issues; they were neither strongly correlated to each other (r < 0.8 for all pairs) nor had high generalized variance inflation factors (GVIF < 4) (*car* package in R: (Fox & Weisberg, 2011)). From each full model set, we identified candidate models that included only models whose dAICc scores were < 4 from the model with the lowest AICc score (Burnham et al., 2011) (models in bold font in Supplementary Tables 4-9). We then determined parameter estimates by model-averaging each set of candidate models using the zero-averaging approach (Burnham & Anderson, 2002; Grueber et al., 2011). This approach weakens the effect sizes of predictors that only appear in a minority of models within the candidate set. It is therefore more useful (than the natural averaging method) in cases where the aim is to determine which (among multiple) factors have the strongest effect on a response variable (Grueber et al., 2011; Nakagawa & Freckleton, 2010). For all parameter interpretations, we set the alpha level at 0.05.

Results:

(Q1) Tests for phylogenetic signals:

Mean species-level scores of both dominance network metrics -- transitivity and dominance certainty -- showed moderate phylogenetic signals (Table 2). When we repeated the analyses including only free-living groups (27 datasets across 7 species), the results showed a strong phylogenetic signal for dominance metrics (K statistics >>1: Table 2). Grooming metrics appeared to show weak phylogenetic signals, although some metrics (eigenvector distribution, density, clustering coefficient) showed moderate signals among free-living groups only (Table 2). Given the relatively small number of species, our tests of phylogenetic signals lacked statistical power (~ 20-35%). Yet, results from the randomization significance tests were mostly consistent with our estimations of the strength of the signals from the K statistic (Table 2). Moreover, they were also robust to phylogenetic branch length variation, with results from the consensus phylogeny being largely consistent with those across a tree ‘block’ of 10 phylogenetic trees extracted from the *10KTrees* website (Supplementary Table 2).

(Q2-4) The effect of dominance metrics, social style, and sociodemographic factors on grooming metrics:

Table 3 shows the zero-averaged coefficients and parameter estimates from candidate GLMM sets (dAICc < 4 from the model with the lowest AICc score) shortlisted from the complete model sets for grooming density and clustering coefficient. Our criterion shortlisted 9 models for groom density, and 16 for groom clustering coefficient, and did not include the ‘null’ or ‘random effect only’ model which had a dAICc > 7 or higher from the candidate sets (Supplementary Table 8, 9). Model averaged coefficients revealed that group size strongly influenced both grooming density and clustering coefficient in the predicted directions. Specifically, model-averaged coefficients from the shortlisted candidate GLMMs for density and clustering coefficients revealed that larger groups showed less dense, but highly clustered or sub-structured grooming networks in comparison with smaller groups (Table 3A, 3B; Figure 2). Further to the highest effect sizes, group size was also the variable with the highest relative importance in both candidate sets, specifically 100% for groom density and 91% for clustering coefficient (Table 3A, 3B). Living condition was the second most important predictor (50% for both metrics), but its effect was not significant. Neither were the effects of female to male sex ratio, or the interaction between group size and living condition. Finally, neither dominance metrics nor social style scale predicted grooming density or clustering coefficient (Table 3A, 3B). In fact, models including social style as a predictor failed to make the candidate set shortlist for groom density.

In contrast to groom density and clustering coefficient, candidate model selection for the complete model sets for grooming centrality indices failed to eliminate the ‘null’ or ‘random effect only’ model (Supplementary Tables 4-7). Zero-based model averaging revealed that none of the predictors had a strong effect on these indices (Supplementary Table 10-13).

Discussion:

In group-living animals, SNA has provided novel approaches to assess variation in aspects of social structure. They improve on traditional approaches based on dyadic interactions alone by addressing higher-order social structure and also by accounting for variation in the extents to which individuals choose to interact, remain peripheral, or engage in social avoidance (Sueur, Jacobs, et al., 2011). Here we examined the impact of phylogenetic relatedness, specifically phylogenetic signals and trait co-variation, as well as sociodemographic factors like group size and living condition on interspecific variation in dominance and grooming social network structure across macaques. We found that while dominance networks showed strong phylogenetic signals, grooming networks showed weak signals and further, were not strongly co-variant with social style or with dominance metrics. Rather, some aspects of grooming networks – density and clustering coefficient – were strongly influenced by group size independent of their current living condition. Below we discuss our findings in depth, and offer avenues for future comparative assessments of primate social network structure.

Previous studies among macaques have established strong phylogenetic signals in some aspects of social structure (e.g. dominance steepness and counter-aggression: (Balasubramaniam et al., 2012a)), but moderate-to-weak signals in others (e.g. kin-bias: (Thierry et al., 2008)). Consistent with this pattern, we found moderate to strong phylogenetic signals for aspects of female dominance networks, but weak signals for grooming networks. Specifically, both transitivity and dominance certainty exhibited degrees of signal that are close to what is expected under a Brownian motion model of evolution (Blomberg et al., 2003). This finding extends earlier findings of strong phylogenetic signals on group-level aspects of dominance structure based on dyadic interactions (e.g. hierarchical steepness, counter-aggression: (Balasubramaniam et al., 2012a)), to broader patterns of triadic motifs (transitivity), and indirect connections that reflect the flow structure of dominance pathways between both interacting and non-interacting individuals (dominance certainty: (Fujii et al., 2013; Fushing et al., 2011); see Methods).

Phylogenetic signals were even stronger when we analyzed only free-living groups of macaques, despite a reduction in sample size from 10 to 7 species (Blomberg et al., 2003). This may be due to the differences in living conditions between groups of closely related species. In captivity, spatial constraints and/or management strategies may force animals to interact that might avoid one another after one or two decided outcomes (Duboscq et al., 2013; McCowan et al., 2008). This may result in greater than expected degrees of reversals in agonistic success and hence, greater uncertainty in dominance relationships. Unfortunately, limited datasets prevented an analysis of phylogenetic signals among captive groups alone (11 out of 38 datasets: 5 species). Nevertheless, the detection of strong phylogenetic signals among free-living macaques (27 out of 38 datasets: 7 species) builds on previous studies that have either included both captive and free living groups (Balasubramaniam et al., 2012a) or only captive groups (Sueur, Petit, et al., 2011; Thierry et al., 2008). It is unlikely that the observed signals are ‘artifacts’ of correlations between phylogeny and current conditions, since previous comparative studies across primates have shown a general lack of correspondence between phylogeny and socioecology (Koenig et al., 2013; Ménard, 2004; Okamoto & Matsumura, 2002). Further, the signals were detected despite the fact that a fraction of the free-living groups in our dataset were exposed to food provisioning by humans (Table 1), although predation pressure, another socioecological factor (van Schaik, 1989), was either very low or absent. This suggests that phylogeny predicts a major component of the variance in dominance structure among free-living macaques, in spite of being exposed to varying socioecological factors such as resource distribution (Sterck et al., 1997; van Schaik, 1989). Nevertheless, our findings don’t entirely rule out an adaptive component. For instance, the concept of social reaction norms proposes that aspects of social structure may change dynamically by responding to socioecological and environmental factors, but within the limits posed by a species- or lineage-typical range of responses that may be linked to phylogenetic closeness (Berman & Thierry, 2010). Moreover, phylogenetic signals, rather than being linked to ancestral genetic splits, may be outcomes of adaptations by ancestral species dispersing into historically similar environments (Kamilar & Cooper, 2015). We suggest that future assessments of the bases of phylogenetic signals in social network traits focus on phylogeographic approaches (Lemey et al., 2009; Ree & Smith, 2008). A comparison of the reconstructed social networks and geographic ranges of ancestral primate taxa may provide better insights into whether phylogenetic signals in primate social networks are indeed ‘artifacts’ of adaptive responses in their evolutionary past.

In contrast to dominance metrics, grooming networks showed weak phylogenetic signals and further, did not co-vary with dominance metrics. A possible explanation is that co-variation between social network traits isn’t always linear or systematic (but see Thierry et al.’s (2008) findings on co-variation between traits associated with conciliatory tendencies across macaques). Further, it may be discernible at levels of organization other than species, for instance across lineages (Thierry, 2000). Yet the lack of a strong effect of species-typical social style on grooming networks, consistent with the detection of weak phylogenetic signals since social style and phylogeny are correlated (Thierry et al., 2000), may be seen as evidence to refute this argument. A more likely explanation is that grooming metrics may come under the influence of current socioecological and/or sociodemographic factors.

Among all the primate genera, macaques are presently unique in the extent to which interspecific variation in social traits is consistent with phylogeny and social style (Balasubramaniam et al., 2012a; Sueur, Petit, et al., 2011; Thierry et al., 2008; Thierry et al., 2000). Yet we found that group size, and not dominance metrics or species-typical social styles, strongly influenced aspects of grooming networks. Specifically, larger groups of macaques showed more clustered but less dense grooming networks than smaller groups. It is possible that the effect of group size could be an artifact of differences in living condition, since captive groups were significantly smaller than free-living groups (see Methods). Yet grooming metrics were neither strongly influenced by living condition, nor by an interaction between group size and living condition (Table

3A, 3B). This suggests that the effect of group size on grooming metrics may more likely have socioecological underpinnings. Specifically, one school of thought is that living in larger groups and/or environments where resources are clumped or seasonal heightens levels of within-group contest competition (or WGC) for resources (Koenig et al., 2013; Sterck et al., 1997; van Schaik, 1989). This may lead to despotic, nepotistic primate societies characterized by both steep and transitive dominance structure (Majolo et al., 2009), and more modular, sparsely connected grooming community structures (Griffin & Nunn, 2012). In comparison, smaller groups may show weaker WGC and the opposite characteristics that are indicative of greater social tolerance. An alternative perspective is that individuals in large groups may also face spatial or time constraints on their abilities to interact consistently with all other group members (Berman & Thierry, 2010; Dunbar, 1992; Korstjens et al., 2010). This may in turn result in modular or clustered but sparser social networks in larger groups, in which individuals may come into contact with each other less frequently (Griffin & Nunn, 2012). Given the lack of a clear association between group size and dominance networks in our dataset (Pearson's correlation: Group size vs. transitivity: $n = 38, r = -0.08, p = 0.61$; group size vs. dominance certainty: $n = 38, r = 0.02, p = 0.88$), our findings point to a spatiotemporal rather than a resource-competition based explanation. Yet final conclusions await the expansion of our dataset to include additional groups and species, and comparable operational measures of resource distribution (see below).

Unlike grooming density and clustering coefficient, grooming centralization indices were not influenced by dominance metrics, social style, or sociodemographic factors. This lack of concordance could be because of how these indices were computed.

For instance, the exclusion of males from our grooming networks may have masked skew in grooming centrality towards dominants. In despotic macaques, high-ranking males may be among the most attractive grooming partners for females who may gain benefits such as access to social support and/or resources (Schino, 2001; Silk et al., 2003; Sueur, Petit, et al., 2011). To ensure uniformity across datasets, we computed centrality metrics from unweighted relationships based on all female-female grooming connections. It is possible that rather than their overall connectedness, female dominance status could be related to their degree and/or eigenvector centrality based on *specific types* of grooming connections; for instance grooming connections with non-kin or that are directed up the hierarchy may provide access to rank-related benefits such as resource tolerance and support in conflicts, and/or reciprocally in the short or long-term (reviewed in (Henzi & Barrett, 1999)). Should comparative data be available, such assessments may generate centralization indices that better reflect affiliative social network structure among female primates.

Our findings should lead naturally to future work that assesses the influence of additional socioecological factors on grooming network structure. Yet such assessments may prove complicated. For instance, we currently lack a consistent operational measure of resource abundance and distribution that may be used in comparative contexts across a wide range of taxa (Clutton-Brock & Janson, 2012). Another challenge is assessing the effects of infectious disease risk on social networks. For instance, increased parasite infection risk may select for individuals to engage fewer partners and hence, lead to the evolution of more clustered or modular networks in larger groups (Griffin & Nunn, 2012; Nunn, 2012; Nunn et al., 2015). At the same time, possessing more connections/ social partners also seems to have clearly-documented *benefits* of socially buffering individuals against infectious risk in some societies via stress mitigation and/or the enhancement of immune function (e.g. free-living Barbary macaques: (Young et al., 2014); captive rhesus macaques: (Balasubramaniam et al., 2016)). The spatial distribution of females may also influence male reproductive tactics, i.e. the extent to which males show reproductive skew by being able to monopolize mating opportunities which may in turn influence female social networks (Schülke & Ostner, 2013). Stemming from this consideration, the 'paternal relatedness hypothesis' posits that in species where male reproductive skew is high, the emergence of numerous kinship ties both from maternal and paternal sides will generate denser, less clustered, and decentralized social networks indicative of greater social tolerance, in comparison to species where male reproductive skew is low (Schülke & Ostner, 2008, 2013). Across eight species of macaques, (Schülke & Ostner, 2008) conclude that male reproductive skew co-varies with species-typical social style grade. More definitive conclusions await the ability to draw interspecies links between reproductive skew and female social networks, and indeed male-male social relationships. Finally, comparative studies on intraspecific variation in primate sociality are fewer in comparison to those on interspecific variation (Clutton-Brock & Janson, 2012). Thus, future work should attempt to extend the validity of our findings by examining the impact of both epigenetic and socioecological factors on intraspecific variation in dominance and affiliative social network structure.

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Table 1: Macaque datasets analyzed in the study

Group ID	Species (*Macaca*)	Social Style	Study Location	Source or Citation	Group Size	Adult Females	Living Condition[b]
1	*fuscata*[a]	1	Yakushima, Japan	Ventura et al. (2006)	25	8	Free-living
2	*fuscata*[a]	1	Yakushima, Japan	Ventura et al. (2006)	50	21	Free-living
3	*fuscata*	1	Koshima, Japan	Duboscq et al. (2016); Romano et al. (2016)	45	21	Free-living
4	*fuscata*	1	Koshima, Japan	Duboscq et al. (2016); Romano et al. (2016)	45	20	Free-living
5	*fuscata*	1	Koshima, Japan	Duboscq et al. (2016); Romano et al. (2016)	45	20	Free-living
6	*fuscata*	1	Rome Zoo, Italy	Schino et al. (2007)	57	23	Captive
7	*fuscata*	1	Rome Zoo, Italy	Schino et al. (2007)	57	23	Captive
8	*fuscata*	1	Paris Zoo, France	Petit et al. (1997)	22-24	9	Captive
9	*mulatta*	1	University of Cambridge, Madingley, UK	Desportes & Thierry (unpub)	16	7	Captive
10	*mulatta*	1	Cayo Santiago, Puerto Rico	Balasubramaniam et al. (2014)	135	30	Free-living [c]
11	*mulatta*	1	Cayo Santiago, Puerto Rico	Balasubramaniam et al. (2014)	33	10	Free-living [c]
12	*mulatta*[a]	1	Yerkes Primate Center, USA	de Waal & Luttrell (1989)	51-62	13	Captive
13	*assamensis*	2	Tukreshwari Temple, Assam, India	Cooper & Bernstein (2008)	28	14	Free-living [c]
14	*assamensis*	2	Tham Pla Temple, Thailand	Ogawa (*unpub*)	47	14	Free-living [c]
15	*assamensis*	2	Shivapuri Nagarjun National Park, Nepal	Ogawa & Koirala (*unpub*)	25	8	Free-living
16	*fascicularis*	2	Primatological Station, Kassel University, Germany	Butovskaya et al. (1995)	9	7	Captive
17	*fascicularis*	2	Primatological Station, Kassel University, Germany	Butovskaya et al. (1995)	13	9	Captive
18	*thibetana*	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	39	8	Free-living [c]
19	*thibetana*	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	42	9	Free-living [c]
20	*thibetana*	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	42	9	Free-living [c]
21	*thibetana*	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	52	10	Free-living [c]
22	*thibetana*	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	49	10	Free-living [c]

23	*thibetana*	2	Mt. Huangshan, China	Balasubramaniam et al. (2011)	37	10	Free-living [c]
24	*arctoides*[a]	3	Yerkes Primate Center, USA	de Waal & Luttrell (1989)	14	12	Captive
25	*radiata*	3	Mysore, India	Cooper et al. (2007)	41-49	13	Free-living [c]
26	*sylvanus*	3	Middle Atlas Mountains, Morocco	McFarland & Majolo (2011)	19	8	Free-living
27	*sylvanus*	3	Middle Atlas Mountains, Morocco	McFarland & Majolo (2011)	29	10	Free-living
28	*sylvanus*	3	Middle Atlas Mountains, Morocco	Molesti & Majolo (2013)	18	7	Free-living
29	*sylvanus*	3	Rocamadour, France	Sosa (2014)	55	24	Free-living [c]
30	*sylvanus*	3	Rocamadour, France	Sosa (2014)	55	24	Free-living [c]
31	*sylvanus*	3	Rocamadour, France	Sosa (2014)	55	24	Free-living [c]
32	*nigra*	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	50	18	Free-living
33	*nigra*	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	21	Free-living
34	*nigra*	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	21	Free-living
35	*nigra*	4	Tangkoko Reserve, Indonesia	Duboscq et al. (2013)	80	24	Free-living
36	*tonkeana*	4	Primatology Center, Strasbourg, France	Thierry (1985); Demaria & Thierry (2001)	16	9	Captive
37	*tonkeana*	4	Orangerie Zoo, Strasbourg, France	De Marco et al. (2010)	21	7	Captive
38	*tonkeana*	4	Primatology Center, Strasbourg, France	Thierry (1985); Demaria & Thierry (2001)	29	11	Captive

[a] Groups excluded from computation and analyses of grooming network metrics on account of either (a) non-availability of data, or (b) too few (< 7) individuals

[b] Criteria for designation of group's living-condition: Free-living: within their natural geographic distribution, or an unfenced area outside of their natural geographic distribution; Captive: housed within a fenced enclosure

[c] Free-living groups that were regularly food-provisioned by humans

Codes for Social Style (Thierry, 2007): (1) Highly Despotic, (2) Mildly Despotic, (3) Mildly Tolerant, (4) Highly Tolerant

Table 2: Results of tests for phylogenetic signals among macaque dominance and grooming social Network metrics. K: Blomberg's Kappa coefficient; P: significance from Randomization tests (Blomberg et al. 2003)

Behavioral Metric	All Datasets (n = 10)		Only Datasets of Free-living Groups (n = 7)	
	K	P	K	P
Dominance Metrics				
Transitivity	0.892	0.081	**1.704**	0.022*
Dominance Certainty	0.893	0.078	**1.634**	0.023*
Grooming Network Metrics				
Degree Coefficient	0.689	0.200	0.625	0.283
Eigenvector Coefficient	0.654	0.205	0.722	0.238
Degree Distribution	0.367	0.673	0.396	0.523
Eigenvector Distribution	0.364	0.716	0.837	0.111
Density	0.691	0.183	0.846	0.120
Clustering Coefficient	0.406	0.567	0.836	0.165
Modularity	0.448	0.533	0.605	0.323

Bold font: K values (> 1) indicate strong phylogenetic signals
* $P < 0.05$; (*) $0.05 < P < 0.1$
Phylogenetic tree used was the Bayesian MCMC consensus tree from the 10ktrees website (Arnold et al. 2010)

Table 3: Summary of zero-averaged coefficients of the predictors from the candidate models (dAICc < 4 from the model with the lowest AICc score) for (A) groom density and (B) groom clustering coefficient.

(A)

	B [a]	Adj SE	z	Pr (>|z|)	Importance
(Intercept)	0.03	0.18	0.16	0.87	
Group Size	-0.63	0.16	3.84	<0.01**	1
Living Condition (Captive vs Free-living)	-0.32	0.36	0.87	0.38	0.55
Dominance Certainty	0.16	0.27	0.57	0.57	0.3
Sex Ratio	-0.02	0.10	0.21	0.84	0.13
Living Condition* Group Size	0.01	0.10	0.07	0.95	0.05
Transitivity	0.00	0.04	0.08	0.93	0.04

(B)

	B	Adj SE	z	Pr (>|z|)	Importance
(Intercept)	-1.67	0.27	6.12	<2e-16***	
Group Size	0.62	0.32	1.94	0.05*	0.91
Living Condition (Captive vs Free living)	0.40	0.54	0.73	0.46	0.5
Social Style (Grade 1 vs Grade 2)	0.21	0.40	0.54	0.59	0.36
Social Style (Grade 1 vs Grade 3)	0.14	0.41	0.33	0.74	
Social Style (Grade 1 vs Grade 4)	-0.35	0.60	0.59	0.55	
Dominance Certainty	-0.22	0.44	0.51	0.61	0.3
Living Condition* Group Size	-0.02	0.20	0.10	0.92	0.06
Sex Ratio	0.00	0.13	0.00	1.00	0.1
Transitivity	-0.01	0.07	0.08	0.94	0.06

[a] Effect sizes are standardized, comparable values (Gelman et al., 2009)

* $p \leq 0.05$

** $p < 0.01$

Data are based on 34 groups representing 9 species of macaques

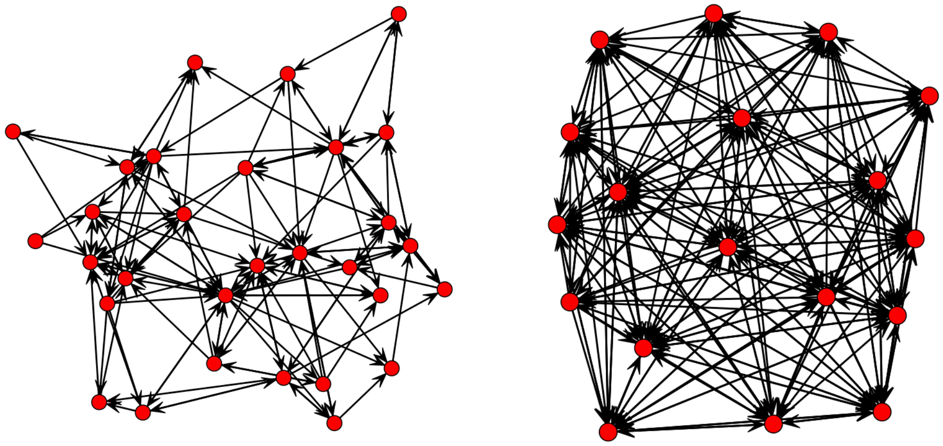


Figure 1: Unweighted grooming social networks from a (A) rhesus macaque (*M. mulatta*) (Balasubramaniam et al. 2014; n = 29 individuals), and a (B) Sulawesi crested macaque (*M. nigra*) (Duboscq et al. 2013; n = 19 individuals) group. Circles represent individual adult females, and lines connecting them represent unweighted edges of grooming relationships between females

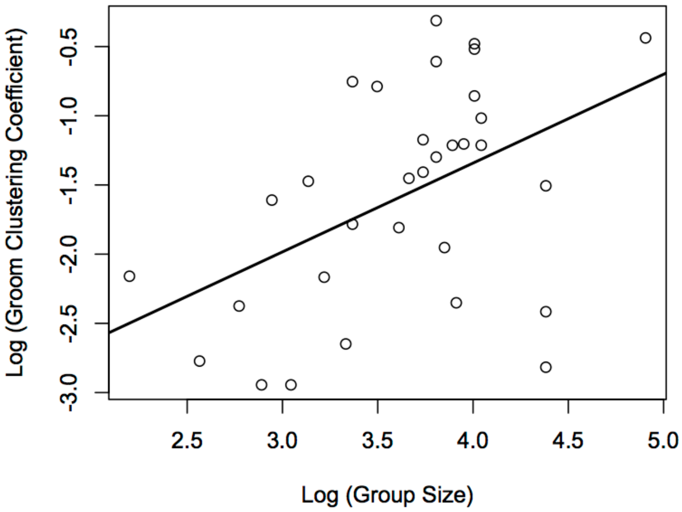
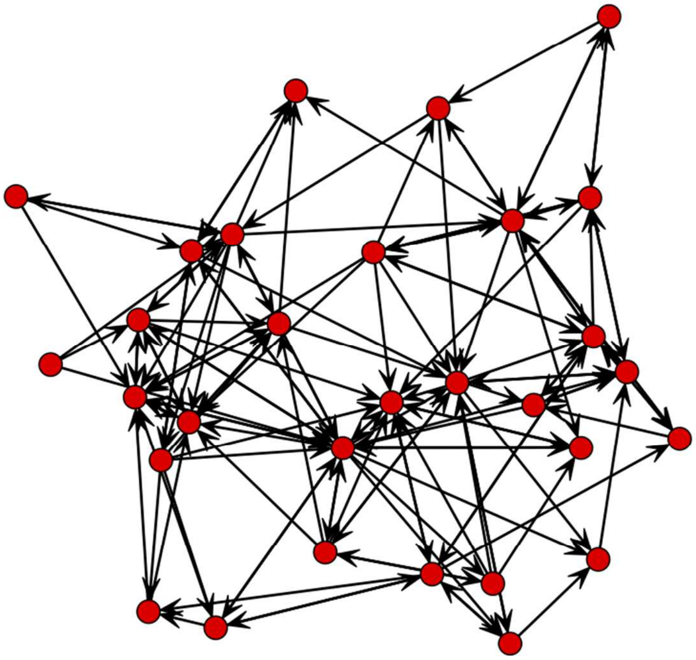


Figure 2: Relationship between group size and grooming clustering coefficient across 34 macaque datasets representing 9 species

- We examined the evolutionary bases for variation in macaque social networks
- Dominance networks showed phylogenetic signals, but grooming networks were linked to group size
- Social networks may be influenced by both ancestry and socioecology



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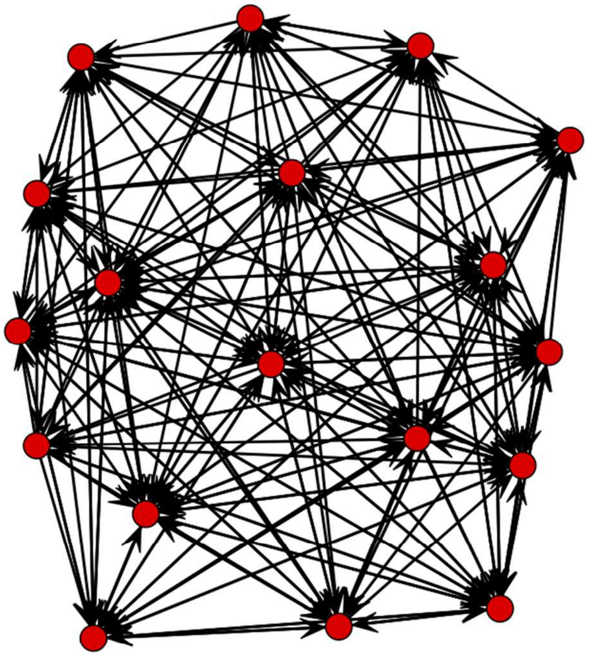

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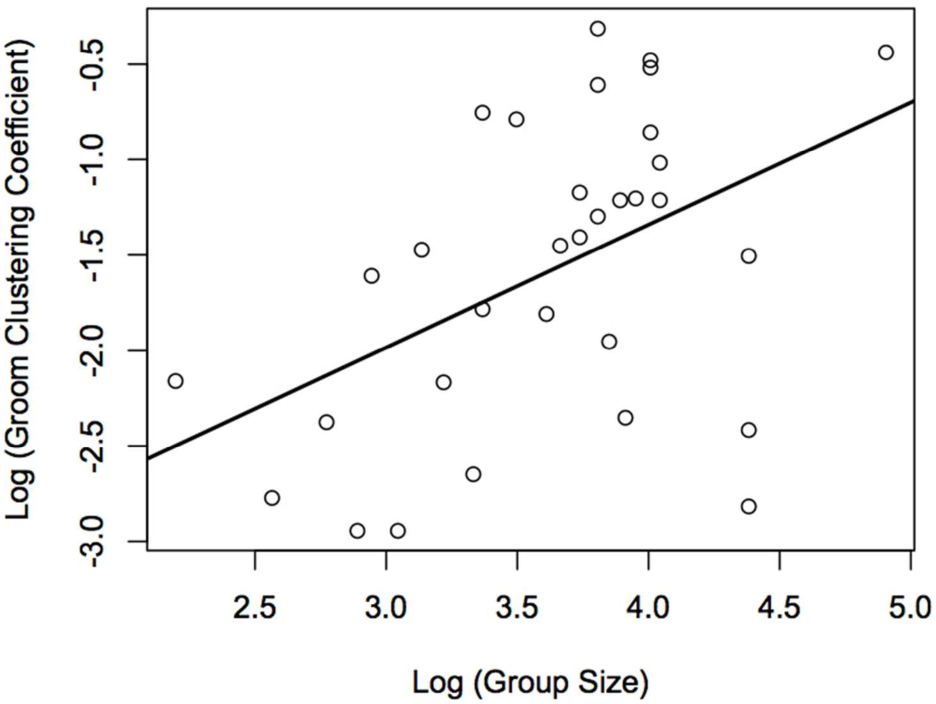

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