Ageing in a collective: The impact of ageing individuals on social network structure

Erin R. Siracusa[a*], André S. Pereira[a,b], Josefine Bohr Brask[c], Josué E. Negron-Del Valle[d], Daniel Phillips[d], Cayo Biobank Research Unit, Michael L. Platt[e,f,g], James P. Higham[h], Noah Snyder-Mackler[d,i,j], Lauren J. N. Brent[a]

Affiliations:
[a]School of Psychology, Centre for Research in Animal Behaviour, University of Exeter, Exeter, UK
[b]Research Centre for Anthropology and Health, Department of Life Sciences, University of Coimbra, Portugal
[c]Department of Applied Mathematics and Computer Science, Technical University of Denmark, Kongens Lyngby, Denmark
[d]Center for Evolution and Medicine, Arizona State University, Arizona, USA
[e]Department of Neuroscience, University of Pennsylvania, PA, USA
[f]Department of Psychology, University of Pennsylvania, PA, USA
[g]Department of Marketing, University of Pennsylvania, PA, USA
[h]Department of Anthropology, New York University, New York, USA
[i]School of Life Sciences, Arizona State University, Arizona, USA
[j]School for Human Evolution and Social Change, Arizona State University, Arizona, USA

*corresponding author; email: erinsiracusa@gmail.com

Abstract

Ageing affects many phenotypic traits, but its consequences for social behaviour have only recently become apparent. Social networks emerge from associations between individuals. The changes in sociality that occur as individuals get older are thus likely to impact network structure, yet this remains unstudied. Here we use empirical data from free-ranging rhesus macaques and an agent-based model to test two things: (1) how age-based changes in social behaviour influence an individual's level of indirect connectedness in their network, and (2) how social ageing feeds up to affect overall network structure. Our empirical analyses revealed that female macaques became less indirectly connected as they aged for some, but not all measures examined, suggesting that ageing animals can remain well integrated in some social contexts.

Our agent-based model showed that aged-based changes in social behaviour can scale up to the network level. Networks with a higher proportion of old individuals were less connected and less cohesive. We did not find similar effects of age distribution on the structure of empirical networks, which may reflect limited age variation in our data. Overall, our results suggest a potentially important and underappreciated role of age in the structure and function of animal collectives.

Introduction

The costs and benefits of an animal's behaviour toward members of their collectives can shape lifespans, life history evolution, and the pace of senescence. For example, the support that cooperative breeding species receive from non-breeding helpers may lead to longer lifespans than those of related solitary species [1]. The transfer of enhanced ecological knowledge to close relatives during collective foraging may have contributed to the evolution of reproductive senescence and prolonged post-reproductive lifespan (i.e., menopause) in female killer whales [2–4]. Differentiated relationships formed between groupmates have also been linked to enhanced longevity in a range of group-living taxa [5]. It is therefore clear that living in collectives can alter the adult ageing process. However, an important question is whether ageing, in turn, influences the behaviour of adults in collectives, and ultimately the structure of collectives themselves.

Growing evidence suggests that older adults differ in their social behaviours from young ones [6–11]. One pattern that seems to be emerging across taxa is that older adults interact with fewer individuals than do younger adults, concentrating social relationships on close associates and kin [6,12–15]. Given that social networks are an emergent feature of association rules between individuals [16], shifts in patterns of social behaviour with age could also affect high-order network structure. Age-based changes in social behaviour could therefore scale up to alter an

individual's connections to the partners of their social partners (their indirect connectedness [17]) as well as the overall structure ("topology") of the social network, both of which can have consequences for disease transmission [18–23], information transfer [24–26], the cohesive movement of groups [27,28], and many other eco-evolutionary dynamics [29,30]. Yet little attention has been given to understanding the impact of social ageing for the polyadic social world or the structure of the collective.

Recent work has offered some glimpses into how measures of indirect connectedness can differ between young and old adults. In some species, older adults have measures of indirect connectedness that suggest they have partners who are themselves not well connected [9,31], (but see [32,33]), and that they are less effective at reaching disparate nodes in the network compared to younger adults [32–34]. In contrast, older adults are more strongly embedded in cliques or clusters in their networks compared to younger adults in some species [9], but not in others [31,33]. However, most research to date has compared differences in measures of indirect connectedness among adults of different age classes (e.g., old versus young), but has lacked the longitudinal data required to quantify how the social positioning of individuals changes across their lifetimes. Such longitudinal analyses have the potential to reveal important patterns that might otherwise be masked by differences between individuals or cohorts [35]. Tracking within-individual changes in measures of indirect connectedness is essential for more firmly placing changes in sociality across the lifespan within the larger ageing phenotype and therefore understanding the causes and consequences of these patterns of social senescence [36].

Populations composed of a greater proportion of older (or younger) adults may also be structured in meaningfully different ways, and this could affect important processes such as communication and cooperation. For example, the loss of old individuals through age-related

disease or trophy hunting can disrupt intergenerational flow of accumulated social and ecological knowledge, impeding collective movement and the ability to locate critical resources [4,37–40]. The age structure of a group can also regulate the behaviour of younger individuals [41,42], influencing aggression rates and social cohesion [43]. The impact of diminished cohorts of younger individuals on higher-order network structure is less well understood, but likely to have repercussions for network connectivity and cohesiveness given that younger adults are more socially active in many populations [8,10,12–14]. Despite the established ecological and evolutionary importance of network structure [29,30] the underlying drivers of variation in network topology remain understudied [44–47]. Ageing, as an important process underlying patterns of individual-level variation in sociality, might therefore provide a window into how simple processes can generate complex network structures [48,49].

Using both empirical data and a theoretical model, we explore how social ageing of individuals relates to measures of indirect connectedness and overall network structure in a group-living primate, the rhesus macaque (*Macaca mulatta*), which is an emerging model in social ageing research [36,50]. Rhesus macaques are highly social cercopithecine primates that live in matrilineal kin-groups and exhibit clearly differentiated social relationships with kin-biased affiliation [51–53]. Patterns of social interactions and social attention vary from adulthood into old age [6,32,54]. Critically, as female rhesus macaques grow older, they reduce the size of their social networks, and focus their social effort on a few important partners including close kin [6]. Despite this, females do not reduce the rate at which they engage in social interactions as they age, indicating that although their ego-networks get smaller, older females continue to invest the same amount of time into fewer relationships [6].

Here, we set out to test if age-based social changes relate to measures of an individual's level of indirect connectedness [17,55], and if they scale up to influence network structure as a whole. Individual-level social network metrics, including measures of direct associations and indirect connectedness to the wider social world, relate to underlying, putatively simple, social differences or processes, such as individual-level variation in general sociability or reassociation tendency [48]. For example, an individual's general tendency to be sociable can be intuitively quantified using a direct network metric (e.g., strength, or the sum of the weights of an individual's ties to their partners), or using an indirect metric (e.g., weighted eigenvector centrality, which measures how well-connected an individual is to its partners and how well connected those partners are to others [48]. Drawing on this idea that underlying processes can predict an individual's position in the network, and on the age-based changes in social behaviour we have documented in rhesus macaque females, we made predictions for four common measures of indirect connectedness: eigenvector centrality, betweenness, closeness, and clustering coefficient. Adult female rhesus macaques maintain their strength of grooming ties to others as they age [6]. We therefore predicted that weighted eigenvector centrality would also remain stable with age. We also previously found that as female rhesus macaques age, they increase their likelihood of interacting with certain partners, especially their kin. That is, ageing females increase both their tendency to reassociate with others, and their tendency to interact with someone from their own sub-group. Individuals with higher within-group association tendencies mix less widely in their networks and those with greater reassociation tendency are less likely to associate with new individuals and connect disparate parts of the network [48]. Therefore, we predicted that as females aged, they would have lower measures of betweenness and closeness, but a higher clustering coefficient. Betweenness calculates the number of shortest paths between others in a network that

128 pass through an individual, thus individuals with low betweenness have a low capacity for linking
129 discrete clusters in a network [56]. Closeness measures the inverse distance to all other individuals
130 in the network, and so the lower an individual's closeness score, the more difficult it is for them
131 to reach others or to be reached [56]. Clustering coefficient measures how densely (or sparsely)
132 the network is clustered around a focal individual, with a high clustering coefficient indicating that
133 an individual's partners are highly connected to each other [56].

134 To determine if age-based changes at the individual level can facilitate changes in overall
135 network structure we built an agent-based model to simulate how changing proportions of old
136 individuals in a network affects network structure. We simulated two simple changes in
137 individuals' interaction patterns with age based on our previous findings in female rhesus
138 macaques. We then used empirical data from 19 networks of female rhesus macaques to explore
139 whether the simulated results were borne out under natural conditions. Using both the simulated
140 networks and empirical networks we determined how changing proportions of old individuals in
141 the network was related to three common measures of global network structure: mean degree,
142 network diameter and transitivity. Mean degree represents the average number of ties that each
143 individual has to others in the network. Diameter measures the longest path length in the network
144 and provides a measure of overall connectedness. Transitivity captures the level of clustering in
145 the network [56]. We predicted that networks with a greater proportion of old individuals would
146 be more sparsely connected due to older animals having fewer social partners (i.e., have lower
147 mean degree and network diameter). Given greater kin clustering with age, we expected
148 networks with more old individuals would be more clustered (i.e., have higher transitivity). Our
149 results provide a first step to understanding how individual changes in social tendencies with age

can scale up to global network structure, offering important insight into the consequences of shifting demography for the structure and function of collectives.

Methods

Study population and data

Data used in this study were collected on a well-studied population of rhesus macaques on the island of Cayo Santiago, off the southeastern coast of Puerto Rico. The current population is maintained by the Caribbean Primate Research Center (CPRC) and is descended from 409 macaques that were introduced to the island from India in 1938. The animals are food supplemented and provided with ad libitum access to water. There is no medical intervention, and so the major causes of death at this predator-free site are illness and injury [52,57]. The CPRC staff collect demographic data five days per week and thus track dates of birth and death of all individuals with a high degree of accuracy.

Subjects were mature adult females 6 years and older [58] from 6 naturally formed mixed-sex social groups. We used data collected between 2010-2017, a time period for which we had detailed behavioural data from which to estimate social networks. We collected behavioural data between 07:30 and 14:00, which are the working hours of the field station, using 10-min focal animal samples and recording all behaviours continuously [59]. We balanced data collection to ensure equal sampling of individuals throughout the day and over the course of the year, resulting in approximately the same number of focal samples per individual per year. Female rhesus macaques have a strict dominance hierarchy with maternal rank inheritance and youngest ascendency [60]. We therefore established dominance ranks for all females in a given year using observed win-loss interactions (as per [61,62]). Rank was assigned as “high” (≥ 80% of other females dominated), “medium” (50%-79% of other females dominated) or “low” (≤

176 49% of other females dominated).

177 Because individuals showed the clearest age-based changes in their grooming
178 associations [6], we used grooming interactions to build social networks. Grooming behaviour
179 was collected by recording the duration of a grooming bout along with the identities of the
180 interactants and the direction of grooming. We focused only on interactions between adult
181 females and did not include interactions with males as we wanted to avoid capturing changes in
182 socio-sexual behaviour with age. Given that the behaviour of juveniles' is commonly influenced
183 by their lack of independence from their mother we also did not include interactions with
184 juveniles of either sex. We built 19 grooming networks from the following group-years (group F
185 2010-2017; group HH 2014; group KK 2015; group R 2015-2016; group S 2011; group V 2015-
186 2016), with data availability based on the focus of projects over time given limited person power.
187 The average size of our networks was 50.7 (± SE = 3.9) adult females. All network metrics were
188 calculated in R (version 4.2.0; [63]) using the igraph package (version 1.3.1; [64]).

189

190 **Investigating the relationship between age and indirect connectedness**

191

192 To assess age-based changes in indirect connectedness we used weighted network
193 metrics, as these are more robust and provide higher resolution than binary measures [67]. In
194 these weighted networks, edges represented the undirected rate of grooming between a pair of
195 individuals (seconds of grooming/total number of hours that both individuals were observed in
196 focal animal samples). For these analyses we set out to test how individuals' level of indirect
197 connectedness to their social network changed from prime adulthood into later life. At six years
198 old, females are deemed adults [58] and previous research on the macaque population of Cayo
199 Santiago has shown that, for females that survive to reproductive age, the median lifespan is 18
200 years with a maximum lifespan of about 30 years [50,68]. In our dataset, the median age of adult

201 females was 10-years. To capture later-life changes in indirect connectedness we thus focused
202 our analyses on individuals aged 10 and older (in line with previous ageing studies in this system
203 [6]. Females ranged between 10 and 28 years old. We had 563 macaque years of data over 204
204 unique females, with an average of 2.8 years of data per individual (range: 1-8 years; Fig. S1).
205 Because there was variation in the age-ranges over which individuals were sampled, we used a
206 within-individual centering approach to capture changes in indirect connectedness across
207 individuals' lifespans [69]. Briefly, following the methodology of van de Pol & Wright (2009)
208 we split our age term into a between-individual effect (calculated as the mean age of an
209 individual across all observations; hereafter called average age) and a within-individual effect
210 (calculated as the deviation of an individual's age from their mean age; hereafter called within-
211 individual age). This within-age term was our primary variable of interest and reflects how an
212 individual's deviation from its age affects its indirect connectedness in the network.

213 We fit four models with our four response variables of interest: eigenvector centrality,
214 betweenness, closeness, and clustering coefficient. All statistical models included average age
215 and within-individual age as continuous fixed effects. Given the strict dominance hierarchy
216 exhibited by female rhesus macaques [60], we assessed whether social status affected the change
217 in an individual's measures of indirect connectedness with age [6] by fitting an interaction
218 between rank and within-individual age in all models. We removed the interaction when not
219 significant. We included individual ID, group, and year, as random effects to account for
220 repeated observations and to capture any variation in indirect connectedness measures that might
221 be due to differences between individuals, groups, or years. We also fitted within-individual age
222 as a random slope over individual ID to capture any among-individual variation in the change in
223 indirect connectedness with age. We had no biological reason to expect non-linearities in the

relationship between age and measures of indirect connectedness given that we were looking at changes from prime adulthood to old age and we've previously found a linear relationship between direct measures of connectedness and age [6]. Nevertheless, we fit a model with quadratic terms for within-individual age and average age and compared that model to the model with only linear age terms using leave-one-out cross-validation in the brms package (version 2.17.0) [66]. The quadratic terms never improved the model fit and so were not considered further. For the eigenvector centrality model, we logit-transformed the response variable to improve model fit and fitted a model with a Gaussian error distribution. For betweenness we fitted a model with a zero-inflated Poisson distribution. For closeness and clustering coefficient we fitted models with a Beta error distribution and a zero-one-inflated Beta error distribution, respectively.

Investigating the relationship between age distribution and network structure

Agent-based model

The purpose of the model was to gain insights into how age-based changes in sociality may affect global network structure – specifically how the age distribution of the population impacts overall network structure. Our general approach was therefore to model artificial populations where social behaviour depends on age, and use these to investigate the relationship between age distribution and global network metrics.

We were particularly interested in the potential effects of the age-dependencies observed in the rhesus macaque system on Cayo Santiago [6]. As mentioned above, female rhesus macaques have been observed to change two aspects of their sociality with age: their number of social partners, and the proportion of partners that are kin [6]. We therefore included kinship as an attribute of individuals in the model, and parameterised the model based on our empirical

data.

More specifically, the model simulates social networks of varying age distributions, in which the probability that two nodes (i.e., individuals) have an edge (i.e., a grooming link) depends on age and kinship of the individuals. Individuals belonged to two age categories (old adults and young adults, hereafter "old" and "young") and two kin categories (kin and non-kin). This gives 6 dyad types, which we denote by the age categories of the two individuals and their kinship status (e.g. old/old kin). We established the linking probability (i.e., the chance of having an edge in the social network) for each dyad type based on the mean proportion of dyads of each type that had an edge across the 19 empirical grooming networks. The linking probability for dyads that were constituted of old individuals who were related to each other (i.e., old/old kin) was 0.33; for old/old non-kin dyads it was 0.02; for old/young kin dyads it was 0.37; for old/young non-kin dyads it was 0.05; for young/young kin dyads it was 0.27 and for young/young non-kin dyads it was 0.08. We fixed group size at 50 individuals, which approximates the mean number of adult females in real groups on Cayo Santiago (mean ± SE = 50.7 ± 3.9). Each simulated network had 10 clusters of individuals who were related to each other (i.e., kin groups) with 5 individuals in each. Kinship was determined by kin group membership: individuals in the same kin group were kin and individuals in different kin groups were non-kin. The number of individuals within each kin group mirrors the mean number of close adult female kin (relatedness coefficient ≥ 0.125) that each adult female rhesus macaque had in our empirical data (mean ± SE = 5.2 ± 0.87).

Each simulation round (i.e., construction and quantification of one network) proceeded as follows: We first randomly drew the number of old individuals in the group (n_{old}) from a uniform distribution with the range [0, 50]. We then randomly assigned all 50 group members to age-

272 groups (n_{old} old individuals and n_{young}= 50-n_{old} young individuals) and kin groups. This allowed
273 the age structure of the groups to vary from only young individuals to only old individuals. We
274 then constructed the social network by drawing links, where the chance of each dyad getting a
275 link depended on their dyad type (link probabilities given above). To determine whether a dyad
276 was given a link, we extracted a random value from a binomial distribution with a sample of 1
277 and probability equal to the linking probability of the type of dyad. If the extracted value was 1,
278 the dyad was given a link, if it was 0, the dyad was not given a link.

279 To confirm that the model was working as intended, we ran 10000 simulations (i.e., we
280 generated 10000 networks), from which we calculated the proportion of dyads of each type that
281 had a link. We confirmed that the means of these proportions corresponded well to their
282 respective empirical linking probability (Fig. S2). Furthermore, to ensure that the conclusions
283 from the model were not highly sensitive to the linking probability estimates, we investigated
284 how the shape of the relationships between the proportion of old individuals and the network
285 metrics changed when the difference between linking probabilities of old and young individuals
286 became smaller. Our endpoint was the case where there was no difference between the social
287 behaviour of old and young individuals (i.e., their respective linking probabilities converged to
288 the same values). We ran the model for this extreme case, for the original data-based values, and
289 for five other sets of linking probabilities, which were at regular distances between the original
290 values and the endpoint values (Table S1). For each of these cases, we ran 10000 simulations.
291 Under high sensitivity, any observed correlations would disappear quickly (e.g., at the first
292 reduction of difference in linking probabilities between age groups), whereas a more gradual
293 reduction would indicate robustness to the input. Given that our input values are only estimates
294 of the real values, robustness to the input values is important for drawing general conclusions

295 about the potential effects in the real system.

296 To investigate the relationship between age distribution and network structure, we ran
297 100000 replicates of the simulation (i.e., generated 100000 networks) and visualised the
298 relationship between the proportion of old individuals and network mean degree, diameter, and
299 transitivity. Additionally, we used the agent-based model to investigate if we should expect to
300 find relationships between the proportion of old individuals and network metrics in the empirical
301 analysis. To do this, we limited the number of old individuals in each network to between 2 and
302 10 (i.e., 4-20% of the group, mirroring the empirical data), and we ran 19 simulations (mirroring
303 the 19 empirical networks). We repeated this 50 times (i.e., 50 sets of 19 networks) to gauge the
304 consistency of the results.

305

306 ***Empirical analyses***

307 To assess the relationship between age distribution and network structure, we built
308 undirected, unweighted networks (where edges simply represented the presence of a grooming
309 relationship or not) to align with our agent-based model. Our networks included all females aged
310 6 and older. We had three response variables of interest and fitted a separate model for each:
311 mean degree, diameter, and transitivity. To ask if age distribution relates to network structure, we
312 included the proportion of old individuals as a continuous predictor in all our models. Since 18 is
313 the median age of death in this population and maximum lifespan is about 30 years, we
314 considered individuals above 18 to be "old" [50,68]. The proportion of old females in our 19
315 networks ranged from 0.03 to 0.19 (Fig. 1). Given that rhesus macaques live in matrilineal
316 groups with kin-biased behaviour [51,70], we included the average relatedness of the network as
317 a continuous covariate to account for differences between groups in general relatedness. We also

included density as a continuous fixed effect in the models of diameter and transitivity to account for the fact that density can drive variation in other global network metrics. We included year as a random effect to account for yearly variation that might affect network structure. We fit all models with a Gaussian error distribution. To account for a potential non-linear relationship between age distribution and network structure we fit all models with a quadratic term for proportion of old individuals and compared that to the model with only linear terms using leave-one-out cross-validation in the brms package (version 2.17.0; [66]). The quadratic terms never improved model fit and so were not considered further.

Statistical analyses

All empirical models were fitted in a Bayesian framework with different error structures and random effects dependent on the data analysed (see above). We conducted all analyses using R (version 4.2.0; [63]) and fitted all models in the Bayesian software STAN [65] using the brms package (version 2.17.0; [66]). All fixed effects were given weakly informative priors (see Supplementary Information for more details). We ran all models for 10,000 iterations across two chains with a warm-up period of 2,000 iterations. We assessed model convergence by examining trace plots to assess sampling mixing and by ensuring Rhat = 1. We considered estimates of fixed effects to be significantly different from zero when the 95% credible intervals of the posterior distribution did not overlap zero.

Results

Relationship between age and indirect measures of network connectedness

Female macaques did not show any change in eigenvector centrality with age (within-

individual age: β = -0.04; 95% CI = -0.30, 0.24; Fig. 2A-B, Table S2). That is, as females aged, the strength of their relationships to their partners, and to their partners' partners, remained stable. We did find evidence of a within-individual decline in betweenness with age, suggesting older individuals were less effective at reaching disparate nodes in the network. This effect was rank dependent and seems to be driven primarily by a decline in betweenness as high-ranking individuals got older (within-individual age:rankH: β = -0.35; 95% CI = -0.41, -0.29; Fig. 2C-D, Table S3), although mid-ranking individuals also showed greater declines in betweenness with age than did low-ranking females (within-individual age:rankM: β = -0.14; 95% CI = -0.18, -0.09; Fig. 2C-D, Table S3). Individuals showed a reduction in their closeness with age (within-individual age: β = -0.18; 95% CI = -0.35, -0.02; Fig. 2E-F, Table S4), meaning they were harder to reach and be reached in the network. There was no within-individual effect of age on clustering coefficient, that is, how cliquish individuals were (within-individual age: β = 0.04; 95% CI = -0.06, 0.14; Fig. 2G-H, Table S5).

Relationship between age distribution and network structure

Agent-based model results

Shifting group demographics in age appeared to have important consequences for network structure (Fig. 3; Fig. S3). Specifically, our simulations showed that as the proportion of old individuals in the population increased, mean degree (i.e., the mean number of partners that each individual associated with) decreased (Fig. 3D), and the diameter of the network (i.e., the longest path length in the network) increased (Fig. 3E), as expected. Network transitivity (i.e., the degree of clustering in the network; Fig. 3F) showed little variation in relation to age-based distribution. Overall, these results suggest that compared to networks with more young

individuals, networks with more old individuals are sparser and less cohesive but are not substantially different in how clustered they are. The patterns described above were only gradually reduced when the difference in social behaviour between young and old individuals was reduced, indicating that conclusions are robust to input parameter values (Fig. S4). When we limited the sample size and variation in age distribution to those of the empirical data (i.e., 19 networks constituted by 4-20% of old individuals) we found no clear effects of age distribution on network structure (Fig. 4C-D). These results hint that we might not expect to find a strong effect of age-based changes in sociality on the structure of 19 empirical networks.

Empirical results

We found little evidence that groups with a greater number of old individuals were structured differently from groups with fewer old individuals. Networks were not more sparsely connected as the proportion of older animals increased. We found no overall effect of the proportion of old individuals in the group on mean degree (β = -2.76; 95% CI = -10.24, 5.25; n = 19; Fig. 4A, Table S6), or network diameter (β = 2.02; 95% CI = -6.21, 10.00; n = 19; Fig. 4B, Table S7). Older networks were also not more clustered or cliquish, as measured by transitivity (β = 0.17; 95% CI = -0.31, 0.65; n = 19; Fig. 4C, Table S8).

Discussion

Age has begun to emerge as an important attribute shaping the social decisions of individuals [6,7,14]. This implies that it is a potentially significant feature underlying the behaviour of animals in collectives. Here we have shown that age-based changes in social behaviour are likely to have important effects on higher-order network structure. As individuals aged, they showed changes in some, but not all of their indirect measures of connectedness. Furthermore, our agent-based model provides evidence that older populations can have

substantially different network structures than younger populations. While this suggests that age plays a role in the overall structuring of rhesus macaque networks, this effect was not detected, and may not have been detectable, in our empirical data.

In line with our predictions, we found no evidence for changes in eigenvector centrality with age. This was expected because female rhesus macaques maintain the amount of time they engage in social interactions as they get older [6], allowing them to continue to have strong connections to some of their partners, and (indirectly) to the partners of their partners. A similar pattern has been observed in a population of wild rhesus macaques in China whereby older individuals had fewer partners but exhibited similar weighted eigenvector centrality to those of younger individuals [32]. Unexpectedly, we did not find any evidence that clustering coefficient increased as individuals aged in this population. Females increase their preference for grooming kin as they age [6], suggesting that within-group (e.g., homophilic) tendencies increase with age, which should lead to greater clustering as females from the same matriline would cluster together in the network. However, although kin-biases increase with age, they exist for females of all ages [53]. It is therefore possible that ties with kin are the main driver of clustering coefficient scores regardless of age. Pruning a few non-kin relationships as an individual ages could thus have a relatively minor impact on their clustering coefficient, leading to stable values for this metric across the adult lifespan. In general, the stability of weighted eigenvector centrality and clustering coefficient across the adult lifespan suggest that older animals can remain socially central and well-integrated in some respects, despite other aspects of their social life changing (e.g., fewer partners overall, and the patterns observed below). Old individuals may therefore continue to reap some of the advantages of social relationships [5].

414 As predicted, we found declines in betweenness and closeness with age. As individuals
415 got older, they had less influence on and became less well-connected to the wider network.
416 These metrics are associated with an individual's level of reassociation tendency and within-
417 group association [48]. In other words, the more likely individuals are to reassociate with the
418 same partners, and to select partners of similar characteristics to themselves, the less they mix
419 with the wider network and the less likely they are to connect distinct subgroups (i.e., have high
420 betweenness) or be easily reached by all others in the network (i.e., have high closeness). We've
421 previously shown that ageing rhesus macaque females have fewer partners, but engage with
422 those partners more often, and increase their preference for close relatives. In other words, while
423 mean dyadic association strength to associates increases with age, mixing with the wider network
424 should decline [6]. Our betweenness and closeness results seem to reflect these underlying
425 changes in behavioural patterns. The declines in betweenness with age were rank dependent,
426 with mid-ranking and high-ranking rhesus macaque females showing a greater decline in
427 betweenness with age than low-ranking individuals. This may simply be due to a floor effect –
428 because low ranking individuals have such low betweenness to begin with, there is little capacity
429 for further decline with age.

430 Generally, our findings demonstrate that how indirectly connected an individual is to
431 their social world can change across their lifespan. How an individual is positioned in the wider
432 social environment can modulate their exposure to information [26,71], parasites [18,72], and
433 pathogens [21–23]. Individuals with high betweenness and closeness occupy a critical position in
434 the acquisition and transfer of 'goods' within a network [17,55,73]. Decreases in both of these
435 measures of indirect connectedness with age may benefit aged individuals who may experience
436 greater susceptibility to disease or illness as a result of immunosenescence [74]. Such benefits

437 need not imply that individuals actively change complex network positions with age. By
438 changing simple behavioural rules or processes with age, changes in polyadic ties with age are
439 likely to emerge [48]. Measures of indirect connectedness have been linked to fitness proxies
440 including future social status [75,76], survival [77,78], and reproductive success [61,76,79].
441 Indirect network metrics can be an even stronger predictor of fitness proxies [17,79] than
442 measures of direct dyadic associations and may more strongly reflect the underlying behavioural
443 rules that give rise to individual differences in sociality [48]. As such, documenting how ageing
444 shapes the polyadic social world may be particularly relevant for understanding how changes in
445 sociality across the lifespan influence patterns of senescence and fitness in later life.

446 In addition to age being associated with changes in the behaviour and social
447 connectedness of animals living in groups, our simulations provide evidence that age can also
448 impact the overall structure of those groups. By modelling age-based differences in two simple
449 interaction patterns, we found that the age composition of a group can have important
450 consequences for its cohesiveness and connectedness. As predicted, mean degree declined and
451 diameter increased as the proportion of old individuals increased, while transitivity exhibited no
452 strong relationship to age-distribution. Contrary to the results of the agent-based model, we
453 found no relationship between age distribution and network metrics in the observed macaque
454 data (Fig. 4). The impact of age distribution on network structure may only be detectable at the
455 extreme ends of the age distribution. That is, populations made up of very large numbers of
456 young, or old, individuals may diverge in structure at detectable levels, whereas populations
457 within a smaller range of age distributions may not. Although our empirical dataset ranged from
458 3-19% of individuals in the group classed as 'old', this may not have been wide enough to detect
459 differences in network structure. Results from our simulation were, as would be expected, the

most extreme at the more extreme ends of the age distributions examined, and when we restricted our simulated networks to approximately 3-19% of individuals classed as 'old', we found no relationship between the proportion of old individuals and network structure. We may additionally have been unable to detect an effect of age distribution on network structure given the amount of data available. Nineteen rhesus macaque networks from 6 groups were collected across 8 years, which represents a considerable investment of research time and effort. But when we restricted our agent-based model to a similar sample size, age distribution did not predict network structure. However, it is also possible that our empirical results reflect a true null result if there are processes occurring that our model has not accounted for. Our model, like all models, is a simplistic version of the real world and does not fully replicate the complete suite of changes that might occur with age.

The aim of our agent-based model was to capture two simple changes in individual-level behaviours with age that have been identified across a wide range of taxa. Although the model has the potential to be generalizable to other systems, it was parameterized based on data from the macaque system and so its outputs may not hold in species that do not have a matrilineal kin structure or low levels of modularity. Future work in other systems, conditions, and contexts could reveal consequences for network structure that are even more stark. For example, more dramatic differences between age classes in the overall probability of forming a social tie may be expected in societies where the probability of connecting decreases with age but there is no compensatory increase in the probability of forming ties with kin. This could lead to stronger absolute effects on global network metrics, including substantial changes in transitivity, and thus would likely have further consequences for network connectivity and spreading processes. However, a greater proportion of older individuals in a population may not always lead to

483 changes in network structure. This can occur, of course, if individuals do not change their social
484 behaviour with age, but also in scenarios where age-based changes in sociality do exist. Within-
485 individual changes in social behaviour with age do not necessarily lead to between-individual
486 differences [69]. A cohort may start out very sociable due to, say, their environmental conditions
487 at birth. Even though members of this cohort become less sociable as they age, they could exhibit
488 similar average levels of sociality to a younger, less social, cohort. This would result in no
489 differences between old and young individuals in their social tendencies and therefore no effects
490 of age distribution on network structure. However, while cohort effects might occasionally mask
491 ageing effects, it seems unlikely that they would do so consistently. Future research may
492 therefore seek to assess at what point between individual differences can negate the effects of
493 within-individual changes with age.

494 Our model provides a glimpse into the powerful effects that age-based changes in
495 behaviour can have on network structure, offering a deeper understanding of the potential
496 importance of demographic changes for the structure and function of collectives. Much attention
497 has been given to the potential for the social structure of populations to be affected by the
498 removal of older individuals, for example through practices like trophy hunting or fishing
499 [80,81]. This is relevant given that older individuals can play a critical role in their social groups
500 through leadership [4,37], intergenerational transfers [38], and the stabilisation of social
501 relationships [82]. Despite the importance of the loss of older individuals from networks, our
502 results suggest that asking what happens when populations contain large numbers of older
503 individuals is an equally salient question.

504 In humans, population ageing is poised to be one of the most significant social
505 transformations of the 21st century, facilitated by falling fertility rates and increasing longevity

[83,84]. Meanwhile, in other group-living species, anthropogenic challenges, including climate change, poaching, disease outbreaks, and pollution, among others, are likely to cause major population declines and demographic shifts [85]. The consequences of declining fertility and/or increasing mortality rates may be further exacerbated by the concomitant shifts in age structure and resulting implications for network structure and function. For instance, declines in cohesiveness and structural connectedness in older networks may limit or slow the transfer of information [24,86], restrict the potential for cooperation [87] or reduce the stability of populations [30], feeding back to further limit population growth. Alternatively, such changes could reduce the vulnerability of populations to infectious diseases or parasites [30,88] or enhance cooperation if network modularity is increased [89]. Consequently, through its effects on network structure, shifting age demography may have broader implications than previously appreciated for group dynamics and persistence and warrants further research.

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Data availability: All data and code associated with the analyses will be made publicly available on the Figshare Repository following acceptance of the manuscript.

Competing Interest Statement: The authors declare no competing interests.

Figure 1. Distribution of ages in each of the 19 empirical macaque networks. The dotted black line at age 18 indicates the median age of death in this population.

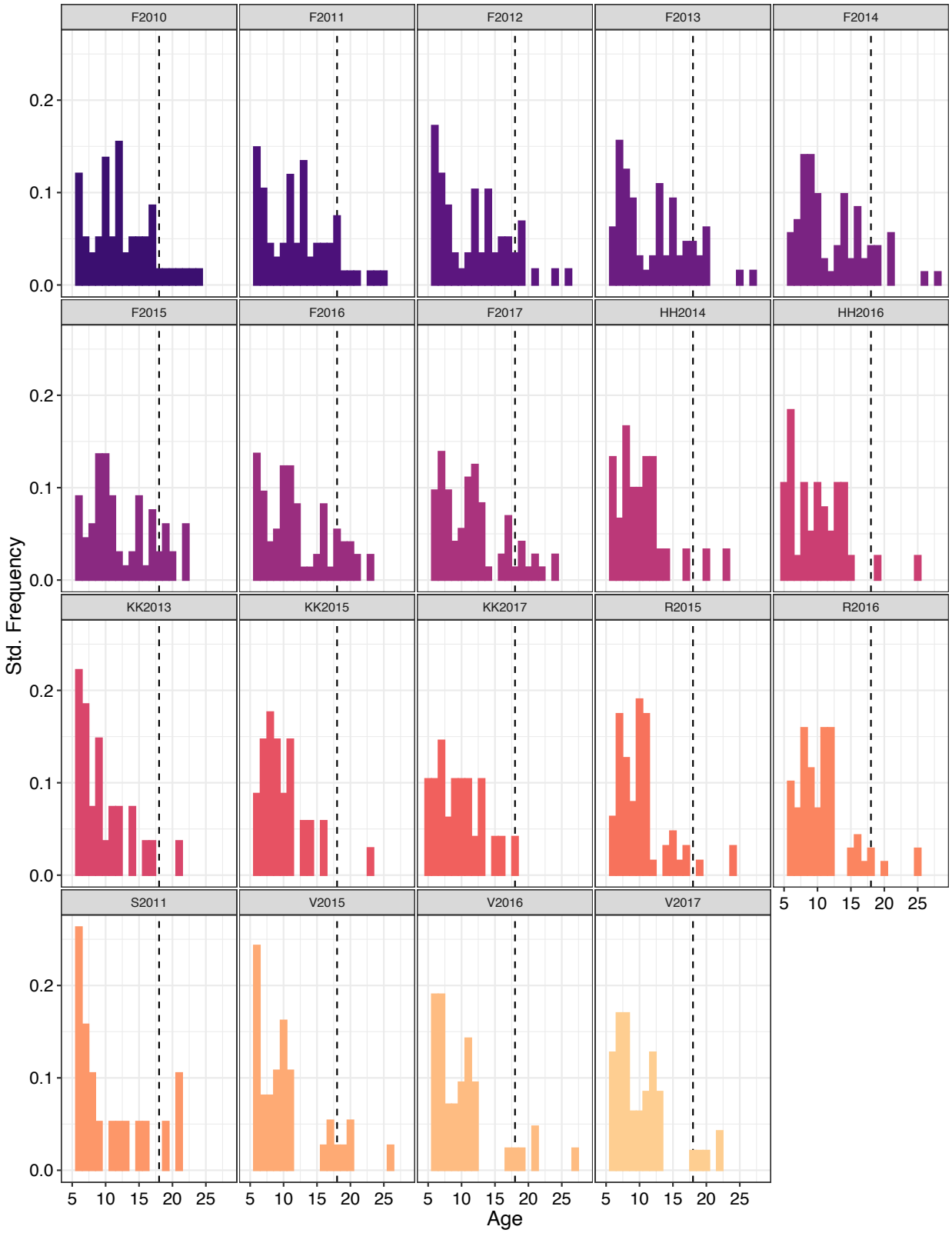


Figure 2. Relationship between within-individual changes in age and indirect measures of connectedness including (A & B) eigenvector centrality, (C & D) betweenness, (E & F) closeness, and (G & H) clustering coefficient in female rhesus macaques. In **A, C, E, G** the points represent raw data. Shaded grey bars indicate 95% confidence intervals around the predicted values. In **B, D, F, H** effect sizes and 95% credible intervals for all fixed effects and interaction terms are shown. Instances where the 95% CI overlaps zero are coloured in purple.

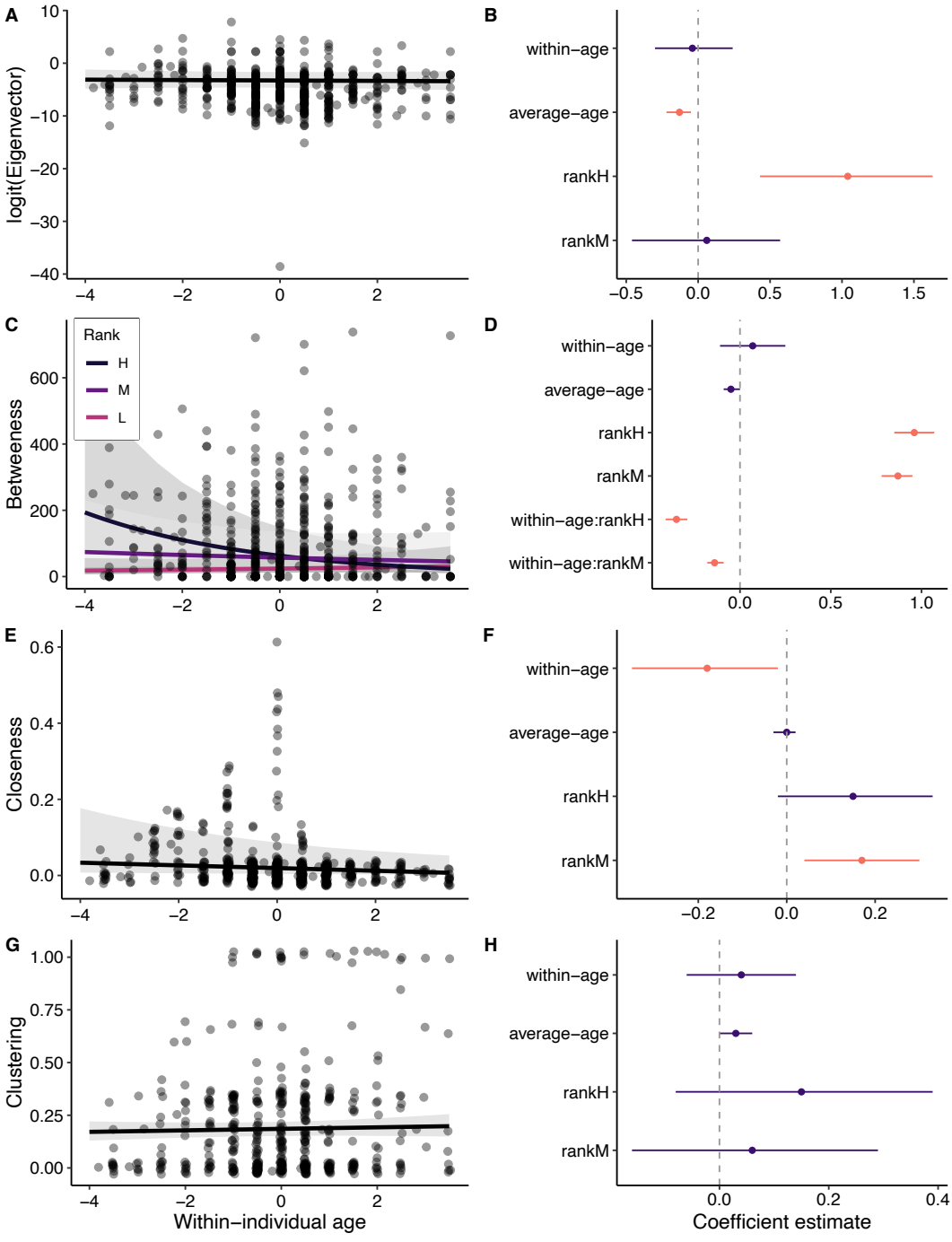


Figure 3. (**A-C**) Example networks from the agent-based model illustrating differences in network structure with the proportions of old individuals in the network equal to 0 (**A**), 0.5 (**B**) and 1 (**C**). Node colour represents kin groups where nodes of the same colour belong to the same kin group. (**D-F**) Results from the agent-based model showing relationship between the proportion of old individuals and (**D**) mean degree, (**E**) diameter, and (**F**) transitivity. Data points from the 100K simulations are shown with a small amount of jitter introduced to show overlapping points and are fitted with a smoothing term.

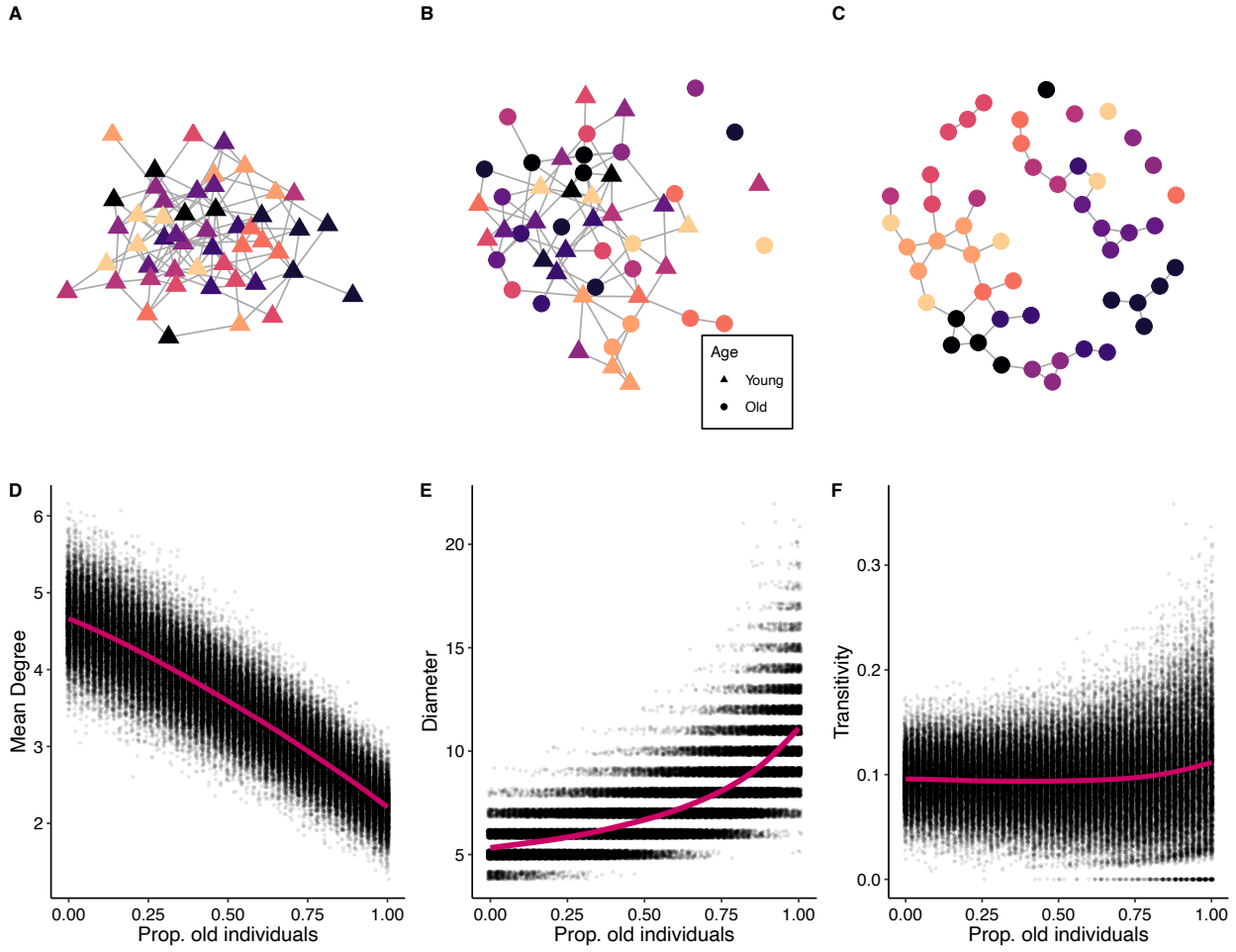
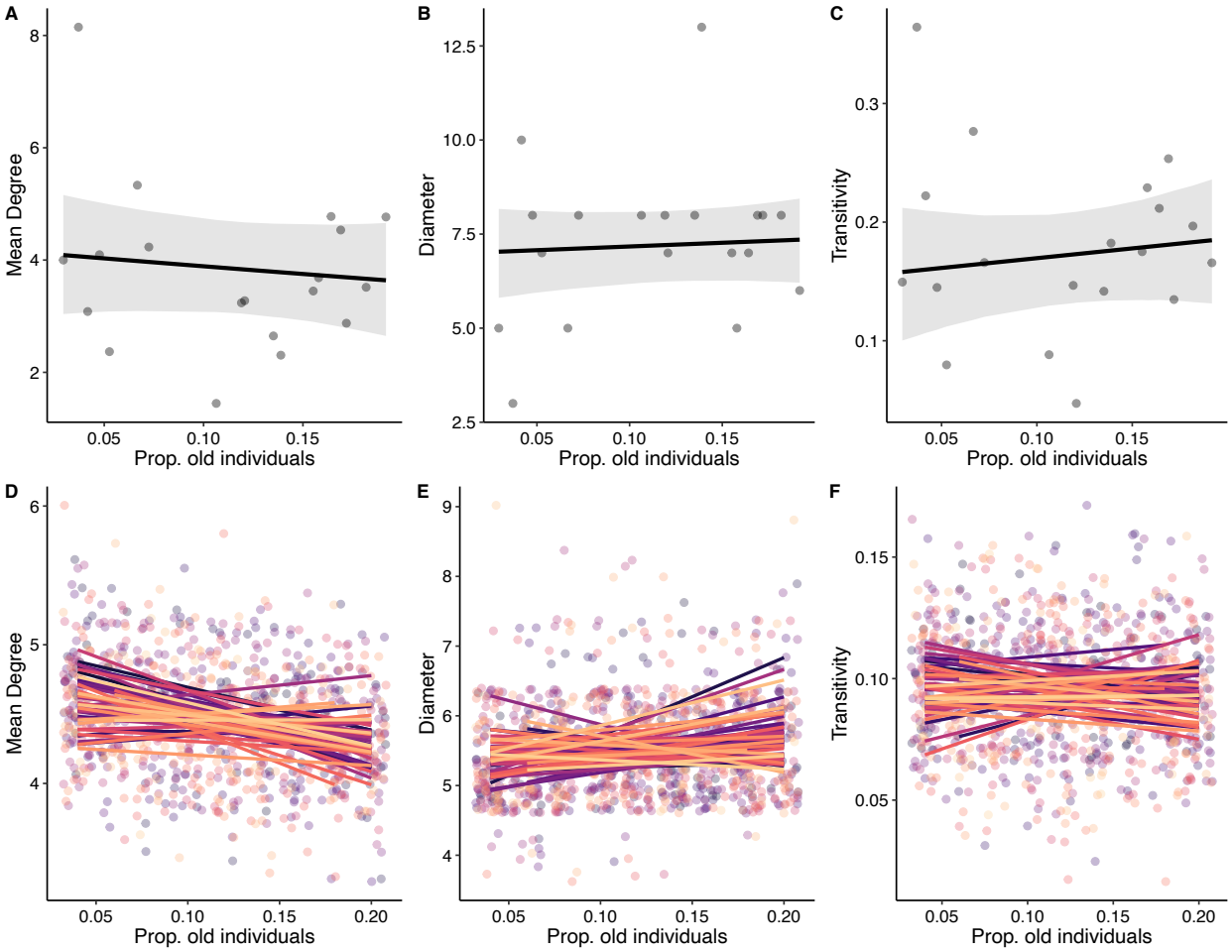


Figure 4. (**A-C**) The relationship between the proportion of old individuals in female rhesus macaque networks and: (**A**) mean degree, (**B**) network diameter, and (**C**) network transitivity. Points represent raw data and shaded grey bars indicate 95% confidence intervals around the predicted values from models. (**D-F**) Relationship between the proportion of old individuals and (**D**) mean degree, (**E**) network diameter, and (**F**) transitivity based on 19 simulations from the agent-based model where the proportion of old individuals in the population was restricted between 0.04 and 0.20. We re-simulated these 19 networks with limited age variation 50 times to help ensure our results were robust. Each colour represents a different 'bout' of 19 networks. Data points are shown fitted with a linear smoothing term.



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