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RESEARCH ARTICLE

Group and individual social network metrics are robust to changes in resource distribution in experimental populations of forked fungus beetles

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Abstract

1. Social interactions drive many important ecological and evolutionary processes. It is therefore essential to understand the intrinsic and extrinsic factors that underlie social patterns. A central tenet of the field of behavioural ecology is the expectation that the distribution of resources shapes patterns of social interactions.
2. We combined experimental manipulations with social network analyses to ask how patterns of resource distribution influence complex social interactions.
3. We experimentally manipulated the distribution of an essential food and reproductive resource in semi-natural populations of forked fungus beetles *Bolitotherus cornutus*. We aggregated resources into discrete clumps in half of the populations and evenly dispersed resources in the other half. We then observed social interactions between individually marked beetles. Half-way through the experiment, we reversed the resource distribution in each population, allowing us to control any demographic or behavioural differences between our experimental populations. At the end of the experiment, we compared individual and group social network characteristics between the two resource distribution treatments.
4. We found a statistically significant but quantitatively small effect of resource distribution on individual social network position and detected no effect on group social network structure. Individual connectivity (individual strength) and individual cliquishness (local clustering coefficient) increased in environments with clumped resources, but this difference explained very little of the variance in individual social network position. Individual centrality (individual betweenness) and measures of overall social structure (network density, average shortest path length and global clustering coefficient) did not differ between environments with dramatically different distributions of resources.

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5. Our results illustrate that the resource environment, despite being fundamental to our understanding of social systems, does not always play a central role in shaping social interactions. Instead, our results suggest that sex differences and temporally fluctuating environmental conditions may be more important in determining patterns of social interactions.

KEYWORDS

Bolitotherus cornutus, experimental populations, forked fungus beetle, resource distribution, social interactions, social networks

1 | INTRODUCTION

Patterns of social interactions impact many ecological and evolutionary processes, including how diseases spread among individuals (Adelman et al., 2015; Silk et al., 2019; VanderWaal et al., 2014), information transmits through populations (Allen et al., 2013; Aplin et al., 2015; Webster et al., 2013) and selection acts on individual phenotypes (Farine & Sheldon, 2015; Formica et al., 2011). Both individual social behaviours and population dynamics drive observed patterns of social interactions (reviewed in Croft et al., 2016 and Shizuka & Johnson, 2020). For example, individuals with fast exploratory personalities interact more often and with more conspecifics (Aplin et al., 2013; Snijders et al., 2014), and social associations among individuals increase after the death of a group member (Firth et al., 2017). Given the widespread importance of social interactions, it is essential to understand what creates variation in social interactions (Croft et al., 2016). As recent research focuses on how behavioural and demographic processes generate patterns of social interactions, we often ignore that the distribution of resources also structures how individuals interact with each other (He et al., 2019; Spiegel & Pinter-Wollman, 2020).

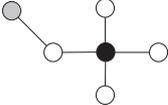
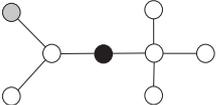
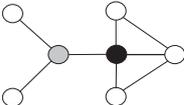
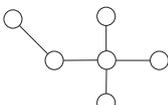
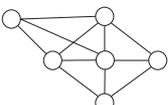
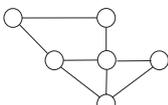
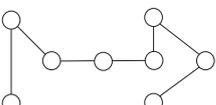
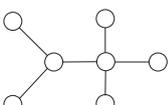
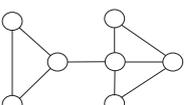
Variation in the distribution of resources is a foundation of our understanding of social systems. Resource distribution impacts everything from mating systems, to sociality, to foraging systems, to migration patterns (Cresswell et al., 2011; Emlen & Oring, 1977; Macdonald, 1983; Shuster & Wade, 2003). Building on this classical research base, there is re-emerging interest in how the distribution of resources structures social interactions and social networks. Recent work has found that resource distribution, abundance and complexity directly and indirectly determine the spatial distribution of individuals, thereby influencing encounter rates and patterns of social interactions in often contradictory ways (reviewed in He et al., 2019). For example, complex habitats restrict the movement of individuals, which reduces free interactions among individuals and decreases social connectivity in sticklebacks (Webster et al., 2013). In other systems, complex habitats funnel interactions into limited space, which increases social connectivity in sleepy lizards (Leu et al., 2016). Habitats with few resources have limited space for interaction, leading to increased social connectivity in many vertebrate taxa (Bachorec et al., 2020; Lantz & Karubian, 2017; Lattanzio & Miles, 2014) but decreased social interconnectedness in others (Burns et al., 2020; Foster et al., 2012; St Clair et al., 2015). Furthermore, habitats with aggregated food resources cause shore crabs to form larger cliques

and interact with more individuals (Tanner & Jackson, 2012) but likewise cause individuals in a simulation using area-restricted search foraging to interact with fewer individuals (Spiegel et al., 2017). The conflicting effects of resources on social interactions across species underscore the complex role of the environment in structuring how individuals interact and demand more empirical work to disentangle the effect of resources on social interactions.

One of the most powerful ways to study social interactions is with social network analysis. Social networks describe complex social patterns that emerge from simple dyadic social interactions and have been increasingly used to answer questions about both individual social behaviours and group social structures (Croft et al., 2008; Farine & Whitehead, 2015; Krause et al., 2015; Snijders et al., 2017). For example, group network metrics describe the connectivity or cliquishness of an entire population, whereas individual network metrics describe how connected, centrally located, or cliquish an individual is within its population (Table 1). These two social network levels affect ecological and evolutionary processes differently. Group cliquishness and network connectivity impact how information and diseases transmit (Allen et al., 2013; Aplin et al., 2015; VanderWaal et al., 2014; Webster et al., 2013). The connectivity, centrality and cliquishness of individuals, however, influence individual fitness (Formica et al., 2020; Oh & Badyaev, 2010). Integrating individual and group social network metrics provides a comprehensive picture of social interactions and offers a unique opportunity to test how resource distribution impacts complex social interactions.

Combining experimental manipulations with social network analysis is logistically challenging but provides critical insight into the proximate mechanisms that structure social networks (Croft et al., 2016). In this study, we manipulated the distribution of an essential food and reproductive resource in experimental populations of a mycophagous beetle. Forked fungus beetles *Bolitotherus cornutus* live on wood-rotting polypore bracket fungi growing on logs in the forests of eastern North America (*Ganoderma applanatum*, *Ganoderma tsugae* and *Fomes fomentarius*; Liles, 1956). Bracket fungi are critical resources for forked fungus beetles, as beetles eat fungus tissue, females oviposit on fungi, larvae develop entirely inside fungus brackets and adult beetles interact on the surface of those brackets (Liles, 1956; Pace, 1967; Wood et al., 2018). Mating interactions between males and females, antagonistic interactions between males fighting for access to mates and proximity interactions between neighbouring beetles all occur on fungus brackets (Brown

TABLE 1 Individual and group social network metrics of connectivity and cliquishness. Visualizations of social networks include nodes (circles) representing individuals and edges (lines) between circles representing social interactions between individuals. Grey nodes denote individuals with low network positions and black nodes denote individuals with high network positions. All measures are weighted by social interactions (Opsahl, 2009)

Metric	Definition	Visualization	
Individual network position			
Strength (individual connectivity)	Number of social interactions and social partners of a focal individual		
Betweenness (individual centrality)	Number of shortest paths connecting pairs of individuals that pass through a focal individual		
Local clustering coefficient (individual cliquishness)	Proportion of social partners of a focal individual that interact with each other		
Metric	Definition	Low	High
Group Network Structure			
Network density	Number of social interactions in a network out of all possible social connections		
Average shortest path length	Average of the shortest path lengths that connect all pairs of individuals in a network		
Global clustering coefficient	Proportion of all social partners in a network that interact with each other		

& Bartalon, 1986; Conner, 1988; Formica et al., 2012; Formica et al., 2020; Mitchem et al., 2019; Pace, 1967).

Social networks built from proximity interactions have been extensively studied in wild populations of forked fungus beetles (Formica et al., 2012; Formica et al., 2020). Wild populations are spatially subdivided among logs with bracket fungi, and most beetles remain on a single log for the entirety of a breeding season (Heatwole & Heatwole, 1968; Ludwig, 2008; Whitlock, 1992). Non-random social network structures and the fitness consequences of individual positions vary among logs (Formica et al., 2020). Individual connectivity (strength) and individual centrality (betweenness) are highly repeatable and covary with male mating success (Formica et al., 2012; Formica et al., 2017; Formica et al., 2020; Table 1). Individual cliquishness (local clustering coefficient), however, does not appear to be repeatable and only rarely has been found to impact male mating success (Formica et al., 2012; Formica et al., 2017; Formica et al., 2020; Table 1).

In addition to social networks and selection varying across wild populations (Formica et al., 2020), logs vary with respect to multiple environmental variables, including the species, size, number and distribution of fungus brackets. To disentangle these oftentimes covarying dimensions of environmental variation and to explicitly

test how resource distribution influences the patterns of social interactions, we manipulated the distribution of fungus brackets in replicate populations of forked fungus beetles. Previous analyses on data collected from this same experimental design investigated how the distribution of fungus brackets structures patterns of space use and found that beetle home range size dramatically decreased when fungus brackets were clumped, which concentrated individuals' space use around clumps of resource (Costello, 2020). Building on the results from our prior work as well as previous studies (Spiegel et al., 2017; Tanner & Jackson, 2012), we expected cliquishness, centrality and connectivity at both the individual and group levels to differ across fungus resource distributions.

2 | MATERIALS AND METHODS

2.1 | Experimental populations

We quantified the effect of fungus resource distribution on social networks in 12 experimental populations of forked fungus beetles. We built 2.44 m × 2.44 m × 1.22 m outdoor enclosures to house

experimental populations at Mountain Lake Biological Station (Giles County, Virginia). Each enclosure contained a 2.34 m × 0.52 m wooden shelving unit that simulated a log. Each artificial log held 54 polypropylene filter bags (SacO₂) filled with hardwood sawdust. In all, 18 of these bags were inoculated with a locally isolated strain of the beetle's host fungus, *Ganoderma tsugae* (Sharondale Mushroom Farm). These inoculated bags produced fungus brackets of the same genotype, age and volume. We interspersed inoculated bags with uninoculated bags to create space between resources. We covered all bags with tulle fabric to provide a surface that beetles could easily move across to travel between fungus brackets.

To test how the distribution of resources shapes social networks, we manipulated the distribution of the bracket fungi along the log. In six of the experimental populations, we aggregated the fungus brackets into three discrete clumps. In the other six, we evenly dispersed the fungus brackets along the log. After a 3-week observation period, we reversed the resource distribution in each replicate while retaining the same group memberships (Figure 1). The six experimental populations with clumped fungus brackets during the first observation period experienced evenly dispersed fungus brackets during the second observation period and vice versa. We replaced the fungus brackets with fresh fungi when we switched the resource distribution treatment, ensuring that each experimental period began with fresh, unused fungus. By exposing each group of beetles to both resource distribution treatments, we controlled for any demographic or behavioural differences between our experimental populations. We isolated individuals for 4 days between observation periods, as previous work demonstrates that this resets social networks (Formica et al., 2017).

We founded each experimental population with 36 beetles. Beetles were collected from 126 different logs in Giles County,

Virginia. Gene flow is sufficient to maintain genetic homogeneity among logs in this metapopulation (Wood et al., 2013). To minimize social familiarity among experimental beetles, we assigned a maximum of three beetles collected from the same log to the same experimental population. Each population was setup with the same sex ratio (18 males and 18 females) and similar body size distributions (linear model with elytra length as the dependent variable and population as the fixed effect: $F_{11,420} = 0.114$, $p = 0.9998$; average elytra length: 6.93 mm). We replaced five beetles that died within the first 3 days of the experiment with beetles of the same sex and size. Experimental population densities (one male per fungus bracket) fell within the range of densities observed in wild populations (Conner, 1989; Formica et al., 2011). This experiment did not require ethical approval.

2.2 | Social networks

We built social networks from observations of dyadic social interactions between beetles in each experimental population. We made observations three times per day (06:30, 14:30 and 21:30) for two 3-week periods (June 27–July 17, 2018 and July 27–August 16, 2018). We acclimated beetles to their enclosures for 36 hours before beginning observations. During observations, we systematically searched each population for beetles. All beetles were labelled with a unique identification code printed on florescent paper and affixed to their elytra with light-cured acrylic (Tuffleye Wet-A-Hook Technologies). We used ultraviolet light to easily detect the fluorescent tagged beetles in the enclosures.

When a beetle was observed, we identified all social partners of that beetle. We defined social partners as beetles mating, touching

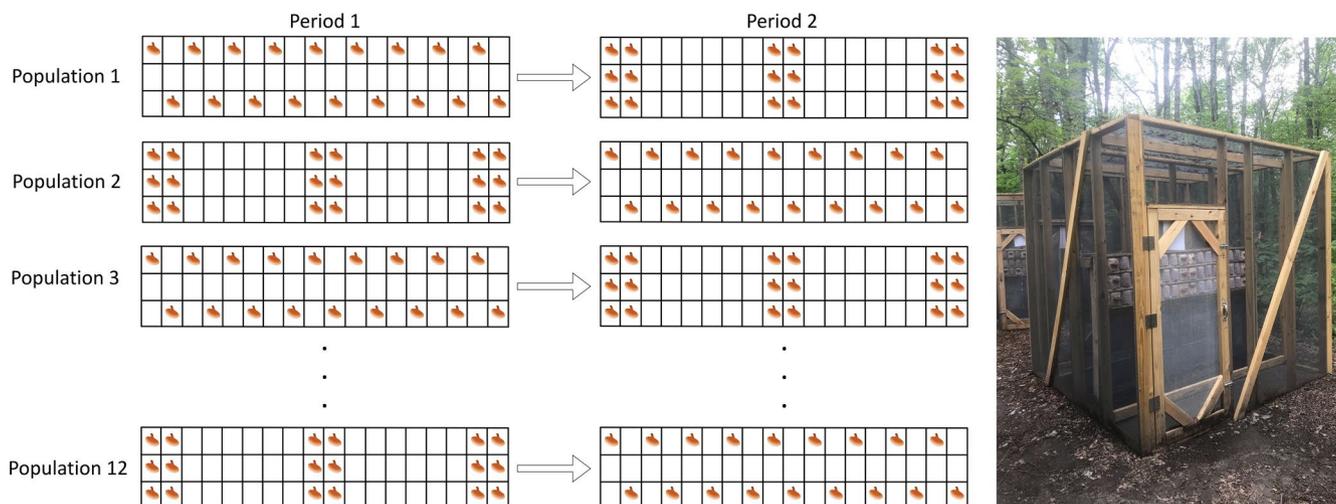


FIGURE 1 Schematic of the experimental design and photograph of an outdoor enclosure. Each of 12 experimental populations contained 54 sawdust-filled bags, 18 of which were inoculated with fungus (indicated above with an orange cartoon fungus bracket) and 36 of which were uninoculated. Every population experienced one of two resource distribution treatments during the first 3-week observation period. Fungus brackets were either dispersed evenly across the log or in three discrete clumps. During the second 3-week observation period, the resource distribution treatment was reversed in each population. This design ensured that every group of beetles experienced both resource distribution treatments and that the number of populations with each resource distribution treatment did not differ across observation periods. Photo credit: Caitlin McIver

and in close proximity. Our definition of social partners follows past work in this system and includes beetles within 5 cm, several body lengths, of each other (Formica et al., 2012; Formica et al., 2017; Formica et al., 2020). At this distance, beetles reorient towards one another, which often directly leads to other behaviours such as males initiating mating behaviours with nearby females and antagonistic behaviours with nearby males (Formica et al., 2012; Formica et al., 2017; Formica et al., 2020). We used pairwise physical proximity to define each dyadic interaction rather than assuming that individuals interact with each other's partners (the 'gambit of the group'), an important distinction when considering how to test hypotheses in animal social networks (see Statistical Analyses below; Croft et al., 2011).

We constructed undirected, weighted social networks from our observations of social interactions using the simple ratio index. The simple ratio index converts pairwise social interactions into weighted network edges, ranging from 0 for beetles never observed together to 1 for beetles always observed together (Croft et al., 2008; Ginsberg & Young, 1992). Observations of interactions with unidentifiable beetles (2.76% of all interactions) were not included in the constructed networks. To accurately represent the social environment, we included beetles that died during the experiment ($N = 32$) in network creation but not in subsequent data analyses. Over the course of the experiment, 1–5 beetles died in each experimental population. We built separate both-sex social networks for each experimental population during each observation period for a total of 24 social networks.

We calculated a variety of social network metrics that describe the connectivity, centrality and cliquishness of individuals within the network (Table 1). Strength describes individual connectivity by calculating how many different social partners an individual interacts with and how often (with an alpha weighting parameter of 0.5; Opsahl, 2009). Individual betweenness provides a description of individual centrality and is calculated as the number of shortest paths that connect pairs of individuals and pass through a focal individual (Opsahl, 2009). Although individual betweenness is measured at the level of the individual, individual betweenness depends on the structure of the whole network. Local clustering coefficient describes individual cliquishness by measuring how many social partners of an individual interact with each other (Croft et al., 2008). Note that beetles with one or no partners have undefined local clustering coefficients and therefore were not included in models analysing local clustering coefficient. We dropped 10 beetles (four beetles from the distributed treatment and six beetles from the clumped treatment) from the local clustering coefficient analysis. However, these disconnected beetles have calculable strength and betweenness values and were included in all other models. Strength, betweenness and local clustering coefficient were all calculated as weighted metrics in the `TNET` package in `R` (Opsahl, 2009).

We additionally calculated overall connectivity and cliquishness of groups (Table 1). Network density measures how connected a group of individuals is by quantifying the number of connections observed out of all possible connections in a network (Wasserman & Faust, 1994). Average shortest path length likewise describes how

connected a network is by calculating the average of the shortest path lengths that connect every pair of individuals (Opsahl, 2009). Global clustering coefficient describes how cliquish a network is by calculating the proportion of social partners in a network that interact with each other (Opsahl, 2009). Average shortest path length and global clustering coefficient were calculated as weighted metrics in the `TNET` package in `R` (Opsahl, 2009), and network density was calculated as a weighted metric in the `SNA` package in `R` (Butts, 2016). Networks were visualized in the `IGRAPH` package in `R` (Csardi & Nepusz, 2006).

2.3 | Statistical analyses

To test how resource distribution impacts individual strength, individual betweenness and local clustering coefficient, we used linear mixed-effect models with resource distribution treatment, sex, elytra length, the number of times observed and observation period as fixed effects and beetle identification nested within experimental population as random effects. We standardized continuous variables by both mean and variance. Individual network metrics are inherently non-independent, thereby violating the assumptions of most parametric statistical tests (Croft et al., 2011; Farine, 2017; Farine & Whitehead, 2015). We used node permutations to address this issue of non-independence. While some studies advocate for the use of datastream permutation methods to statistically account for common observation biases (Farine, 2017), our approach avoids many common observation biases by directly observing dyadic social interactions between known and easily identifiable individuals, all brightly labelled to be highly visible, in uniform experimental enclosures. Additionally, datastream permutations produce high false-positive error rates when testing null hypotheses in social networks, making node permutations a more appropriate method for testing hypotheses in our social networks (Croft et al., 2011; Puga-Gonzalez et al., 2020; Weiss et al., 2021).

Our node permutations randomly shuffled all variables used in the linear mixed models without replacement among all individuals to create 5000 permuted datasets. This permutation method breaks the relationship between each fixed effect and social network metric in the permuted datasets. We tested for statistical significance by comparing the estimate extracted from our linear mixed model using the observed dataset to a distribution of estimates extracted from the same model using the permuted datasets. We calculated p values as the proportion of permuted estimates that are more extreme than the observed estimate. Models were built in the `R` package `GLM-TMB` (Brooks et al., 2017), and the `R` package `EMMEANS` was used to calculate marginal means (Lenth, 2018).

We measured the effect sizes of all variables in our linear mixed models using Cohen's f^2 (Cohen, 1988). Cohen's f^2 measures the proportion of variance explained by the fixed effect relative to the proportion of variance unexplained by the model. Notably, effect sizes measured by Cohen's f^2 are standardized by how well the model explains variance. The `R` package `performance` calculated Nakagawa's

TABLE 2 Estimates and significance values from linear mixed models exploring how resource distribution treatment impacts individual network metrics. Model estimates are reported for continuous variables and marginal means are reported for categorical variables. *p* values are calculated as the proportion of permuted model estimates that are more extreme than the observed model estimate. Significant *p* values at the $\alpha = 0.05$ level are bolded

Fixed effect	Individual strength $R^2 = 0.29$			Individual betweenness $R^2 = 0.73$			Local clustering coefficient $R^2 = 0.009$		
	Estimate	<i>p</i> value	Effect size (f^2)	Estimate	<i>p</i> value	Effect size (f^2)	Estimate	<i>p</i> value	Effect size (f^2)
Treatment	Clumped: 2.80 Dispersed: 2.65	0.022	0.008	Clumped: 21.8 Dispersed: 22.1	0.83	0.0005	Clumped: 0.55 Dispersed: 0.52	<0.0002	0.002
Sex	Male: 2.39 Female: 3.05	<0.0002	0.12	Male: 18.8 Female: 25.0	<0.0002	0.39	Male: 0.55 Female: 0.52	<0.0002	0.002
Elytra length	0.03	0.35	0.002	1.19	0.15	0.054	0.0005	0.86	<0.0002
Number of observations	0.52	<0.0002	0.19	8.13	<0.0002	1.22	-0.007	0.033	0.0004
Observation period	Period 1: 2.87 Period 2: 2.57	<0.0002	0.032	Period 1: 26.7 Period 2: 17.1	<0.0002	0.12	Period 1: 0.51 Period 2: 0.56	<0.0002	0.005

marginal R^2 values used in our calculations of Cohen's f^2 (Lüdecke et al., 2021).

We used two-sample matched-pairs *t*-tests to test whether network densities, average shortest path length and global clustering coefficients differed between resource distribution treatments. Social network metrics that describe the overall structure of the network do not violate assumptions of non-independence, and parametric statistics can be used to compare networks of similar sizes (Croft et al., 2011; James et al., 2009). We also visually inspected whether network structure of individual populations differed between resource distribution treatments.

Figures were built in the R package GGPLOT2 (Wickham, 2016). All analyses were conducted in R version 3.6.2 (R Core Team, 2019).

3 | RESULTS

We constructed social networks from a total of 11,491 observed social interactions (867 male–male social interactions, 2765 female–female social interactions and 7859 male–female social interactions) among 400 individual beetles in 12 experimental populations. Of these social interactions, 3626 were mating interactions. We observed a similar number of social interactions in populations in environments with clumped fungus (5734 total interactions; range: 398–577 interactions per population) and dispersed fungus (5757 total interactions; range: 358–558 interactions per population). Individual beetles varied in the number of times they were observed interacting during an observation period (range: 1–71; mean \pm standard deviation: 33.55 ± 11.63 social interactions). We observed an average of 1.86 interactions per interacting pair, but the number of interactions per dyad ranged from 1 to 11.

Resource distribution had a significant but small effect on both individual strength and local clustering coefficient (Table 2; Figures 2 and 3a,c). Individual strength was higher in environments with clumped fungus (marginal mean with 95% confidence interval: 2.80 ± 0.12) than with dispersed fungus (marginal mean with 95% confidence interval: 2.65 ± 0.12 ; $p = 0.022$; Table 2; Figures 3a and 4a). However, resource distribution only explained 0.8% of the variance in individual strength relative to unexplained variance (Cohen's $f^2 = 0.008$). Similarly, beetles had higher local clustering coefficient when fungus brackets were clumped together (0.55 ± 0.014) than when fungi were evenly dispersed across the log (0.52 ± 0.014 ; $p < 0.0002$; Table 2; Figures 3c and 4c). Despite the significant difference in local clustering coefficient across environments with different resource distributions, the effect size of resource distribution on local clustering coefficient was small due to the limited amount of variance in local clustering coefficient explained by the model (Cohen's $f^2 = 0.002$; $R^2 = 0.009$). Individual betweenness did not differ across resource distribution treatments (Table 2; Figures 3B and 4B).

Females had higher individual strength (female: 3.05 ± 0.12 ; male: 2.39 ± 0.12 ; $p < 0.00002$; Cohen's $f^2 = 0.12$; Table 2; Figure 4) and betweenness (female: 25.00 ± 2.10 ; male: 18.80 ± 2.40 ; $p < 0.00002$; Cohen's $f^2 = 0.39$; Table 2; Figure 4) than males, whereas males

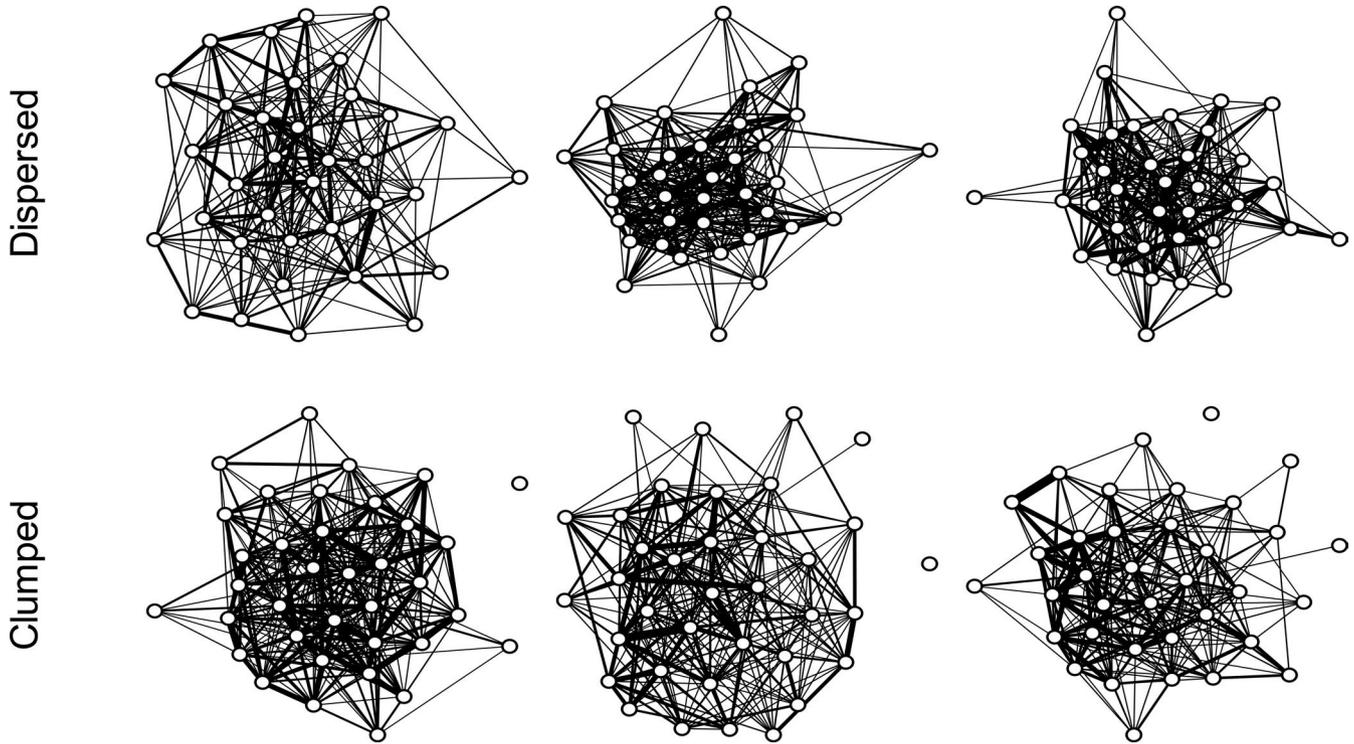


FIGURE 2 Visualizations of networks from populations experiencing dispersed or clumped resource distributions during the first observation period. Line thickness is proportional to the simple ratio index, and individual nodes are plotted using an algorithm that places highly connected nodes close together. Network visualizations include all beetles, even beetles that died. Individual and group social network metrics do not visually differ between the dispersed and clumped resource distribution treatments

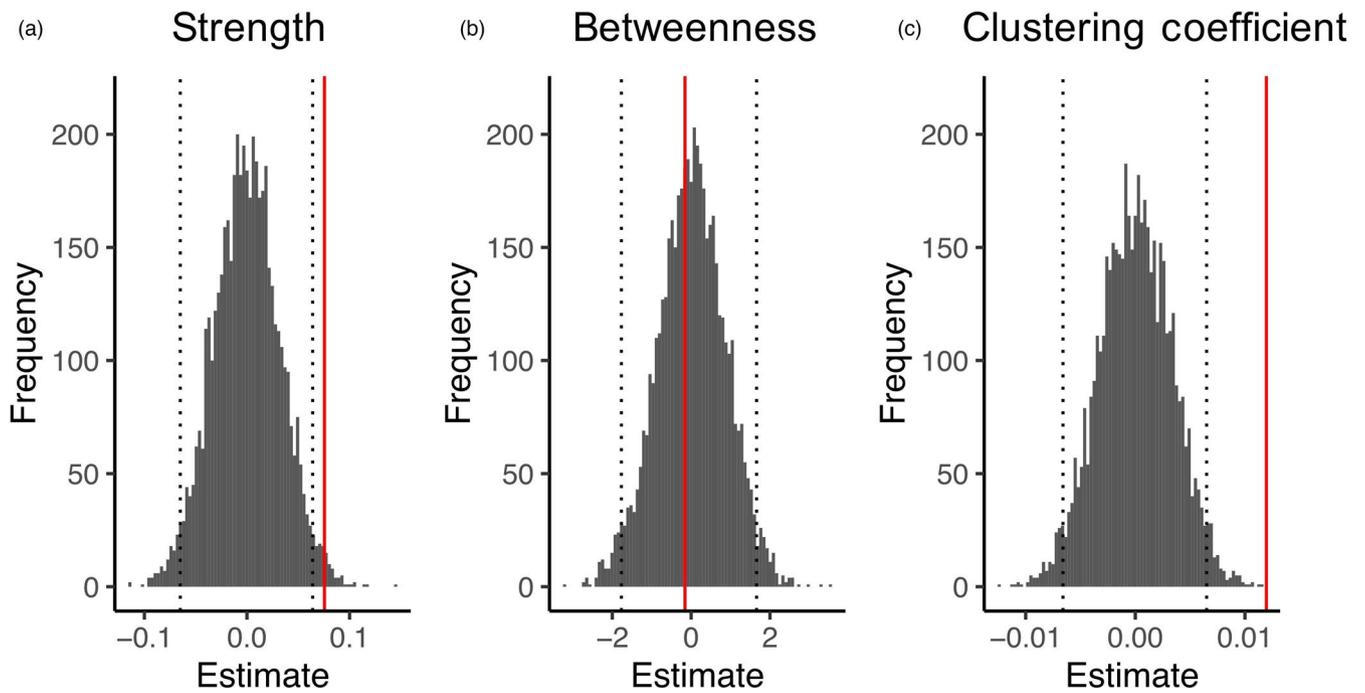


FIGURE 3 The distribution of permuted model estimates for the effect of resource distribution on (a) individual strength, (b) individual betweenness and (c) local clustering coefficient illustrates how the node permutations evaluate statistical significance. Black dotted lines indicate threshold estimate values. Values more extreme than the threshold estimate values are significant at the $\alpha = 0.05$ level. Observed model estimates are indicated by the red line and differ significantly from permuted model estimates in panels a and c

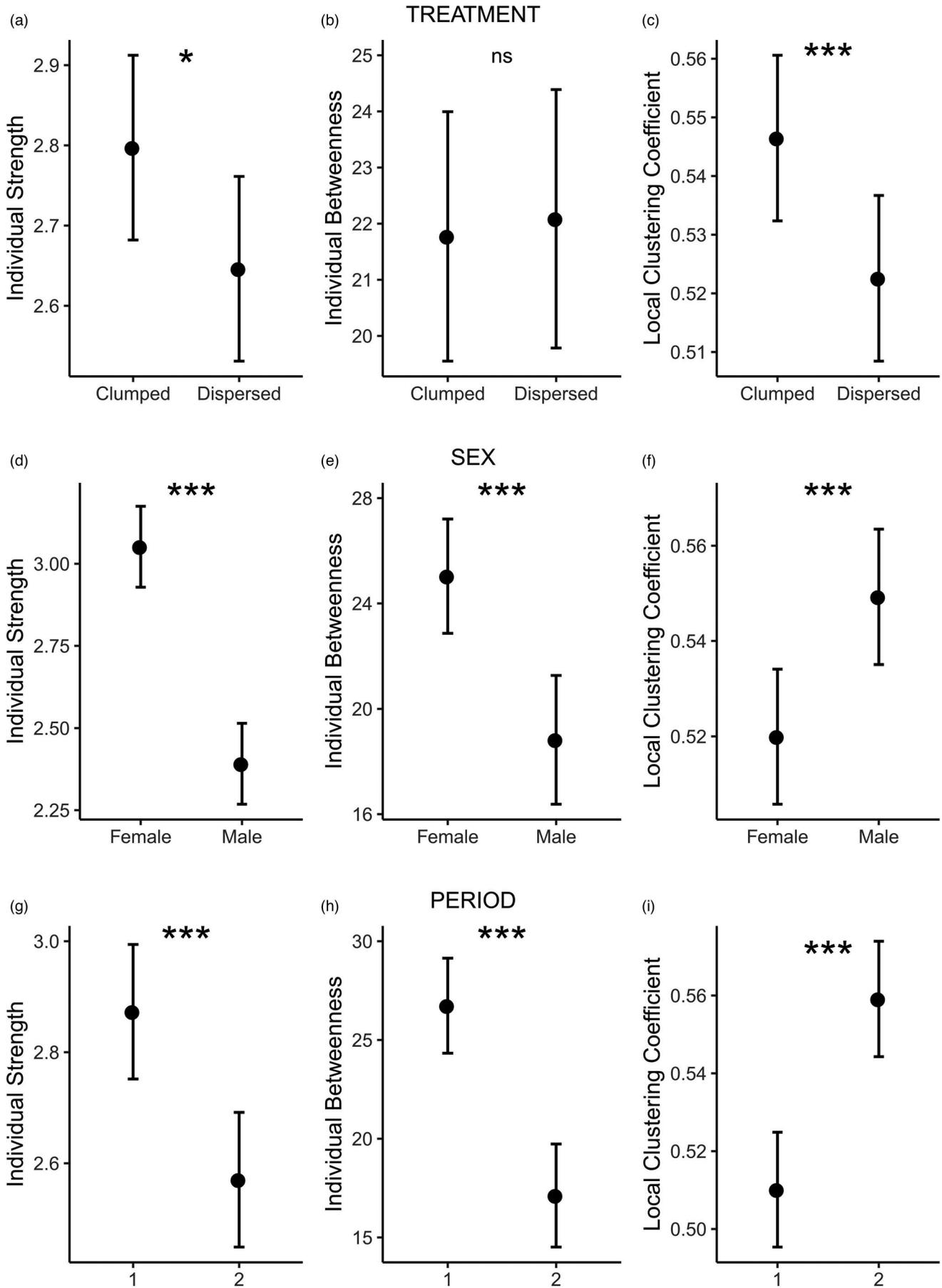


FIGURE 4 Marginal means with 95% confidence error bars extracted from linear mixed models that use observed data to test how the distribution of fungus resources (a–c), sex (d–f) and observation period (g–i) affects individual strength, individual betweenness and local clustering coefficient. Statistical significance was evaluated as the proportion of permuted model estimates that were more extreme than the observed model estimate. ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

experienced higher local clustering coefficient (female: 0.52 ± 0.014 ; male: 0.55 ± 0.014 ; $p < 0.00002$; Cohen's $f^2 = 0.002$; Table 2; Figure 4). Similarly, individual strength (period 1: 2.87 ± 0.12 ; period 2: 2.57 ± 0.12 ; $p < 0.00002$; Cohen's $f^2 = 0.032$; Table 2; Figure 3) and betweenness (period 1: 26.71 ± 2.40 ; period 2: 17.10 ± 2.60 ; $p < 0.00002$; Cohen's $f^2 = 0.12$; Table 2; Figure 4) were higher during observation period 1, while local clustering coefficient was higher during observation period 2 (period 1: 0.51 ± 0.015 ; period 2: 0.56 ± 0.015 ; $p < 0.00002$; Cohen's $f^2 = 0.005$; Table 2; Figure 4). Unsurprisingly, beetles observed more often had higher individual strength, individual betweenness, and local clustering coefficient (Table 2). Beetle elytra length did not impact any individual network metrics (Table 2).

Overall network structure did not differ across resource distribution treatments (Figures 2 and 5). The distribution of fungi did not impact network density (clumped mean \pm standard deviation: 0.43 ± 0.04 ; dispersed mean \pm standard deviation: 0.43 ± 0.05 ; $t_{11} = -0.02$; $p = 0.99$), average shortest path length (clumped: 1.48 ± 0.15 ; dispersed: 1.44 ± 0.13 ; $t_{11} = 0.83$; $p = 0.43$) or global clustering coefficient (clumped: 0.54 ± 0.03 ; dispersed: 0.52 ± 0.05 ; $t_{11} = 1.17$; $p = 0.27$).

4 | DISCUSSION

Our experiment reveals that resource distribution has a very small effect on individual social interactions and no effect on group social network structures. We found that individual connectivity (individual strength) and individual cliquishness (local clustering coefficient) of forked fungus beetles *Bolitotherus cornutus* significantly increased in environments where fungus resources were aggregated in clumps, but this difference explained very little of the variance in individual social network positions. Furthermore, individual betweenness, a measure of individual centrality that depends on the overall structure of the social network, did not change where resources were clumped. Likewise, overall network connectivity (network density and average path length) and network cliquishness (global clustering coefficient) did not differ across resource distribution treatments. Taken together, our results illustrate a surprisingly limited impact of resource distribution on individual and group social network metrics.

The small effect of resource distribution on individual social network position contrasts with patterns observed in environments with different resource abundances (Bachorec et al., 2020; Davis et al., 2016; Foster et al., 2012; Lantz & Karubian, 2017). For example, red-backed fairywrens *Malurus melanocephalus* and Egyptian fruit bats *Rousettus aegyptiacus* concentrate around resources and interact more often when food resources are scarce (Bachorec et al., 2020; Lantz & Karubian, 2017). Meanwhile, killer whales *Orcinus orcas* and degus *Octodon degus* interact in closed

cliques when food resources are abundant (Davis et al., 2016; Foster et al., 2012). In forked fungus beetles, our previous analyses of the same experimental populations established that beetles in environments with clumped fungus resources occupied dramatically smaller home ranges concentrated around fungus resources (Costello, 2020). Surprisingly, these overlapping home ranges did not translate to a difference of large effect in individual connectivity, cliquishness or centrality across environments with different resource distributions.

Unlike resource distribution, sex had a large effect on individual social network position. Differences in social network position are often observed between sexes but depend on both the species and the type of social network. Similar to our previous work in forked fungus beetles (Formica et al., 2017), we found that males and females differed in their individual connectivity, centrality and cliquishness. Females held more connected and central positions within their network, whereas males interacted more often in cliques. Social interactions in our experimental populations more often occurred among female beetles (24% of interactions) than among male beetles (7.5% of interactions). Females may have had higher individual connectivity and centrality than males if males avoided competitive interactions with other males. Furthermore, females may have interacted in fewer cliques as a direct result of males rarely interacting with other males (i.e. females interacting with two males did not often form closed cliques, whereas males interacting with two females did). The differences in individual network position between the sexes provide insight into how social behaviours of one sex may influence individual network positions of the other sex. Notably, unlike resource distribution, sex explained a large proportion of variance in individual connectivity and centrality. The difference in effect size between resource distribution and sex underscores the finding that individual characteristics, and not resource distributions, play an outsized role in shaping individual social interactions.

Surprisingly, no measure of social network structure varied across resource distribution treatments. Our experimental manipulation did not support the conclusion that real biological differences in social network structure are influenced by resource distribution. Instead, we found strikingly similar mean network structure values in environments with clumped and distributed resources. In fact, mean network density was identical in the different resource distribution treatments. Our network-level analysis of 12 experimental populations has limited power and underscores the scale required to compare network structure across experimental treatments with statistical power to reject a null hypothesis, although other experimental studies of comparable scale in this and other study systems have detected significant differences in social network structure across different experimental

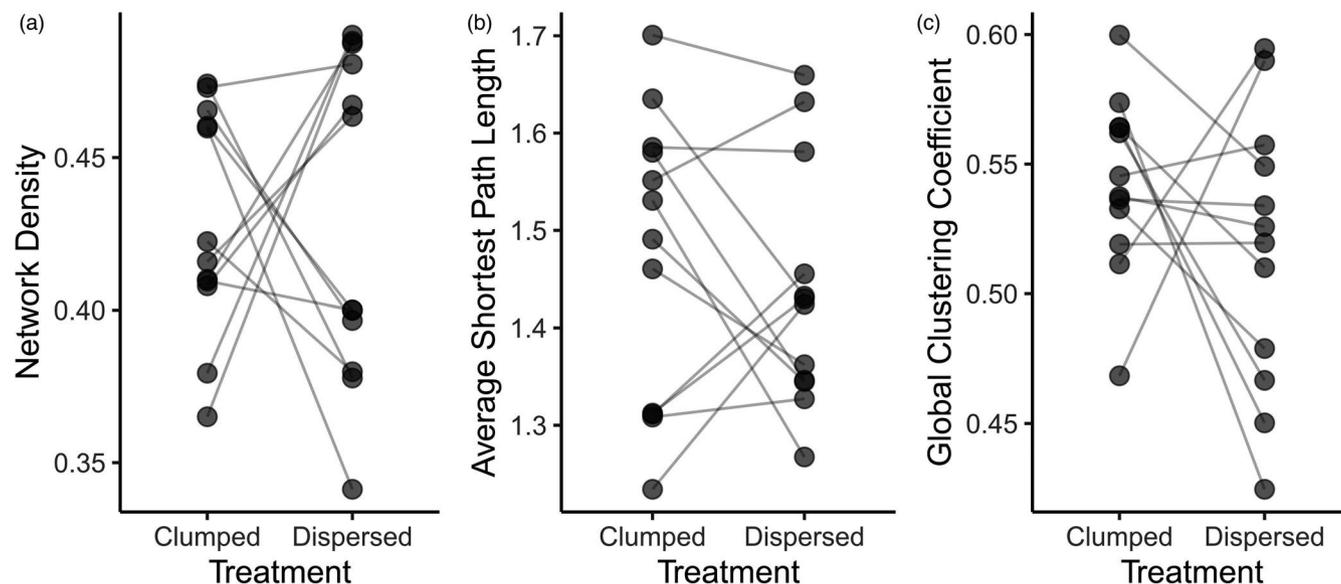


FIGURE 5 The (a) network density, (b) average shortest path length and (c) global clustering coefficient of each population in each resource distribution treatments. Lines connect social network traits of the same population in different resource distribution treatments. Paired *t*-tests revealed that the distribution of resources did not impact overall network structure

treatments (Ruch et al., 2015; Leu et al., 2016; Burns et al., 2020; Cook et al., 2022). In one study in forked fungus beetles that applied a similar experimental approach, five experimental populations composed of socially active forked fungus beetles had higher network density, average shortest path length and global clustering coefficient than five populations composed of socially inactive beetles (Cook et al., 2022). Thus, although our power to detect a difference in social network structure may have been low, we conclude that the observed lack of difference between resource distribution treatments likely reflects biological reality, not statistical insufficiency.

One potential explanation for the lack of effect of resource distribution on social network structure is that groups of individuals may produce repeatable social network structures regardless of ecological conditions. In captive populations of forked fungus beetles experiencing laboratory conditions, social network structures remained consistent in groups of beetles that reformed networks after social isolation (Formica et al., 2017). However, in our experiment, we saw that experimental populations of the same group of beetles did not produce consistent network structures in environments with different distributions of fungus resources (Figure 5). An alternative explanation for the lack of effect of resource distribution on social network structure is that temporal variation in abiotic variables such as rainfall and temperature may have greater impacts on variation in group social network structure. Our finding that observation period substantially influenced variation in individual connectivity and centrality is consistent with this interpretation. Without control populations that did not experience a change in the distribution of fungus resources, we could not quantify whether temporally varying environmental conditions impacted group social network structures. It is also worth noting that, even though previous analyses on data collected from this same experimental design revealed

dramatic changes in beetle space use behaviour across resource distribution treatments (Costello, 2020), we may have needed to employ more extreme resource distribution treatments to detect different social network structures. One final point is that we analysed social network metrics from both-sex networks that included all social interactions and that the impact of resource distribution on social networks may differ for single-sex and mating-only networks. Further work is warranted to understand the underlying causes of variation in social network structure.

Previous work on forked fungus beetles reveals the evolutionary implications of the limited impact of resource distribution on individual social network positions. In a wild metapopulation, individual connectivity and centrality but not cliquishness of male forked fungus beetles influenced individual mating success (Formica et al., 2020). Furthermore, individual connectivity and centrality but not cliquishness were highly repeatable in captive populations of forked fungus beetles (Formica et al., 2017). As such, both individual strength and individual betweenness are candidates for evolutionary change. Here, we found that individual strength and individual betweenness are unlikely to meaningfully vary across wild populations with different fungal distributions and across generations as the distribution of fungi on a log changes through time. The invariance of individual strength and individual betweenness across resource distributions highlights the possibility of consistent evolution of individual strength and individual betweenness in forked fungus beetles.

Studies exploring the effect of resource distribution on social network characteristics often focus on either how habitats shape individual positions within social networks (Lantz & Karubian, 2017; Lattanzio & Miles, 2014; Tanner & Jackson, 2012) or overall social network structure (Burns et al., 2020; Webster et al., 2013), but rarely both. We found that resource distribution had limited impacts

on individual and no effect on group network levels. Our results contrast with a study in sleepy lizards which found that habitat complexity increased overall network density but not individual association strength (Leu et al., 2016). More studies need to consider the multi-level nature of social networks, as different social network levels hold different ecological and evolutionary implications (Croft et al., 2016).

5 | CONCLUSIONS

A central tenet of the field of behavioural ecology is the expectation that the distribution of resources shapes social interaction patterns. Instead, we found a surprisingly limited impact of resource distribution on both individual and group social network metrics. Influences of sex differences and temporally fluctuating environmental conditions seemed to be more important determinants of variation in individual social network positions than resource distribution. Future research should explore whether the same factors likewise contribute to variation in group social network structures. Recent literature has emphasized the importance of studying how the resource environment shapes complex social interactions (reviewed in He et al., 2019). Our results, however, illustrate that, despite a priori expectations, the distribution of resources in the environment may not play an integral role in shaping complex social interactions at either the individual or group level.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

R.A.C. designed the study with input from E.D.B. III and V.A.F.; R.A.C. and P.A.C. collected the data; R.A.C. analysed the data with assistance from P.A.C. and V.A.F.; R.A.C. led the writing of the

manuscript. All authors contributed to the drafting of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.69p8cz93x> (Costello et al., 2022).

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