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2 **Resource availability influences global social network properties in Gunnison's prairie**  
3 **dogs (*Cynomys gunnisoni*)**  
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19 **Abstract**  
20

21 Increasingly we are discovering that the interactions between individuals within social groups  
22 can be quite complex and flexible. Social network analysis offers a toolkit to describe and  
23 quantify social structure, the patterns we observe, and evaluate the social and environmental  
24 factors that shape group dynamics. Here, we used 14 Gunnison's prairie dogs networks to  
25 evaluate how resource availability and network size influenced four global properties of the  
26 networks (centralization, clustering, average path length, small world index). Our results suggest  
27 a positive correlation between overall network cohesion and resource availability, such that  
28 networks became less centralized and cliquish as biomass/m<sup>2</sup> availability decreased. We also  
29 discovered that network size modulates the link between social interactions and resource  
30 availability and is consistent with a more 'decentralized' group. This study highlights the  
31 importance of how individuals modify social cohesions and network connectedness as a way to  
32 reduce intragroup competition under different ecological conditions.  
33

34 **Introduction**

35

36 At the heart of any social group is its members. Many factors may influence social group  
37 dynamics, including resource availability, predation, specific social interactions (e.g., tolerance,  
38 despotism), and other ecological parameters (see Lott, 1991 for review). We know, for example,  
39 that the abundance and distribution of resources can have a profound influence on grouping  
40 patterns in a number of species and there is convincing evidence that many social systems  
41 display significant sensitivity to resource availability and distribution by altering home ranges,  
42 territory sizes, mating patterns, and/or group size in response to changing ecological conditions  
43 (Lott, 1991; Jetz & Rubenstein, 2011; Botero & Rubenstein, 2012; Schradin et al., 2012). Thus,  
44 in the absence of additional benefits such as predation risk reduction, increased access to mates,  
45 or kinship-mediated cooperation – the benefits of communal resource defense alone may be  
46 sufficient to favor the formation of stable groups, underscoring the importance of understanding  
47 when and how resources drive social evolution.

48 The past decade has seen a rise in the number of empirical studies that consider the  
49 significance of resource availability when investigating social grouping patterns (Newton-Fisher  
50 et al., 2000; Ansmann et al. 2012; Leu et al., 2016). In parallel, advances in behavioral ecology  
51 have highlighted how understanding these social complexities can be enhanced within the  
52 framework of social network analysis (Wey et al., 2008). Social network analysis has allowed for  
53 a multi-faceted method for describing the complex interactions among individuals, revealed  
54 potentially emergent properties of animal societies, and influenced conservation and  
55 management strategies (Croft et al., 2004; Lusseau & Newman, 2004; Drewe et al., 2009;  
56 Madden et al., 2009; de Silva et al., 2011).

57 It is not surprising then, that our attention is turning toward using social network analysis

58 to understand the social response to resource availability. On theoretical grounds, it is predicted  
59 that the costs and benefits of social associations are likely to change with ecological conditions  
60 and there is considerable broad empirical support for a trade-off between foraging and social  
61 interactions (Croft et al., 2016). Therefore, we might expect to see this trade-off reflected in both  
62 social network properties, where, under favorable resource conditions individuals increase social  
63 interactions resulting in greater social network connectivity, both in local network properties like  
64 individual and global network. Local network properties refer to the individuals and their level of  
65 interaction in dyads and triads (e.g., betweenness, centrality, etc.), while global or group level  
66 characteristics may address things like network size, density, and clustering. Some metrics such  
67 as average path length can be examined at the level of the individual or the network as a whole  
68 (Croft et al., 2008).

69         Recently, there have been a number of studies supporting the hypothesis that resource  
70 availability shapes global group level network properties such that when resource pressure  
71 relaxes, social networks become more tightly connected. For example, in killer whales (*Orcinus*  
72 *orca*), Foster et al. (2012) show that overall network connectivity was significantly correlated  
73 with chinook salmon (*Oncorhynchus tshawytscha*) abundance. Specifically, during periods of  
74 high salmon abundance, the killer whale population became highly clustered indicating the social  
75 network became more highly interconnected. Foster et al. (2012) suggested that during periods  
76 of low food availability killer whales in this population make a trade-off between social  
77 interactions and searching for food.

78         A similar pattern was observed in wild giraffes (*Giraffa camelopardalis*), where stronger  
79 whole network connectivity occurred during the wet season, corresponding to greater food  
80 availability (Prehn et al., 2019). Additional research on African elephants (*Loxodonta africana*)

81 (Wittemyer et al., 2005) and Asian elephants (*Elephas maximus*) (Nandini et al., 2017), also  
82 support the foraging-social interaction tradeoff hypothesis in that both species had stronger  
83 individual social connections and more cohesive networks during the food-abundant wet season.  
84 In another interesting study looking at a different resource-social interaction trade-off, roosting  
85 sites in the insectivorous leaf-roosting bat, *Thyroptera tricolor*, appear to be the critical  
86 ecological resource influencing social network properties. Chaverri (2010) found that the global  
87 clustering coefficients were significantly higher in populations with a higher abundance of  
88 roosting sites.

89 Collectively these studies support the importance of ecological conditions in shaping  
90 emergent properties of social organization and reveal that ecological processes can modify social  
91 network properties at both the local and global scale. A similarity across all of these studies is  
92 that these changes happened across groups of different sizes. Although group size, or network  
93 size, is an important component of network properties, it does not necessarily determine overall  
94 global social network structure (McCabe & Nunn, 2018). This is not entirely unexpected as  
95 network theory predicts that the “sum” of the behavior and interactions of individuals can be  
96 different from the global properties of the network itself (Levorato, 2014).

97 Gunnison’s prairie dogs are an ideal system to evaluate how resource availability impacts  
98 global network structure and properties. First, there is a lack of dominance hierarchies, no  
99 significant relatedness structure, variable individual patterns of association within and across  
100 networks of differing sizes, and affiliative social networks can be consistently and reliably  
101 constructed to reflect social groups using a single behavioral measure, the greet-kiss (Verdolin,  
102 2007, 2008; Verdolin & Slobodchikoff, 2009, Verdolin et al., 2014).

103 Here, we tested the foraging-social interaction trade-off hypothesis in Gunnison's prairie  
104 dogs (*Cynomys gunnisoni*). Specifically, we explore the relationship between aboveground  
105 foraging biomass and global social network properties, while accounting for differences in  
106 network size. Previous experimental research has suggested that individual Gunnison's prairie  
107 dogs contract their individual home ranges within a territory in response to greater food  
108 availability without adjusting overall social group size (Verdolin, 2007, 2008). Therefore, we  
109 predicted that higher aboveground biomass would translate into greater overall network  
110 centralization and clustering reflecting a foraging-social interaction tradeoff.

## 111 **Materials & Methods**

### 112 *Study species and area*

113 Gunnison's prairie dogs are diurnal, highly social ground squirrels whose area is limited to the  
114 grasslands of the Colorado Plateau (Hall & Kelson, 1959). Data for the analyses presented here  
115 are based on behavioral and vegetation data collected from two colonies (HS and CC) from  
116 March-August 2004 and reflect three mutually exclusive populations, CCI, HSI, and HSII. Both  
117 colonies were located within the city limits of Flagstaff, Arizona.

### 118 *Behavioral data*

119 This study uses previously published social networks (Verdolin et al., 2014) constructed using all  
120 occurrences of greet-kissing to evaluate the role aboveground resource biomass has on shaping  
121 global network properties. Briefly, networks were constructed using adult and yearling males and  
122 females, thus inclusive of all potentially reproductive individuals (Verdolin et al., 2014).

123 Verdolin et al. (2014) found that inclusion of both males and did not affect network structure  
124 (see Supplement 1 for additional details on network size and populations). Greet-kissing  
125 behavior is a distinct, easily observable interaction that, when not followed by agonistic behavior  
126 (e.g., fights, chases), signals a mutually tolerant behavior indicative of social group membership

127 (King, 1955; Travis & Slobodchikoff, 1993; Slobodchikoff et al., 2009; Verdolin et al., 2014).  
128 Previous research by Verdolin et al. (2014) demonstrated that greet-kissing is a reliable  
129 behaviour and can be used to construct social networks in Gunnison's prairie dogs.

### 130 *Social Network Metrics*

131 To describe the networks in a global way, we estimated degree-based centralization (*NCI*,  
132 the shape of networks while considering all the connections individuals have within the group),  
133 clustering coefficient (*CC*, the probability that the immediate neighbors of a particular individual  
134 are also connected), the average path length (*APL*, the minimal number of links connecting two  
135 individuals) and the small world index (*SWI*; shows how short is the average path between two  
136 randomly chosen nodes) of all social networks.

137 The network centralization index (*NCI*) quantified the overall shape of the network. If the  
138 degree for node  $i$  is denoted by  $D_i$  and the largest degree is  $D_{max}$ , then the value of *NCI* is:

$$139 \quad NCI = \frac{\sum_i^N D_{max} - D_i}{(N - 1) * (N - 2)}$$

140 The minimal value ( $NCI = 0\%$ ) describes a regular graph, where each node has the same  
141 degree (every individual has the same number of neighbors). The maximal value ( $NCI = 100\%$ )  
142 describes a perfect star, where a single individual is directly connected to every other individual  
143 and there is link between these latter. While rare, this very unique structure does exist in nature,  
144 see Bhadra et al. (2009) for an example. High centralization indicates the presence of one or a  
145 few individuals that dominate the network in a structural sense, while low centralization  
146 indicates a more homogeneous, or democratic, network.

147 The clustering coefficient (*CC*) provides information on how localized information is  
148 spread in the network: high clustering means more intense local circulation, where individuals  
149 are tightly linked to small subgroups and these cliquish subgroups are relatively poorly

150 connected to each other (Wasserman & Faust, 1994). Low clustering means, on the contrary, a  
151 larger diversity of neighbors for an individual, less cliquish structure and information potentially  
152 spreading more freely in the network.

153 The clustering coefficient of node  $i$  ( $CC_i$ ) equals the density of the subnetwork composed  
154 by the neighbors of node  $i$ . This is the probability that its two neighbors  $j$  and  $k$  will be directly  
155 linked to each other. It can be defined as:

$$156 \quad CC_i = \frac{2 * |E(G_i)|}{D_i * (D_i - 1)}$$

157 where  $G_i$  is the subgraph composed of the nodes that are directly linked to node  $i$ ,  $|E(G_i)|$   
158 is the number of edges in this subgraph and  $D_i$  is the degree of node  $i$ . The whole network can be  
159 characterized by the average clustering coefficient calculated for all nodes. We calculated the  
160 weighted clustering coefficient that considers the size of the subgraphs and gives larger weight to  
161 a larger subgroup of neighbors.

162 The distance between two nodes  $i$  and  $j$  in a network ( $d_{ij}$ ) is the minimal number of links  
163 connecting them (i.e. the length of the shortest path length between  $i$  and  $j$ ). The whole network  
164 can be characterized by the average of shortest path lengths ( $APL$ ):

$$165 \quad APL = \frac{\sum_i \sum_j d_{ij}}{2N}$$

166 This quantifies how long (and slow) is the spread of information between any pair of individuals  
167 in the network. It is averaged for all of the path lengths between each pair of nodes, and the path  
168 length for nodes  $i$  and  $j$  is the minimum number of steps connecting them in the network (it  
169 equals 1 for directly linked neighbors; Wasserman & Faust, 1994; Wey et al., 2008). This can be  
170 an indication of the general speed of communication between individuals.

171 Finally, the small world index (SWI) can also be an indication of the general speed of  
172 communication between individuals (Killworth & Bernard 1978). The small world index (SWI)  
173 is measured as

$$174 \quad SWI = \frac{\ln N}{\ln D_{av}}$$

175 where  $N$  is the number of nodes and  $D_{av}$  is average degree. Small world networks may  
176 facilitate rapid dissemination of information as well as disease spread within a network.

177 Combined, these four metrics have been used successfully to provide a straightforward  
178 and informative description of the social dynamics in groups (e.g., marmots: Wey et al., 2008;  
179 paper wasps: Bhadra et al., 2009, Bhadra & Jordán, 2013). All social network metrics were  
180 calculated in UCINET v6.543 (Borgatti et al., 2002).

### 181 *Ecological Variable*

182 We used territory aboveground foraging biomass/m<sup>2</sup> per territory that was estimated for the  
183 social networks used in this study. Aboveground foraging biomass was calculated during  
184 previous research on these prairie dog populations that was focused on exploring the relationship  
185 between resources and social structure (Verdolin, 2007). Briefly, to quantify this value, Verdolin  
186 (2007) estimated territory size. Territory size (TS) in m<sup>2</sup> was calculated using the fixed kernel  
187 density estimator based on locations of social group members. Then, the average dry weight of  
188 food plant samples was calculated by collecting 100-cm<sup>2</sup> samples from fifteen randomly selected  
189 100-m<sup>2</sup> quadrats in each territory. Samples were placed in a flower press, and oven drying them  
190 for 24h before obtaining a dry weight (B). Finally, territory aboveground foraging biomass/ m<sup>2</sup>  
191 (B/m<sup>2</sup>) was estimated by calculating the percent cover from digital samples taken on a given  
192 territory and dividing that by size of the territory in m<sup>2</sup>. Complete details on sampling,  
193 calculation of territory size, and biomass estimates are available in Verdolin (2007). We chose

194 B/m<sup>2</sup> instead of total aboveground foraging biomass because B/m<sup>2</sup> is at a scale we feel is more  
195 relevant to an individual prairie dog.

### 196 *Statistical analysis*

197 Given the potential for multi-collinearity among the social network metrics (Croft et al., 2008),  
198 we conducted a principal components analysis (PCA) analysis with all variables. Bartlett's test of  
199 sphericity returned  $\chi^2$  of 21.092 (p = 0 .002) suggesting that principal components analysis  
200 would be useful. The results of the principal component analysis of the global social network  
201 structure variables is presented in Table 1. Following PCA, only the first principal component  
202 (PC1) had an eigenvector greater than 1 (2.61) and described 65.27% of the variance. From  
203 Table 1 is one can determine that first principal component has positive associations with  
204 network centralization index, cluster coefficient, and small world index, so this component  
205 primarily measures the cohesion of the network, though network centralization index and cluster  
206 coefficient play a larger role in explaining the variation.

207 Biomass/m<sup>2</sup> data were log transformed to reduce heteroscedasticity. We used a  
208 generalized linear regression to determine the relationship between the PC1 and resource  
209 abundance with network size as a covariate in our analyses to explore how food availability and  
210 network size influence global network properties. All statistical analyses were conducted in JMP  
211 Pro 14.

### 212 **Results**

213

214 For the three populations, we used the 14 social networks from interactions among 80 prairie  
215 dogs (CCI: 4 networks, HSI: 5 networks, HSII: 5 networks) constructed in a previous study  
216 (Verdolin et al., 2014), where each node within a network represented one individual (Figure 1).

217 The whole model generalized linear regression using network size and log biomass/m<sup>2</sup> as

218 predictors of network metrics PC1 was significant (whole model:  $R^2=0.75$ ,  $F_{3,10}=10.24$ ,  
219  $P=0.0022$ ), however, their effects were different. As network size increased PC1 decreased  
220 ( $F=23.42$ ,  $P=0.0007$ ), suggesting that larger networks were less clustered (see Figure 2a). As log  
221 biomass/m<sup>2</sup> increased, PC1 increased (see Figure 2b) indicating that as food became more  
222 abundant networks became more clustered ( $F=5.87$ ,  $P=0.0359$ ). The interaction term for this  
223 analysis was not significant ( $F=1.2969$ ,  $P=0.2813$ )

## 224 **Discussion**

225         We compared global network properties across 14 networks of different sizes and show  
226 that overall network size and resource availability play a role in shaping the nature and strength  
227 of global network structure of Gunnison's prairie dog social networks. We assessed whether  
228 properties of social networks emerge as a function of ecological conditions. Our results suggest  
229 that network structure is positively correlated with greater resource availability, in this case  
230 biomass/m<sup>2</sup>. The increased cliquishness may reflect higher levels of social interaction among  
231 individuals within a network in response to relaxed foraging pressure as resource availability  
232 increases.

233         We also discovered that network structure was negatively correlated with network size.  
234 Typically, as group size increases, networks, on average, break down into modules or cliques  
235 (Maldonado-Chaparro et al., 2015; Nunn et al., 2015). Interestingly, we found that, for  
236 Gunnison's prairie dogs, as social networks became larger, they became *less* centralized and *less*  
237 clustered. This may reflect the way in which territorial sociality emerges in this species.  
238 Frequently, the definition of a territory is fairly restrictive and assumes that individuals in a  
239 social group share a territory and that all individuals in a group occupy all portions of that  
240 territory (Burt, 1943; Maher & Lott, 2000).

241           However, in some social systems, including Gunnison's prairie dogs, a group emerges  
242 from overlap of individual home ranges sufficient to allow for communal defense of an overall  
243 resource aggregation rather than complete sharing of territories (voles: Salvioni, 1988; jays:  
244 Brown, 1974; Gunnison's prairie dog: Verdolin, 2007; primates: Willems et al., 2015). In some  
245 cases, this may be difficult to distinguish because individuals are likely to follow opportunistic  
246 behavioral 'rules of thumb' that maximize resource acquisition rather than collective action  
247 (Todd & Gigerenzer, 2000; Willems et al., 2015). Distinguishing between these two is an  
248 ongoing challenge, but research on collective decision-making largely focused on coordinated  
249 movement is yielding some exciting results and social network analysis may provide a way  
250 forward (King & Sueur, 2011). Other analyses that may prove fruitful could examine nonrandom  
251 associations based on behavioral traits like personality

252           Once a group emerges, individuals may utilize several different strategies to reduce  
253 intragroup competition, including modifying foraging strategies, adopting fission-fusion  
254 subgrouping, and/or adjusting individual spatial proximity. There is widespread empirical  
255 support for spatiotemporal flexibility in group association patterns associated with resource  
256 availability (Sundaresan et al., 2007; Aureli et al., 2008; Rubenstein et al., 2015; Haulsee et al.,  
257 2016).

258           The inverse relationship of average path length in PC1 (see Table 1) is logical when we  
259 consider network size as this would be consistent with a more 'decentralized' group. Intragroup  
260 competition for resources would necessarily increase under low availability. We suspect that  
261 modifications of space use result in fewer social interactions and leads to the decentralized  
262 networks reported here. Network size would amplify this effect. Our findings support balancing  
263 social interactions with foraging by adjusting spatial proximity in relatively stable networks. This

264 is similar to what is seen in some other species (Chaverri, 2010; Ansmann et al., 2012; Foster et  
265 al., 2012; Prehn et al., 2019). Previous research indicated that, in response to experimentally  
266 altered resource availability within territories, Gunnison's prairie dogs modified their space use  
267 within the group without a change in overall group size (Verdolin, 2007). By using network  
268 centralization, clustering, small world index and average path length as indicators, we  
269 demonstrate how communal territorial defense and occupancy can be maintained in the face of  
270 intragroup competition costs associated with increasing group size through a decentralization of  
271 the social network.

272         One potential concern with respect to this interpretation is that several of the networks are  
273 small and this may be problematic. However, for average path length specifically, the  
274 relationship between average path length and network size is robust across networks of different  
275 sizes (Steuer & Lopez, 2008). Although it is not surprising that network topologies might vary  
276 considerably in the degree to which they are influenced by network size, we suggest, on basis of  
277 our results and that of other studies, that these patterns may vary in biologically meaningful  
278 ways. Previous research by Wey et al. (2008), Levorato, (2014), and McCabe & Nunn, (2018),  
279 all indicate interactions of individuals within the network do not necessarily characterize the  
280 global properties of the network itself. At the same time, it become very challenging to separate  
281 out how much network size influences these global properties in ways that are meaningful. We  
282 think this aspect warrants further investigation to tease apart how much of the relationship  
283 between network size and global properties can add to our understanding of group-level  
284 dynamics in a species.

285         Past research on Gunnison's prairie dogs clearly supports cooperative territory defense by  
286 both male and female prairie dogs within a social group (Slobodchikoff, 1984; Travis &

287 Slobodchikoff, 1993; Verdolin, 2007). Furthermore, experimental studies manipulating the  
288 spatial and temporal distribution of food abundance has shown that individuals modify their  
289 home range and that, consequently, the collective territory size changes (Verdolin, 2007).  
290 Therefore, we expected that food availability would similarly alter the social interactions among  
291 individual within a group and be evident in the global network properties we measured. Our  
292 results supported this prediction and demonstrate that the influence of resource availability and  
293 network size on cohesion reflect behavioral decisions made by prairie dogs in response to their  
294 perception of the local environment.

295         The implications of this research extend beyond advancing our understanding of the  
296 ecological selection pressures that shape social behavior and have direct applications for  
297 management and conservation. In many areas, human-prairie dog conflicts are common, and  
298 relocation of populations is a tool that is utilized for all four endemic species of prairie dogs  
299 across their ranges. The survival of relocated prairie dogs is highly variable and frequently  
300 extremely low (25-50%) (Roe & Roe, 2004; USFWS, 1991). Although it has been suggested that  
301 the overall number of individuals released is a factor (Robinette et al., 1995), there is evidence  
302 that habitat quality, burrow availability (preferably natural), predator-experience, and moving  
303 intact social groups play a more important role in survivorship (Roe & Roe, 2003, 2004; Shier,  
304 2006; Shier & Owings, 2007).

305         Habitat quality can mean different things, but in the context of relocations of prairie dogs,  
306 the emphasis is on vegetation, soil substrate, slope, and burrow availability (Roe & Roe, 2003),  
307 not aboveground foraging biomass availability. Based on the results presented here, we  
308 recommend that when relocating prairie dogs, it is important to match prairie dogs with areas of  
309 similar resource availability of their original territory and release social groups together in a

310 similar spatial orientation to their original habitat because we know that there are some  
311 individuals that act as bridges across networks (Verdolin et al., 2014) and releasing individuals in  
312 this way can facilitate maintaining the integrity of these interactions as well as keeping the social  
313 network structure intact potentially facilitating higher survival. Additionally, since relocations  
314 often happen quickly with little time to conduct extensive behavioral observations, we also  
315 strongly recommend utilizing greet-kissing behavior to rapidly identify social groups.

316 We acknowledge there are some limitations to the dataset we used, principally that we  
317 have a small sample size of 14 networks and there may be issues comparing with networks of  
318 varying sizes. However, this would be most problematic when attempting a longitudinal or  
319 replicative analysis within a population or a comparative analysis across species (Faust &  
320 Skvoretz, 2002). Additionally, the results we report are consistent with previous research on  
321 Gunnison's prairie dogs, while simultaneously providing new insights. Thus, we feel the results  
322 and interpretation presented are robust.

### 323 324 **Conclusions**

325 By linking social network analysis to resource availability, we can enhance our ability to identify  
326 and assess how key environmental parameters might influence patterns of interactions within  
327 networks. Here, we demonstrated a link between resource abundance, network size, and global  
328 social network properties and provide new evidence that sociality is a flexible behavior pattern  
329 modulated by ecological and local network-level processes. In addition, Gunnison's prairie dog  
330 social networks may trade small world network structure for resilience. However, we don't yet  
331 know whether subgrouping within a network is non-random or functional as in bonded core  
332 groups as in dolphins (Wiszniewski et al., 2009) and elephants (Wittemyer et al., 2005; Schutter  
333 et al., 2014).

334 Further research needs to focus on comparative studies examining taxonomic patterns of  
335 social networks (Farine & Whitehead, 2015), resource availability, and the influence of various  
336 data collection methods (Perkins et al., 2009). Perhaps most importantly, understanding  
337 intraspecific social variation in response to changing conditions can make it possible to predict  
338 whether (and how) social organisms will respond to particular changes in their environment; the  
339 ability to make such predictions is critical to conserving social species facing a variety of  
340 anthropogenic pressures (Sih et al., 2011; Schradin, 2013). We see evidence of this coming from  
341 work on lions where Dunston et al. (2017) also showed that the social network structure of  
342 Africa lion prides was crucial to predicting successful reintroduction. More research along these  
343 lines is necessary, particularly for species of concern or those targeted for reintroductions. For  
344 prairie dogs, where relocations are frequently used, understanding how differences in resource  
345 abundance in new location will influence the existing group social dynamics is critical to  
346 improving outcomes.

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**Figure 1.** The social networks of the 14 social groups: Yellow: HSI-1 (a), HSI -2 (b), HSI -3 (c), HSI-4 (d), HSI -5 (e), HSII-1 (f), HSII-2 (g), HSII-3 (h), HSII-4 (i), HSII-5 (j), CCI-1 (k), CCI-2 (l), CCI-3 (m) and CCI-4 (n). The nodes represent individuals and the lines represent unweighted edges in the network.

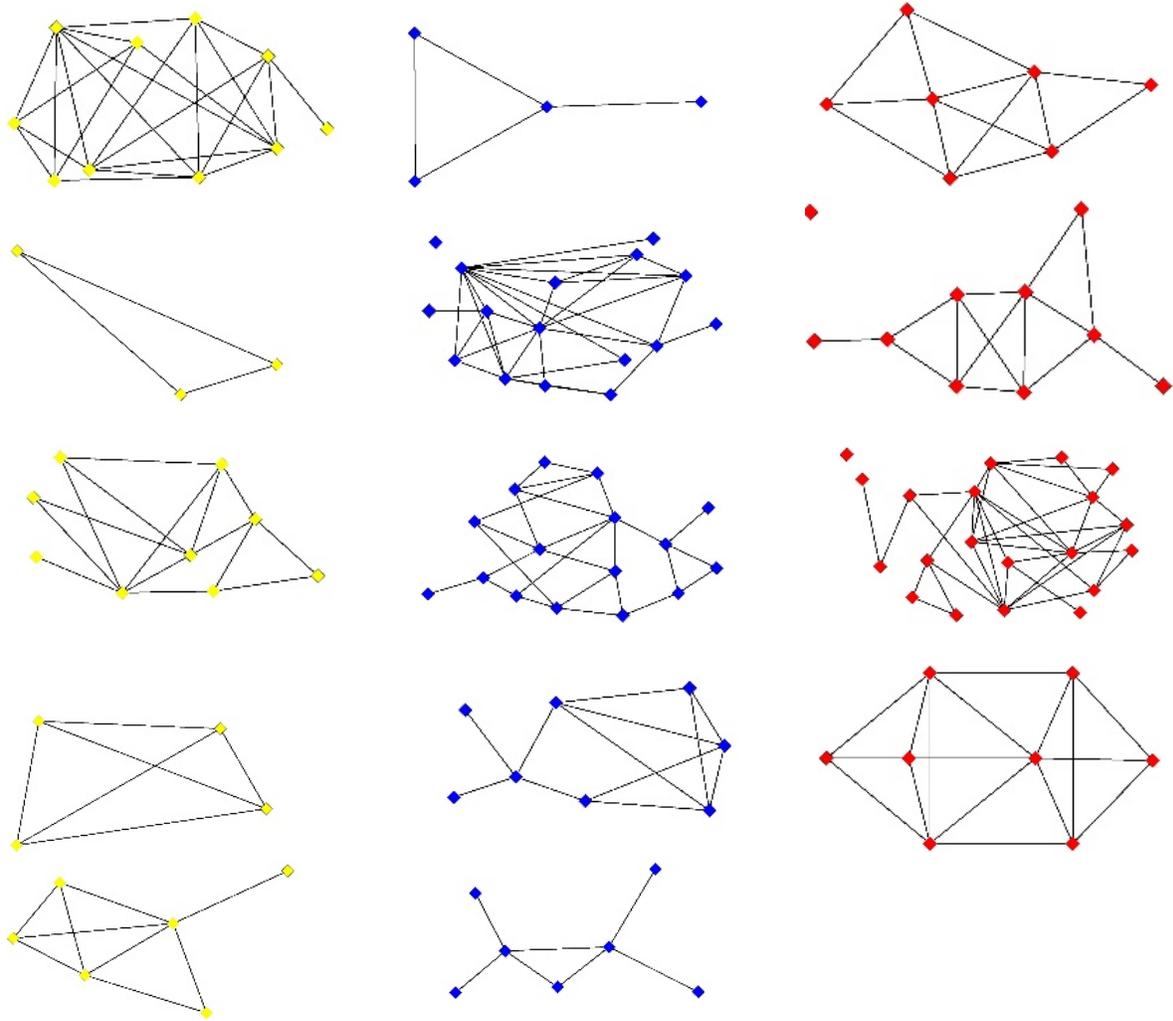
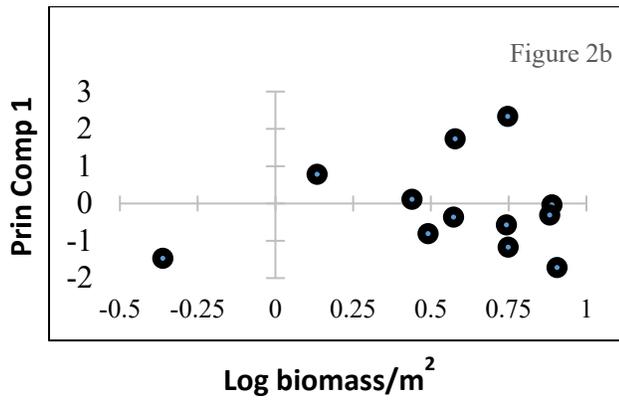
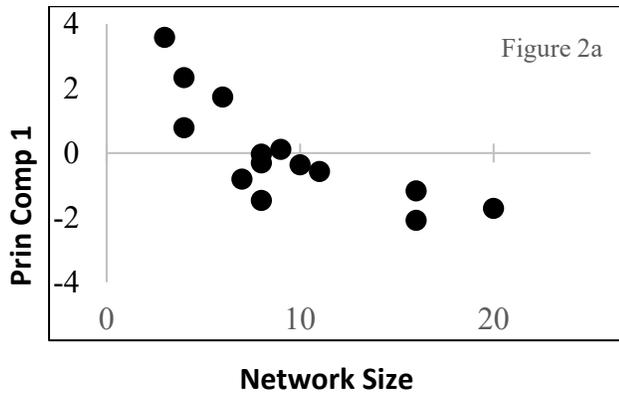


Figure 2a-b. Relationships between (a) PC1 and network size and (b) PC1 and log biomass/m<sup>2</sup>



1 Table 1. Principal component analysis loading matrix, eigenvalues, percent variation  
 2 explained, and significance. Values in bold reflect loadings and eigen values above the  
 3 minimal threshold, as well as  $X^2$  values that yielded significant p-values (also in bold).

<b>Principal Component</b>				
<b>Variable</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>
NCI	<b>0.542</b>	-0.356	-0.149	<b>0.747</b>
CC	<b>0.536</b>	0.035	<b>0.8176</b>	-0.208
APL	<b>-0.542</b>	0.264	<b>0.502</b>	<b>0.619</b>
SWI	0.354	<b>0.896</b>	-0.239	0.122
Eigenvalue	<b>2.61</b>	0.808	0.359	0.221
% Variation	65.27	20.20	8.98	5.551
$X^2$	<b>21.09</b>	4.829	0.601	-
P-value	<b>0.002*</b>	0.498	0.882	-

4