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Title: The topology of spatial networks affects stability in experimental metacommunities

1   The topology of spatial networks affects stability in experimental metacommunities
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8
9   Abstract
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12   Understanding the drivers of community stability has been a central goal in ecology.

13   Traditionally emphasis has been placed in studying the effects of biotic interactions on

14   community variability, and less is understood about how the spatial configuration of habitats

15   promotes or hinders metacommunity stability. To test the effects of contrasting spatial

16   configurations on metacommunity stability, I designed metacommunities with patches

17   connected as random or scale-free networks. In these microcosms, two prey and one protist

18   predator dispersed, and I evaluated community persistence, tracked biomass variations, and

19   measured synchrony between local communities and the whole metacommunity. After 30

20   generations, scale-free metacommunities had lower global biomass variability and higher

21   persistence, suggesting higher stability. Synchrony between patches was lower in scale-free

22   metacommunities. Patches in scale-free metacommunities showed a positive relationship

23   between variability and patch connectivity, indicating higher stability in isolated

24   communities. No clear relationship between variability and patch connectivity was observed

25   in random networks. These results suggest the increased heterogeneity in connectivity of

26   scale-free networks favors the prevalence of isolated patches in the metacommunity, which

27   likely act as refugia against competition—the dominant interaction in this system—resulting

28   in higher global stability. These results highlight the importance of accounting for network

29   topology in the study of spatial dynamics.

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34 **Introduction**
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37 Identifying the drivers of community temporal dynamics, including stability in response to

38 perturbations, has been a central goal in ecology [1–4]. Whether these drivers are biotic,

39 abiotic or some combination of both is largely context dependent, but understanding how and

40 under which circumstances these drivers operate is the key to predicting how systems

41 respond to different scenarios. In community ecology, the concept of "stability" can be

42 defined in multiple ways. Given the difficulty of its study in empirical systems, the

43 operational definitions of stability often differ from the mathematical definition. In a strict

44 sense stability can be defined as the ability of a system to return to its initial conditions after a

45 perturbation [5]. In practice, ecological studies also consider measures of community

46 permanence [6], species persistence or turnover [5], and the temporal invariability of a

47 community descriptor [3,7], as measures of stability. In this study I will use the latter two as a

48 proxy for stability.

49 Historically, much emphasis has been placed on studying biotic drivers of community

50 invariability/stability. In particular, the effects of species interactions have been frequently

51 studied under the diversity-stability relationship framework [2,8–11]. Findings in this field

52 are diverse, but they emphasize the large role that interactions play in community function.

53 Evidence regarding the effects of competition on community stability is varied. Some

54 studies report little to no influence of competition or interaction strength on community

55 variability, but note stronger effects at the population level (Ives et al. 1999). However, other

56 sources report that competition decreases community stability (Yodzis, 1981, Allesina &

57 Tang 2012). Experimental studies have also revealed that interaction strength in competitive

58 communities can not only alter the relationship between community biomass and stability,

59 but also the range of variation of biomass [15]. Other interactions, such as predator-prey,

60   have been described as stabilizing for communities when interaction strength is high, while

61   mutualistic interactions are destabilizing [14].

62   Abiotic drivers of community stability have been seldom addressed as such. Most

63   studies in this context have focused on environmental fluctuations as drivers and although

64   many community-level properties can track changes in abiotic conditions over time [16], it is

65   the species-specific responses to environmental fluctuations that affect diversity-stability

66   relationships [12]. In such cases, compensatory dynamics can confer stability to communities

67   under scenarios of environmental fluctuations [17].

68   Spatial dynamics can have stabilizing effects on metacommunities [18,19] and

69   metaecosystems [20]. Although it was been shown that the pattern of habitat connectivity

70   affect metacommunity persistence [21] and can modulate the importance of the different

71   drivers of metacommunity dynamics [22,23] we currently lack a clear understanding of how

72   it affects metacommunity stability. Thus, we are far from being able to draw general

73   predictions if its effects under complex scenarios. Network topology is a key feature of

74   spatial systems as it can dictate the connectivity pattern between local communities and

75   determine—among other things—the "ease" at which elements can move through the

76   network. For example, random networks are characterized by having nodes (i.e., patches)

77   with very similar number of connections, and therefore their "connectivity" frequency

78   distribution (i.e., degree distribution) follows a Poisson distribution (Fig. 1; top panel) where

79   most patches have an average number of connections and only a few are poorly or highly

80   connected (Erdös & Rényi, 1960). Conversely, in a sparser scale-free network whose degree

81   distribution approximates a power law (Fig. 1; bottom panel), most nodes are poorly

82   connected and only a few are highly-connected hubs [25]. These topological differences can

83   not only determine the network's resilience and robustness against perturbations, but it also

84   control the speed at which "information" (species) can spread. In an ecological scenario, we

85 can think of organisms as information, and their movement should be easier in more

86 homogeneous networks (i.e., random) than in those that are sparser (i.e., scale-free).

87 Dispersal can affect stability through the synchronization of local dynamics [26]. Restriction

88 in the movement of individuals can be the key to maintain asynchrony in metacommunities

89 where local communities are at different stages of consumer-resource fluctuations [27].

90 Similarly in competitive metacommunities high levels of dispersal can lead to competitive

91 exclusion [28,29]. Consequently, if spatial topology determines dispersal, we can expect

92 lower stability in networks that facilitate inter-patch movement.

93   In fact previous studies have shown that network topology has strong and contrasting

94 effects on metapopulation [30] and metacommunity dynamics [31]. Some of the proposed

95 mechanisms behind diversity-stability relationships have also been shown to have contrasting

96 effects between communities and populations. Diversity can foster community stability but

97 have neutral effects on populations [32]. Specifically, competition can enhance community

98 stability but destabilize local populations [7,18]. In this context, understanding how network

99 topology affects community stability and how patch metrics relate to variability, will help to

100 identify those local communities that are more susceptible to extinction and consequently

101 those that should be the target of protective measures for habitat conservation and

102 management.

103   To empirically assess the relationship between habitat configuration and

104 metacommunity stability at the local and regional scale in a system with competitive and

105 predator-prey interactions, I compared experimental metacommunities configured as random

106 or scale-free networks. Given their differences in connectivity, I hypothesize that random

107 metacommunities —the more homogeneous topology— will allow an easier dispersal of

108 organisms across the system, decreasing stability at the local and global scale as a result of

109 the increased likelihood of encountering enemies. Conversely, in scale-free

110   metacommunities, where connectivity is sparser, the higher proportion of isolated patches

111   will allow the persistence of local communities, increasing overall stability.

112

113   **Methods**

114   *Experimental setup*

115   I selected two contrasting network topologies—Erdös-Rényi (from here on random) and

116   scale-free—to represent a biologically plausible range of connectivity in natural

117   metacommunities. Using the R package 'igraph' (v. 1.2.4.1) I created two different 24-patch

118   realizations of each network topology and I used 24-well plates to recreate them as protist

119   landscapes. Each of them was experimentally replicated four times (Fig. 1). For this, I filled

120   each well (i.e., patch) with protist media (0.37 g Protist pellet and 0.07 g Herptivite in 1.4 L

121   of well water bacterized with *Proteus vulgaris*, *Serratia marcesens*, *Bacillus subtilis* and

122   *Bacillus cereus*) and connected them according to the layouts using glass capillary tubes

123   filled with protist media. Each well plate—now considered a 24-patch metacommunity—

124   contained a food web module of three protist species, *Paramecium tetraurelia*, *Paramecium*

125   *bursaria* and *Dileptus anser*. The two bacterivore species (*P. tetraurelia* and *P. bursaria*)

126   were initially inoculated in a third of the local communities/wells at random and the predator

127   *D. anser* was added after four days. Microcosms were allowed to develop as organisms

128   dispersed for over 80 protist generations, during which time I measured the abundance of

129   each species in each local patch by directly counting individuals with a stereomicroscope

130   three times per week.

131   To measure biomass, I took photographs of between 10 and 35 individuals of each

132   species and estimated their surface area using ImageJ [33]. I calculated biomass using these

133   surface area estimations, the value of the density of water and the abundance counts per

134   patch.

135   I defined species persistence as the length of time from the start of the experiment

136   until the first extinction of a species in the metacommunity. A species was considered

137   "extinct" when it was not observed for at least two consecutive samplings.

138

139   *Analysis*

140   To compare the curves of community biomass over time for the two types of networks I used

141   profile analysis using the 'profileR' R package. This analysis allows to compare curves by

142   checking for differences in parallelism and the similarity of response levels [34]. The

143   parallelism portion of the analysis tests whether segments of the curve are oriented similarly

144   between groups (e.g., are parallel). If the answer is positive, then a MANOVA is performed

145   to test for equal levels, and find differences in the average value per group.

146   To evaluate community variability, I used the data of the first 30 days of the

147   experiment (roughly 30 protist generations), which is the period of time when predators were

148   observed. There are multiple ways of defining community stability (see Lehman & Tilman

149   [2000] for more details), but the most common are a measure of temporal variability —such

150   as the coefficient of variation of a community descriptor such as biomass, or its reciprocal

151   [4,7,16,18,35]—or a measure community persistence [5,36].

152   I calculated the coefficient of variation (CV) of total biomass across time (pooling the

153   biomass of all species) both at the metacommunity (per plate) and local level (per well). I

154   evaluated differences in the CV of pooled biomass (community-level estimation) and per-

155   species biomass between network topologies at the metacommunity scale using generalized

156   linear mixed models (GLMMs) with network replicate as a random factor. I measured

157   community persistence as the number of days all species were counted as present in the

158   system and I analyzed the differences using a GLMM with network replicate as a random

159   factor. Additionally, I evaluated metacommunity synchrony by calculating the zero-lag

160   correlations between the time series of community biomass of each local community and

161   total biomass of all other patches, using the Gross et al. (2014) index included in the R

162   package 'codyn' [38]. Differences between topologies in these two descriptors were

163   evaluated using a generalized linear model since the GLMM approach showed that no

164   variance was explained by the random factor.

165   To characterize the patches and their location in the network I used two metrics that

166   have been previously used to describe node position/importance within a metacommunity

167   network [39–41]: degree and closeness centrality. Degree corresponds to the number of links

168   (i.e., neighbors) between a focal patch and other patches in the network. Closeness centrality

169   is measured as the reciprocal of the average shortest path length between a focal node and all

170   the other nodes in the network. Therefore, higher values indicate nodes that are closer to

171   others or "more central". These relationships were also analyzed with GLMMs, in this case

172   with patch metric and network as predictors, and network realization as random factor, and in

173   the case where the random factor did not explain any variance, I used a GLM. Model

174   specifications for all analyses are detailed in the supplementary material as well as the

175   frequency distribution of these patch metrics in the networks used in the study (Figs. S1 and

176   S2).

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178
179   **Results**
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181   All metacommunities showed some temporal variation of biomass. The peak biomass in all

182   metacommunities occurred around day 5 and steeply declined afterwards (Fig. 2). Although

183   both types of metacommunities followed a similar temporal trend, biomass was consistently

184   higher in scale-free metacommunities. This was confirmed with profile analysis, which

185   showed that the network-specific curves were parallel (Hotelling's $T^2 = 8.594$, $F_{11,4} = 3.125$,

186    $p=0.141$) but with different elevations ($F_{1,14}=20.63$, $p=0.00046$).

187   On a global scale, inferred community stability was higher in scale-free

188   metacommunities (Fig. 3) as they showed lower coefficients of variation than random

189   metacommunities (GLMM network: χ_1^2= 9.0219, p = 0.002). Similarly, when comparing

190   stability at the local level scale-free networks showed lower CV values than random

191   ($F_{1,14}$=19.06, p=0.00064). Differences in metapopulation level stability (i.e., measured

192   separately per species) between networks were observed only for *P. tetraurelia* (GLMM

193   network: χ_1^2= 10.551, p = 0.0011; Fig. S3).

194   Metacommunities with different topologies also differed in species persistence (Fig.

195   4A). In scale-free metacommunities the complete 3-species food web module was present in

196   the system for about 10 generations longer than in random metacommunities (GLMM

197   network: χ_1^2= 14.07, p = 0.0001). The reduction of spatial synchrony has been suggested as a

198   promoter of metapopulation [42,43] and metacommunity persistence [44], in this study it

199   could be one of the explanation for the differences in persistence of metacommunities with

200   different topologies. Even though spatial synchrony in both types of metacommunities was

201   generally low (calculations were very close to 0), scale-free metacommunities had lower

202   values than random networks ($F_{1,12}$ = 6.231, p = 0.0281; Fig. 4B).

203   At the local scale, stability decreased in relation to patch closeness centrality only in

204   scale-free metacommunities ($F_{1, 380}$ = 0.747, p = 0.003), while no effect evident for random

205   metacommunities (Fig. 5). Conversely, patch degree had no effect in the stability of local

206   communities.

207
208   **Discussion**
209

210   Network topology had clear effects on overall metacommunity stability. Globally,

211   metacommunities arranged as scale-free networks showed higher levels of functioning (i.e.,

212 as measured by biomass), lower temporal variability, and increased persistence time of all

213 three species.

214   Asynchrony between the dynamics of local patches can have stabilizing effects on

215 communities [4,44]. Downing et al. (2014) studying aquatic food webs in mesocosms found

216 that the stabilizing effects of species asynchrony in their experimental system are more

217 evident when comparing open and closed systems, suggesting this feature is particularly

218 relevant for metacommunities. In this experiment, spatial asynchrony was slightly higher in

219 scale-free metacommunities. Comparing these results with a previous study focused on

220 metapopulations where random and scale-free systems had high but similar values of

221 asynchrony between local patches [30] reinforces the importance of interactions in these

222 systems.

223   Observing the dynamics of local communities also provides insights into the

224 mechanisms driving these differences between topologies. In scale-free metacommunities,

225 there is a positive relationship between patch isolation and stability, which translates into

226 increased global stability likely due to the higher proportion of isolated patches in scale-free

227 than in random metacommunities. These results are opposed to findings by McCann et al.

228 (2005) whose models predict that fragmented or more isolated habitats should be more prone

229 to the destabilizing effects of mobile predators. However, it is likely that in this experimental

230 system isolation creates spatial refugia which dampen the effects of predators on prey. If this

231 is the case, then it is reasonable to expect a decrease in the frequency of negative interactions

232 in scale-free metacommunities. Given the nature of the data collected, I can only approach

233 this by using different combinations of species co-occurrences as a proxy for frequency of

234 interactions. Although it is an imperfect approximation, there was no difference in the

235 frequency of co-occurrences between types of networks (Fig. S4, Table S1), suggesting that

236 connectivity may not have directly affected the occurrence of the interactions but perhaps it

237 modulated their strength.

238   One of the main differences between random and scale-free networks is the

239 differences in the level of connectivity. Random networks are more homogeneous and

240 therefore the transmission of information between distant nodes—in this case dispersal of

241 organisms between patches—is easier and faster than in scale-free networks. Gravel et al.

242 (2016), in a modelling study where connectivity is not addressed explicitly, describe a

243 relationship between stability and dispersal that increases to an asymptote in heterogeneous

244 landscapes, which differs from the trends observed in this study. Even considering that

245 habitat heterogeneity acts as a stabilizing force in metacommunities, and that this factor is

246 absent in this study, it would still be reasonable to expect the same general trend but perhaps

247 with lower stability values, which is not the case in this experiment. However, another aspect

248 of these dynamics suggests that dispersal stabilizes meta-ecosystems by modulating

249 interaction strength in a way that stability in a spatial system depends on interactions

250 averaged across space instead of their local coefficients (Gravel et al. 2016). In this study,

251 topology could modulate this relationship even further, producing the observed differences.

252   The effects of weak interactions in communities can also be idiosyncratic. In general

253 it has been proposed that they have stabilizing properties for communities compared to strong

254 interactions [19,46–48]. Recent studies have shown that different trophic groups contribute

255 differently to metacommunity stability. Particularly, competitive interactions in a food web

256 can weaken spatial synchrony and affect stability [49]. In this case, and given the high

257 frequency in which the competitor species co-occur in comparison to predator-prey co-

258 occurences —and unless interaction strength between predators and prey is high (in this case

259 it is not, see Fig. S5)— it is possible that competition between the two prey species is

260 stronger than predation. If this is true, then the increased isolation in scale-free

261 metacommunities would likely create refugia against competition and not so much against

262 predation. Competition has been described as a destabilizing force for communities [14],

263 therefore the "protection" against it in scale-free networks through refugia, results in an

264 overall positive effect on global stability. I suggest that the increased persistence of the

265 predator in scale-free systems should be considered a consequence of the increased

266 availability of prey but it does not contribute to overall stability *per se*.

267 Other studies have shown that abiotic factors—such as precipitation—have an indirect

268 effect on community variability acting through biotic interactions [16]. It has been suggested

269 that spatial heterogeneity can alter the variability of interaction strength [20] and ultimately

270 community stability and diversity [50], and in this study I show that spatial configuration can

271 determine community stability by creating refugia against competition.

272 Although the experimental setup used in this study only allows to draw limited

273 conclusions regarding long-term community stability, the results presented here encompass

274 over 30 protist generations and provide solid support for the idea of spatial configuration

275 being a key factor in community functioning.

285
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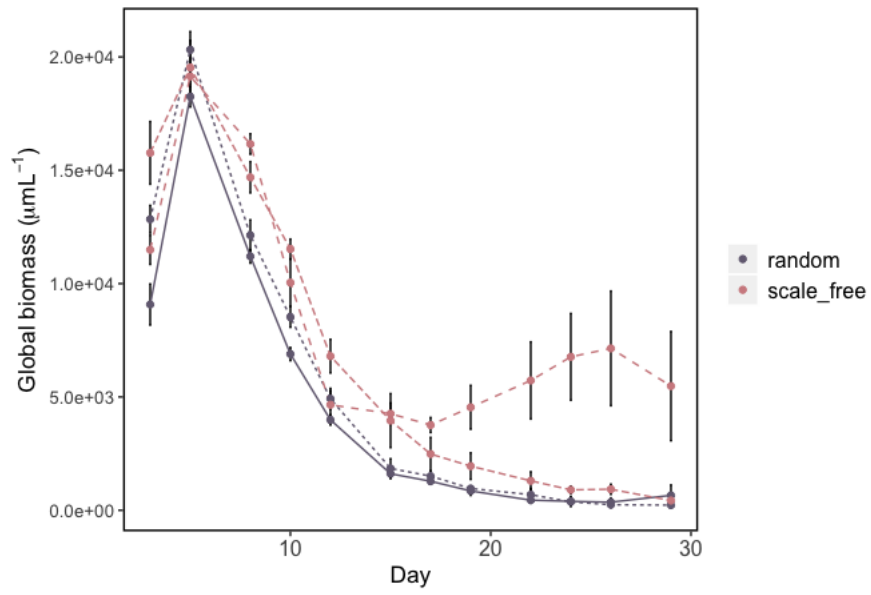
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412 **Figures**
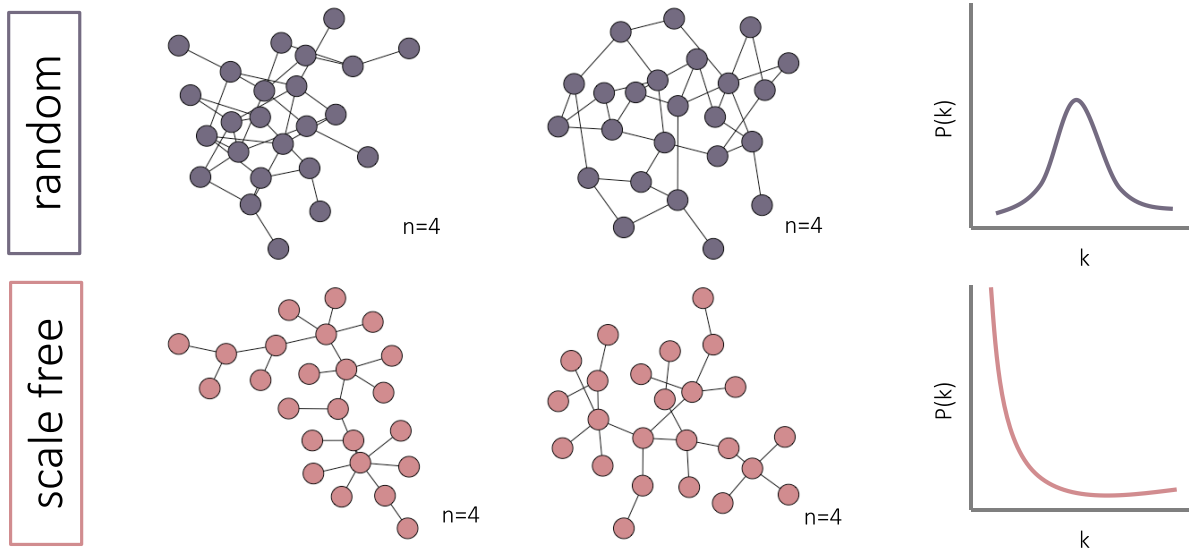
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414 Figure 1. Layouts of random and scale-free networks used in the experiment, and their idealized

415 degree distribution on the right. Each network realization (i.e., layout) was replicated four times
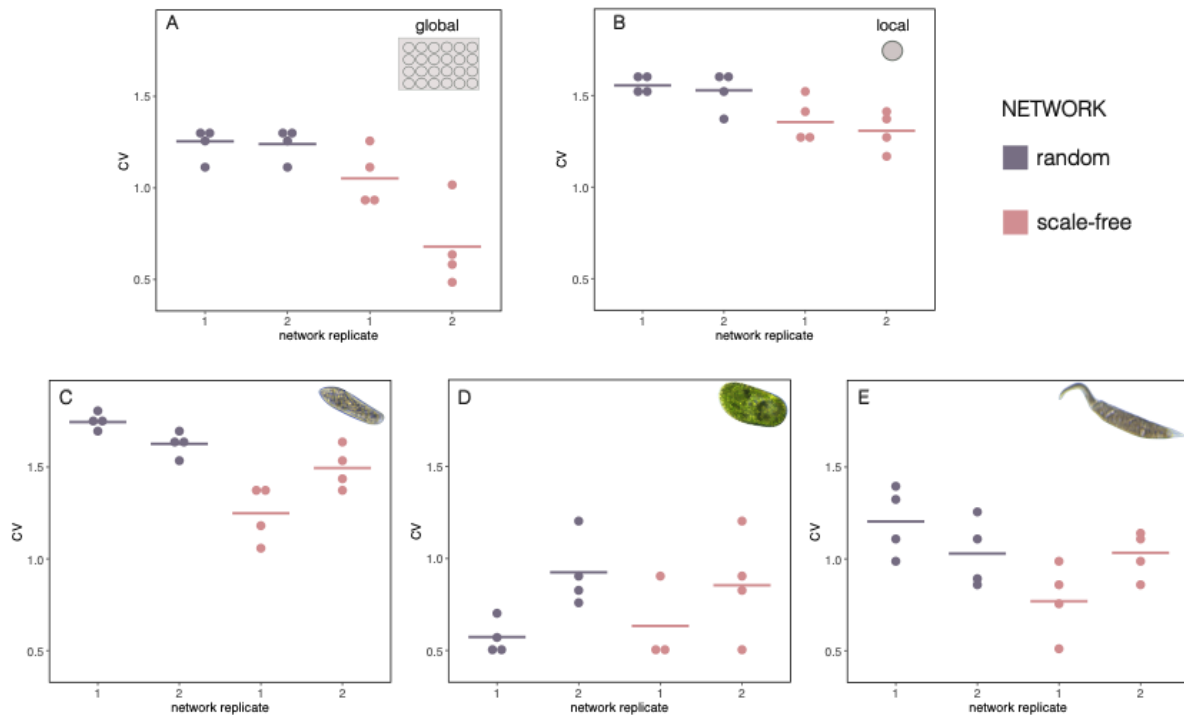
416 in the experiment.

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420 Figure 2. Biomass variation over time, calculated at the metacommunity level for

421 metacommunities connected as random (purple) and scale-free (pink) networks ($\overline{X} \pm$ S.E.; n =

422 4). Same color lines correspond to network-level replicates.

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Figure 3. Metacommunity variability measured as the coefficient of variation (CV) of

biomass in random (purple) and scale-free (pink) (n =4). Horizontal bars represent the mean.

(A) CV corresponds to the variation in community biomass across the entire metacommunity

(all habitat patches considered together), (B) shows the variation of biomass in local

communities (i.e. patches), (C) CV of biomass for *P. tetraurelia,* (D) CV of biomass for *P.*

bursaria, and (E) CV of biomass for *D. anser.*
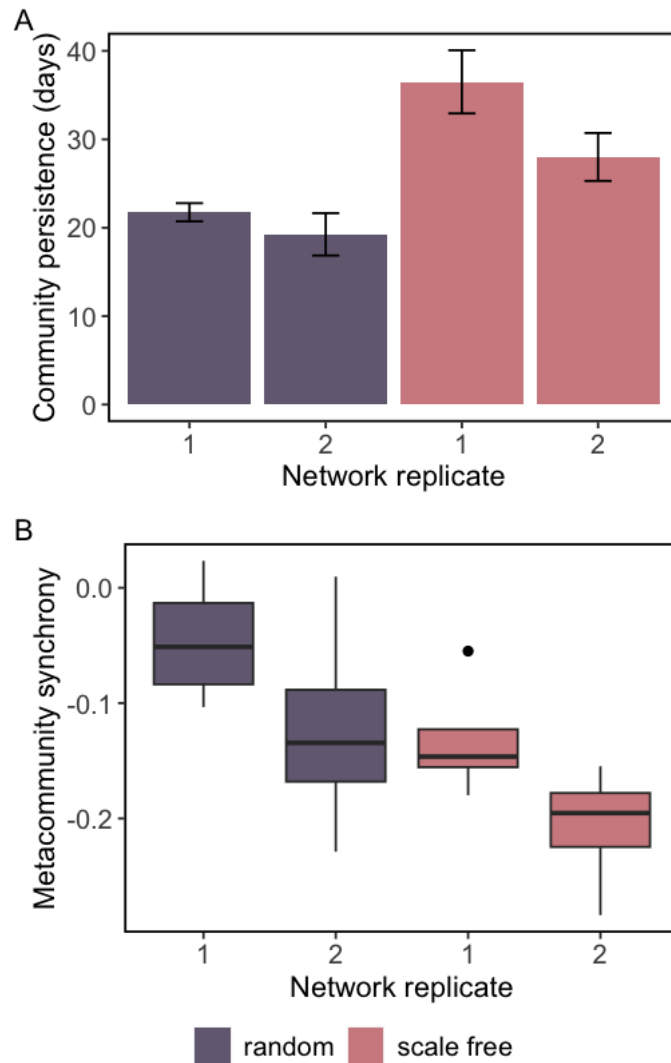
Figure 4. (A) Community persistence in random and scale-free metacommunities, calculated as the number of days all three species were observed present in the system ($\overline{X} \pm$ S.E.; n = 4). (B) Metacommunity synchrony (calculated *sensu* Gross et al. 2014) in random and scale-free metacommunities (n = 4). Same color boxes correspond to network-level replicates. In each boxplot, bold horizontal lines show the median among network replicates, upper and lower hinges represent the first and third quartiles, and whiskers indicate the largest and smallest values.

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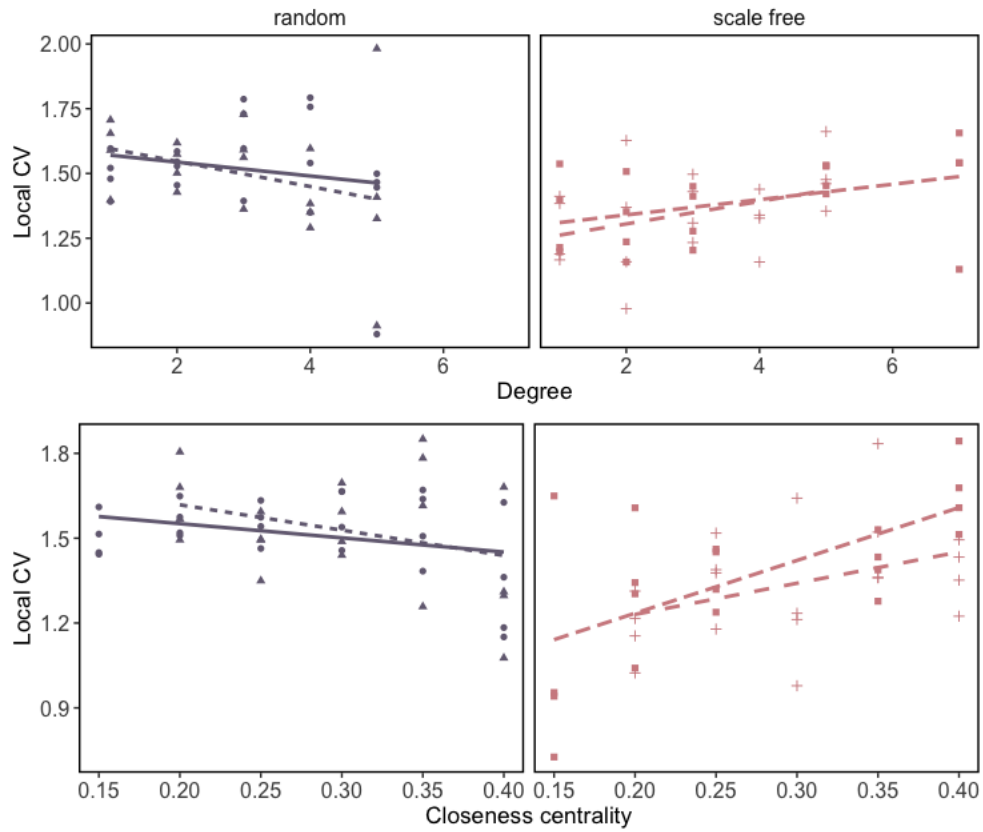
Figure. 5. Local community variation and its relationship with patch degree (top panels) and patch closeness centrality (bottom panels) in random (left panels) and scale-free (right panels) metacommunities. Different symbols within each plot represent different replicate layouts and each data point represents the plate average of patches according to their corresponding network metric.