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

Year: 2024

Version: Accepted version (Final draft)

Please cite the original version:

Arancibia, P. A. (2024). The topology of spatial networks affects stability in experimental metacommunities. Proceedings of the Royal Society B : Biological Sciences, 291(2024), Article 20240567. https://doi.org/10.1098/rspb.2024.0567

The topology of spatial networks affects stability in experimental metacommunities

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Abstract

Understanding the drivers of community stability has been a central goal in ecology. Traditionally emphasis has been placed in studying the effects of biotic interactions on community variability, and less is understood about how the spatial configuration of habitats promotes or hinders metacommunity stability. To test the effects of contrasting spatial configurations on metacommunity stability, I designed metacommunities with patches connected as random or scale-free networks. In these microcosms, two prey and one protist predator dispersed, and I evaluated community persistence, tracked biomass variations, and measured synchrony between local communities and the whole metacommunity. After 30 generations, scale-free metacommunities had lower global biomass variability and higher persistence, suggesting higher stability. Synchrony between patches was lower in scale-free metacommunities. Patches in scale-free metacommunities showed a positive relationship between variability and patch connectivity, indicating higher stability in isolated communities. No clear relationship between variability and patch connectivity was observed in random networks. These results suggest the increased heterogeneity in connectivity of scale-free networks favors the prevalence of isolated patches in the metacommunity, which likely act as refugia against competition—the dominant interaction in this system—resulting in higher global stability. These results highlight the importance of accounting for network topology in the study of spatial dynamics.

Keywords: spatial connectivity, metacommunities, stability, microcosms

Introduction

Identifying the drivers of community temporal dynamics, including stability in response to perturbations, has been a central goal in ecology [1–4]. Whether these drivers are biotic, abiotic or some combination of both is largely context dependent, but understanding how and under which circumstances these drivers operate is the key to predicting how systems respond to different scenarios. In community ecology, the concept of "stability" can be defined in multiple ways. Given the difficulty of its study in empirical systems, the operational definitions of stability often differ from the mathematical definition. In a strict sense stability can be defined as the ability of a system to return to its initial conditions after a perturbation [5]. In practice, ecological studies also consider measures of community permanence [6], species persistence or turnover [5], and the temporal invariability of a community descriptor [3,7], as measures of stability. In this study I will use the latter two as a proxy for stability.

Historically, much emphasis has been placed on studying biotic drivers of community invariability/stability. In particular, the effects of species interactions have been frequently studied under the diversity-stability relationship framework [2,8–11]. Findings in this field are diverse, but they emphasize the large role that interactions play in community function.

Evidence regarding the effects of competition on community stability is varied. Some studies report little to no influence of competition or interaction strength on community variability, but note stronger effects at the population level (Ives et al. 1999). However, other sources report that competition decreases community stability (Yodzis, 1981, Allesina & Tang 2012). Experimental studies have also revealed that interaction strength in competitive communities can not only alter the relationship between community biomass and stability, but also the range of variation of biomass [15]. Other interactions, such as predator-prey,

have been described as stabilizing for communities when interaction strength is high, while mutualistic interactions are destabilizing [14].

Abiotic drivers of community stability have been seldom addressed as such. Most studies in this context have focused on environmental fluctuations as drivers and although many community-level properties can track changes in abiotic conditions over time [16], it is the species-specific responses to environmental fluctuations that affect diversity-stability relationships [12]. In such cases, compensatory dynamics can confer stability to communities under scenarios of environmental fluctuations [17].

Spatial dynamics can have stabilizing effects on metacommunities [18,19] and metaecosystems [20]. Although it was been shown that the pattern of habitat connectivity affect metacommunity persistence [21] and can modulate the importance of the different drivers of metacommunity dynamics [22,23] we currently lack a clear understanding of how it affects metacommunity stability. Thus, we are far from being able to draw general predictions if its effects under complex scenarios. Network topology is a key feature of spatial systems as it can dictate the connectivity pattern between local communities and determine—among other things—the "ease" at which elements can move through the network. For example, random networks are characterized by having nodes (i.e., patches) with very similar number of connections, and therefore their "connectivity" frequency distribution (i.e., degree distribution) follows a Poisson distribution (Fig. 1; top panel) where most patches have an average number of connections and only a few are poorly or highly connected (Erdös & Rényi, 1960). Conversely, in a sparser scale-free network whose degree distribution approximates a power law (Fig. 1; bottom panel), most nodes are poorly connected and only a few are highly-connected hubs [25]. These topological differences can not only determine the network's resilience and robustness against perturbations, but it also control the speed at which "information" (species) can spread. In an ecological scenario, we

can think of organisms as information, and their movement should be easier in more homogeneous networks (i.e., random) than in those that are sparser (i.e., scale-free). Dispersal can affect stability through the synchronization of local dynamics [26]. Restriction in the movement of individuals can be the key to maintain asynchrony in metacommunities where local communities are at different stages of consumer-resource fluctuations [27]. Similarly in competitive metacommunities high levels of dispersal can lead to competitive exclusion [28,29]. Consequently, if spatial topology determines dispersal, we can expect lower stability in networks that facilitate inter-patch movement.

In fact previous studies have shown that network topology has strong and contrasting effects on metapopulation [30] and metacommunity dynamics [31]. Some of the proposed mechanisms behind diversity-stability relationships have also been shown to have contrasting effects between communities and populations. Diversity can foster community stability but have neutral effects on populations [32]. Specifically, competition can enhance community stability but destabilize local populations [7,18]. In this context, understanding how network topology affects community stability and how patch metrics relate to variability, will help to identify those local communities that are more susceptible to extinction and consequently those that should be the target of protective measures for habitat conservation and management.

To empirically assess the relationship between habitat configuration and metacommunity stability at the local and regional scale in a system with competitive and predator-prey interactions, I compared experimental metacommunities configured as random or scale-free networks. Given their differences in connectivity, I hypothesize that random metacommunities —the more homogeneous topology— will allow an easier dispersal of organisms across the system, decreasing stability at the local and global scale as a result of the increased likelihood of encountering enemies. Conversely, in scale-free

metacommunities, where connectivity is sparser, the higher proportion of isolated patches will allow the persistence of local communities, increasing overall stability.

Methods

Experimental setup

I selected two contrasting network topologies—Erdös-Rényi (from here on random) and scale-free—to represent a biologically plausible range of connectivity in natural metacommunities. Using the R package 'igraph' (v. 1.2.4.1) I created two different 24-patch realizations of each network topology and I used 24-well plates to recreate them as protist landscapes. Each of them was experimentally replicated four times (Fig. 1). For this, I filled each well (i.e., patch) with protist media (0.37 g Protist pellet and 0.07 g Herptivite in 1.4 L of well water bacterized with *Proteus vulgaris*, *Serratia marcesens*, *Bacillus subtilis* and *Bacillus cereus*) and connected them according to the layouts using glass capillary tubes filled with protist media. Each well plate—now considered a 24-patch metacommunity—contained a food web module of three protist species, *Paramecium tetraurelia*, *Paramecium bursaria* and *Dileptus anser*. The two bacterivore species (*P. tetraurelia* and *P. bursaria*) were initially inoculated in a third of the local communities/wells at random and the predator *D. anser* was added after four days. Microcosms were allowed to develop as organisms dispersed for over 80 protist generations, during which time I measured the abundance of each species in each local patch by directly counting individuals with a stereomicroscope three times per week.

To measure biomass, I took photographs of between 10 and 35 individuals of each species and estimated their surface area using ImageJ [33]. I calculated biomass using these surface area estimations, the value of the density of water and the abundance counts per patch.

I defined species persistence as the length of time from the start of the experiment until the first extinction of a species in the metacommunity. A species was considered "extinct" when it was not observed for at least two consecutive samplings.

Analysis

To compare the curves of community biomass over time for the two types of networks I used profile analysis using the 'profileR' R package. This analysis allows to compare curves by checking for differences in parallelism and the similarity of response levels [34]. The parallelism portion of the analysis tests whether segments of the curve are oriented similarly between groups (e.g., are parallel). If the answer is positive, then a MANOVA is performed to test for equal levels, and find differences in the average value per group.

To evaluate community variability, I used the data of the first 30 days of the experiment (roughly 30 protist generations), which is the period of time when predators were observed. There are multiple ways of defining community stability (see Lehman & Tilman [2000] for more details), but the most common are a measure of temporal variability —such as the coefficient of variation of a community descriptor such as biomass, or its reciprocal [4,7,16,18,35]—or a measure community persistence [5,36].

I calculated the coefficient of variation (CV) of total biomass across time (pooling the biomass of all species) both at the metacommunity (per plate) and local level (per well). I evaluated differences in the CV of pooled biomass (community-level estimation) and per-species biomass between network topologies at the metacommunity scale using generalized linear mixed models (GLMMs) with network replicate as a random factor. I measured community persistence as the number of days all species were counted as present in the system and I analyzed the differences using a GLMM with network replicate as a random factor. Additionally, I evaluated metacommunity synchrony by calculating the zero-lag

correlations between the time series of community biomass of each local community and total biomass of all other patches, using the Gross et al. (2014) index included in the R package 'codyn' [38]. Differences between topologies in these two descriptors were evaluated using a generalized linear model since the GLMM approach showed that no variance was explained by the random factor.

To characterize the patches and their location in the network I used two metrics that have been previously used to describe node position/importance within a metacommunity network [39–41]: degree and closeness centrality. Degree corresponds to the number of links (i.e., neighbors) between a focal patch and other patches in the network. Closeness centrality is measured as the reciprocal of the average shortest path length between a focal node and all the other nodes in the network. Therefore, higher values indicate nodes that are closer to others or "more central". These relationships were also analyzed with GLMMs, in this case with patch metric and network as predictors, and network realization as random factor, and in the case where the random factor did not explain any variance, I used a GLM. Model specifications for all analyses are detailed in the supplementary material as well as the frequency distribution of these patch metrics in the networks used in the study (Figs. S1 and S2).

Results

All metacommunities showed some temporal variation of biomass. The peak biomass in all metacommunities occurred around day 5 and steeply declined afterwards (Fig. 2). Although both types of metacommunities followed a similar temporal trend, biomass was consistently higher in scale-free metacommunities. This was confirmed with profile analysis, which showed that the network-specific curves were parallel (Hotelling's T^2= 8.594, $F_{11,4}$= 3.125, p=0.141) but with different elevations ($F_{1,14}$=20.63, p=0.00046).

On a global scale, inferred community stability was higher in scale-free metacommunities (Fig. 3) as they showed lower coefficients of variation than random metacommunities (GLMM network: χ_1^2= 9.0219, p = 0.002). Similarly, when comparing stability at the local level scale-free networks showed lower CV values than random ($F_{1,14}$=19.06, *p*=0.00064). Differences in metapopulation level stability (i.e., measured separately per species) between networks were observed only for *P. tetraurelia* (GLMM network: χ_1^2= 10.551, p = 0.0011; Fig. S3).

Metacommunities with different topologies also differed in species persistence (Fig. 4A). In scale-free metacommunities the complete 3-species food web module was present in the system for about 10 generations longer than in random metacommunities (GLMM network: χ_1^2= 14.07, p = 0.0001). The reduction of spatial synchrony has been suggested as a promoter of metapopulation [42,43] and metacommunity persistence [44], in this study it could be one of the explanation for the differences in persistence of metacommunities with different topologies. Even though spatial synchrony in both types of metacommunities was generally low (calculations were very close to 0), scale-free metacommunities had lower values than random networks ($F_{1,12}$ = 6.231, p = 0.0281; Fig. 4B).

At the local scale, stability decreased in relation to patch closeness centrality only in scale-free metacommunities ($F_{1, 380}$ = 0.747, p = 0.003), while no effect evident for random metacommunities (Fig. 5). Conversely, patch degree had no effect in the stability of local communities.

Discussion

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

connectivity may not have directly affected the occurrence of the interactions but perhaps it modulated their strength.

One of the main differences between random and scale-free networks is the differences in the level of connectivity. Random networks are more homogeneous and therefore the transmission of information between distant nodes—in this case dispersal of organisms between patches—is easier and faster than in scale-free networks. Gravel et al. (2016), in a modelling study where connectivity is not addressed explicitly, describe a relationship between stability and dispersal that increases to an asymptote in heterogeneous landscapes, which differs from the trends observed in this study. Even considering that habitat heterogeneity acts as a stabilizing force in metacommunities, and that this factor is absent in this study, it would still be reasonable to expect the same general trend but perhaps with lower stability values, which is not the case in this experiment. However, another aspect of these dynamics suggests that dispersal stabilizes meta-ecosystems by modulating interaction strength in a way that stability in a spatial system depends on interactions averaged across space instead of their local coefficients (Gravel et al. 2016). In this study, topology could modulate this relationship even further, producing the observed differences.

The effects of weak interactions in communities can also be idiosyncratic. In general it has been proposed that they have stabilizing properties for communities compared to strong interactions [19,46–48]. Recent studies have shown that different trophic groups contribute differently to metacommunity stability. Particularly, competitive interactions in a food web can weaken spatial synchrony and affect stability [49]. In this case, and given the high frequency in which the competitor species co-occur in comparison to predator-prey co-occurences —and unless interaction strength between predators and prey is high (in this case it is not, see Fig. S5)— it is possible that competition between the two prey species is stronger than predation. If this is true, then the increased isolation in scale-free

metacommunities would likely create refugia against competition and not so much against predation. Competition has been described as a destabilizing force for communities [14], therefore the "protection" against it in scale-free networks through refugia, results in an overall positive effect on global stability. I suggest that the increased persistence of the predator in scale-free systems should be considered a consequence of the increased availability of prey but it does not contribute to overall stability *per se*.

Other studies have shown that abiotic factors—such as precipitation—have an indirect effect on community variability acting through biotic interactions [16]. It has been suggested that spatial heterogeneity can alter the variability of interaction strength [20] and ultimately community stability and diversity [50], and in this study I show that spatial configuration can determine community stability by creating refugia against competition.

Although the experimental setup used in this study only allows to draw limited conclusions regarding long-term community stability, the results presented here encompass over 30 protist generations and provide solid support for the idea of spatial configuration being a key factor in community functioning.

Acknowledgements

This research was supported by a Rutgers University Graduate Program in Ecology and Evolution Small Grant, and a Ted Stiles award. I thank Peter Morin, Rita Grunberg, Mira Kajanus, Brendan Furneaux, members of the Morin Lab (Rutgers University), and members of the Predictive Community Ecology Group (University of Jyväskylä), for their thoughtful comments on drafts of this manuscript. This manuscript was greatly improved by the feedback provided by two anonymous reviewers.

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Figures

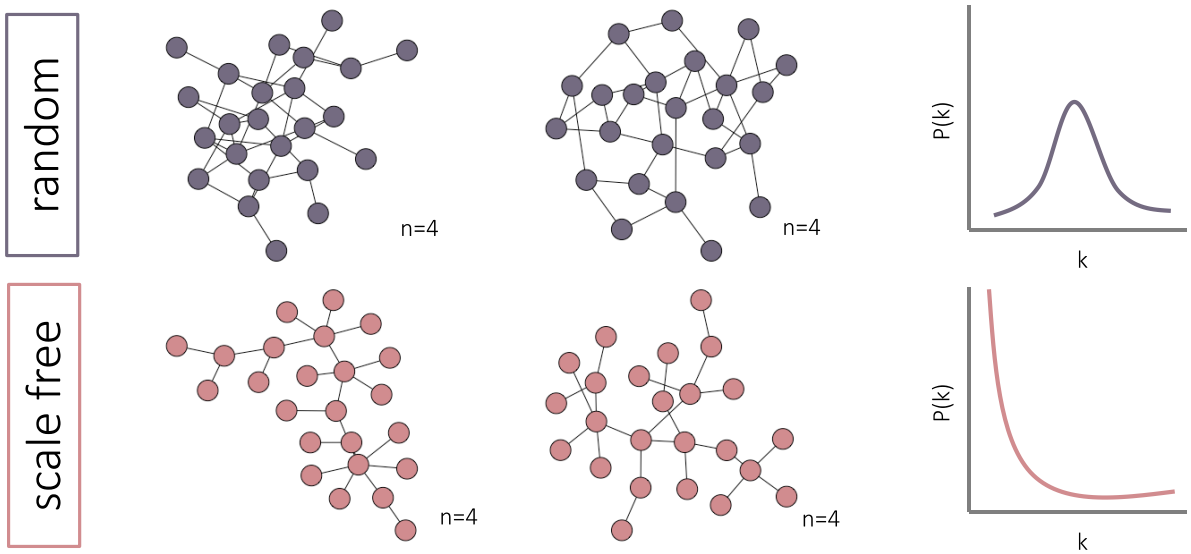

Figure 1. Layouts of random and scale-free networks used in the experiment, and their idealized degree distribution on the right. Each network realization (i.e., layout) was replicated four times in the experiment.

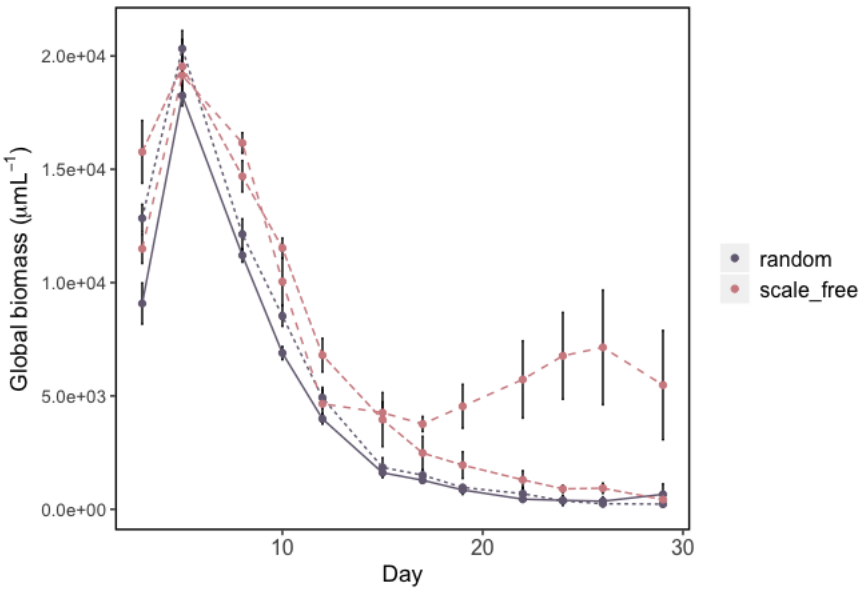

Figure 2. Biomass variation over time, calculated at the metacommunity level for metacommunities connected as random (purple) and scale-free (pink) networks ($\overline{X}$ ± S.E.; n = 4). Same color lines correspond to network-level replicates.

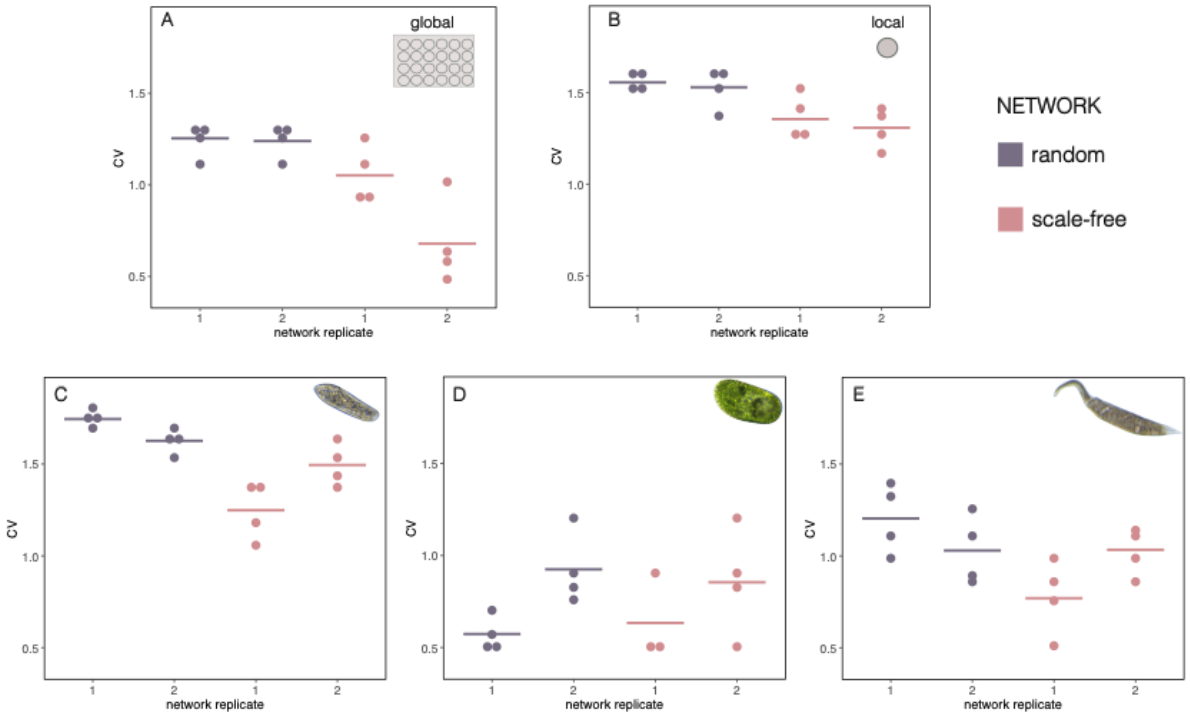

Figure 3. Metacommunity variability measured as the coefficient of variation (CV) of biomass in random (purple) and scale-free (pink) (n =4). Horizontal bars represent the mean. (A) CV corresponds to the variation in community biomass across the entire metacommunity (all habitat patches considered together), (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.*

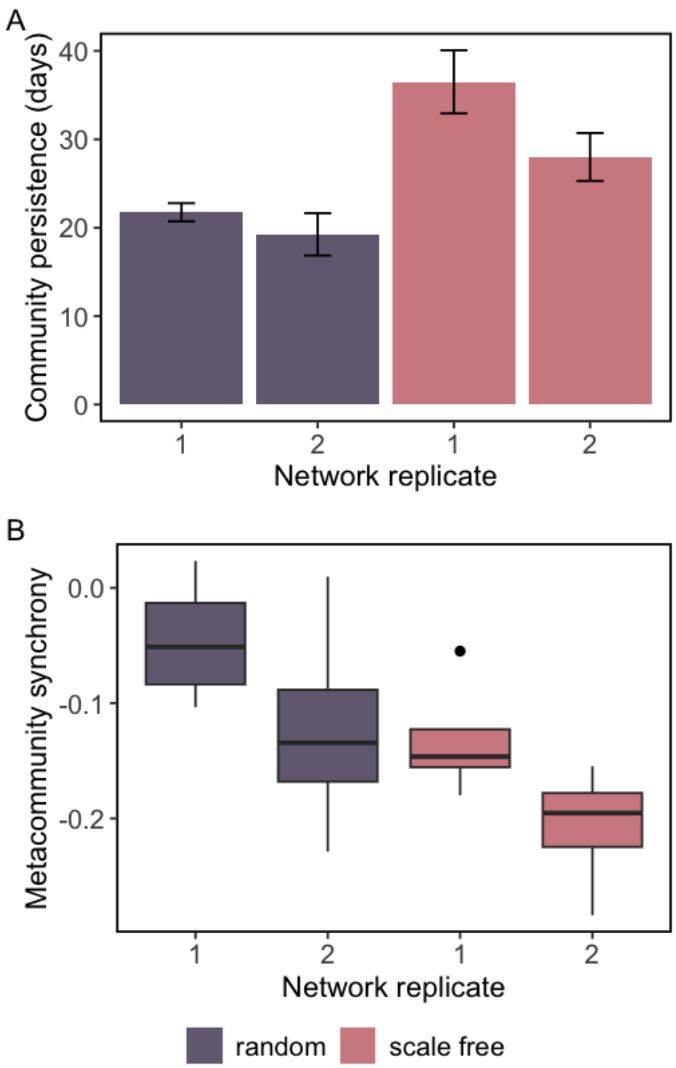

Figure 4. (A) Community persistence in random and scale-free metacommunities, calculated as the number of days all three species were observed present in the system ($\overline{X}$ ± S.E.; n = 4). (B) Metacommunity synchrony (calculated *sensu* Gross et al. 2014) in random and scale-free metacommunities (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.

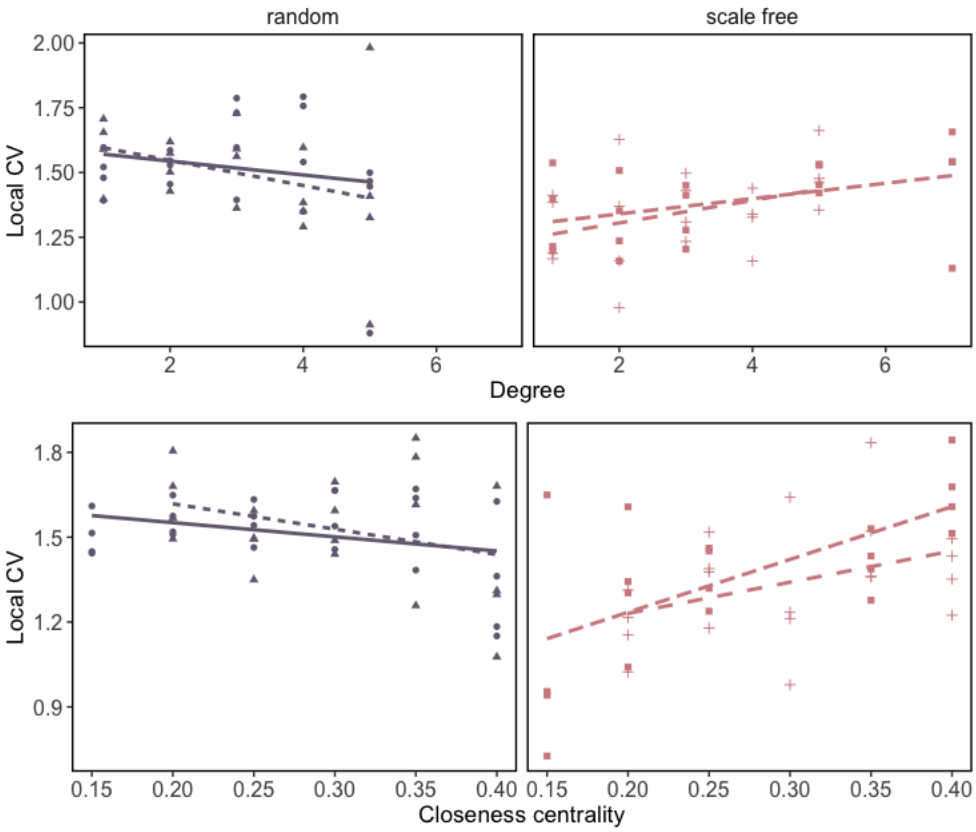

Figure. 5. Local community variation and its relationship with patch degree (top panels) and patch closeness centrality (bottom panels) in random (left panels) and scale-free (right panels) metacommunities. Different symbols within each plot represent different replicate layouts and each data point represents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