

1 Abrupt transitions and its indicators in mutualistic
2 meta-networks: effects of network topology, size of
3 metacommunities and species dispersal

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6 **Abstract**

7 Gradual changes in the environment could cause dynamical ecological networks to
8 abruptly shift from one state to an alternative state. When this happens ecosystem
9 functions and services provided by ecological networks gets disrupted. We, however,
10 know very little of how the topology of such interaction networks can play a role in
11 transitions of ecological networks at a spatial scale. In the event of such unwanted
12 transitions, little is known how statistical metrics used to inform such impending tran-
13 sitions, measured at the species-level or at the community-level could relate to network
14 architecture and the scale of spatial interactions. Here, using fifty-six empirical plant-
15 pollinator networks in a spatial setting, I evaluated the impact of network topology
16 and spatial scale of species interactions on abrupt transitions, and on statistical metrics
17 used as predictors to forecast such abrupt transitions. Using generalized Lotka-Volterra
18 equations in a meta-network framework, I show that species dispersal rate and the size
19 of the metacommunity can impact when an abrupt transition can occur. In addition,
20 forecasting such unwanted abrupt transitions of meta-networks using statistical metrics

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21 of instability was also consequently dependent on the topology of the network, species
22 dispersal rate, and the size of the metacommunity. The results indicated that the plant-
23 pollinator meta-networks that could exhibit stronger statistical signals before collapse
24 than others was dependent on their network architecture and on the spatial scale of
25 species interactions.

26 keywords: meta-networks, mutualistic networks, abrupt transitions, dispersal, early warning
27 signals

28

29 Introduction

30 Ecological systems could abruptly shift from one state to another in response to gradual
31 changes in environmental conditions. Such abrupt transition occurs when environmental
32 conditions cross a specific threshold, the threshold being commonly known as tipping points
33 (Dakos et al., 2018; Scheffer et al., 1993). Tipping points and abrupt transitions are gener-
34 ally observed in ecological systems governed by positive feedback loops. Abrupt transitions
35 can occur in systems ranging from aquatic systems such as algae and macrophytes (Dakos
36 et al., 2018), mutualistic ecological networks (Baruah, 2022; Dakos and Bascompte, 2014;
37 Lever et al., 2014), and populations exhibiting allee thresholds (Hilker, 2010). When such
38 abrupt transitions occurs, the equilibrium stable state of the system jumps to another state
39 where loss of beneficial ecosystem functions and services could occur (Dunne and Williams,
40 2009; Hutchings and Reynolds, 2004; Scheffer et al., 2012). Abrupt transitions, thus, can
41 cause long-term radical changes to ecosystems. However, at the scale of multiple commu-
42 nities connected by species dispersal, very few studies have explored how local network
43 architecture and spatial scale of interactions could impact the timing of abrupt transitions

44 .
45 Mutualistic communities are examples of communities that exhibit positive feedback loops
46 in networks of interactions between two groups of species (Bascompte et al., 2003; Dakos
47 and Bascompte, 2014; Kéfi et al., 2016). While negative interactions such as intraspe-
48 cific competition could have stabilising effects, positive interactions such as those observed
49 in plant-pollinator or mutualistic networks could be destabilising and could result in the
50 presence of alternative stable states (Baruah, 2022). As such due to the presence of such
51 alternative stable states, mutualistic communities can transition from a stable state to an
52 alternative state as environmental change causes a change in the system’s feedback strength
53 (Lever et al., 2020). The spatial context of such transition has somewhat remain unexplored,
54 particularly on the impact of topological and architectural aspects of such systems such as
55 network size, nestedness, or connectance. Previous study on spatial mutualistic systems

56 has suggested that the presence of transitions can be modulated by shift in strength in
57 species phenology or habitat destruction (Fortuna and Bascompte, 2006). Habitat destruc-
58 tion increases the chances of abrupt transition which rewires local networks (Revilla et al.,
59 2015). In addition, with strong mutualistic interactions the amount of habitats required for
60 persistence of all species then depends on the range of species dispersal (Prakash and Roos,
61 2004). However, it is unknown whether topological features of mutualistic networks such as
62 network size or connectance could influence the timing of occurrence of abrupt transition in
63 response to gradual changes in environment. For instance, could larger networks collapse
64 earlier in comparison to smaller networks?

65 Rarely, ecological communities occur in isolation. More often, ecological communities oc-
66 cur in habitat patches across a larger network of patches that is connected by dispersal,
67 which is commonly known as a metacommunity. Metacommunity concept has gained much
68 attention over the last decade and empirical and theoretical studies have provided with
69 an understanding of how local and regional processes work to maintain diversity both at
70 local and regional scale (Limberger et al., 2019; Loreau et al., 2003). Species diversity
71 can stabilize the dynamics of local communities. This stabilization occurs due to differ-
72 ent asynchronous responses of species over time to temporal changes in the environment.
73 Such stabilization due to increases in number of species is generally known as species in-
74 surance effects (Heino et al., 2015; Loreau et al., 2003; Shoemaker and Melbourne, 2016).
75 Species insurance can occur due to interspecific competition (Lehman and Tilman, 2000), or
76 when species response to biotic environment differs from other species (Loreau et al., 2003).
77 Spatial insurance in metacommunities arises when local communities exhibit asynchronous
78 dynamics. This happens when species dispersal rate is limited or when species composition
79 across local communities vary considerably thereby leading to spatial heterogeneity (Walter
80 et al., 2017; Wang and Loreau, 2014). Species dispersal from habitat patches could poten-
81 tially rescue local communities from collapses as environment changes. However, the role of
82 species dispersal on timing of transition of meta-networks remains unknown. For instance,
83 does spatial scale of species interactions and the spread of such ecological networks (number

84 of habitat patches) determine whether network collapses occur earlier or later?

85 Local and regional scale extinctions could occur not only due to local processes such as pre-
86 dation or competition but also due to large scale external disturbances (Cunillera-Montcusí
87 et al., 2021). Large scale disturbances akin to changes in climate could impact species
88 interactions not only locally but also across communities connected in space (Revilla et
89 al., 2015; Thompson and Gonzalez, 2017). In mutualistic communities, changes in the
90 environment could lead to weakening of interactions between species such as phenologi-
91 cal mismatches thereby altering local structure of communities (Forrest, 2015; Kudo and
92 Cooper, 2019; Morton and Rafferty, 2017; Renner and Zohner, 2018; Visser and Gienapp,
93 2019). However, such species mismatches could be rescued when similar communities are
94 accessible to species in a mosaic of communities connected by species dispersal. It is, how-
95 ever, unknown whether such global changes in the environment interacts with local network
96 topological properties to mitigate drastic change. Increases in phenological mismatch could
97 be further compounded by habitat destruction and could lead to substantial changes in
98 network architecture (Revilla et al., 2015). In addition, whether the spatial scale (size of
99 the metacommunity) of such changes matters in the occurrence of transition is somewhat
100 not known.

101 There has been statistical tools developed to inform impending transitions that could occur
102 as environment gradually changes (Scheffer et al., 2012). Abrupt transitions could occur
103 when changes in the environment crosses a certain threshold that pushes the ecological sys-
104 tem towards another alternative state where ecosystem functions could be lost permanently.
105 However, there are statistical tools that been developed to forecast such impending tran-
106 sitions which are commonly known as “early warning signals.” Commonly used signals are
107 temporal autocorrelation and variance that could derived using a sliding window approach
108 (see [Dakos et al. (2012a) for details) from state based temporal data such as abundance
109 or biomass. However, the utility of such signals are dependent on a host of factors that
110 includes sampling requirements (Arkilanian et al., 2020), data quality (Clements et al.,

111 2015), eco-evolutionary factors (Baruah et al., 2021, 2020) and type of species interactions
112 (Baruah et al., 2022; Dakos, 2017; Patterson et al., 2021). One important challenge is to
113 test the utility of such signals in a multispecies context embedded within a spatial scale of
114 species interactions. This is especially relevant as multispecies communities rarely occur in
115 isolation and are generally connected by dispersal among habitat patches. The detection of
116 such signals becomes even more challenging as dynamics of such communities are inherently
117 linked to their topological features which also directly impacts the occurrence of transitions
118 (Baruah, 2022; Dakos and Bascompte, 2014).

119 Here, using fifty-six empirical plant-pollinator networks in a spatial context collated from
120 web-of-life.es database, I explore the effects of topological network features such as network
121 size, connectance, or nestedness on timing of transitions and on indicators of temporal
122 and spatial resilience. Using generalized Lotka-Voltterra equations, I model the ecologi-
123 cal dynamics of spatially-explicit mutualistic meta-networks to global changes in strength
124 in mutualistic interactions. Specifically, using different metacommunity sizes, I show that
125 timing of abrupt transition depends not only how species disperse across habitat patches,
126 but also on local network topological predictors such as network size and connectance of
127 the network. Furthermore, the threshold at which a species could abruptly transition is
128 influenced by the degree of the species, rate of dispersal and also by the size of the meta-
129 community. In addition, how large the metacommunity was also significantly played a role
130 on how early an abrupt transition might occur. Furthermore, when such global transition
131 of mutualistic metacommunities occur, predictability with temporal and spatial resilience
132 indicators also depends on the topological network features and on the rate of dispersal of
133 species. These results argue the importance of understanding the dynamics of communi-
134 ties from a spatial perspective and highlights the importance of network architecture on
135 biodiversity maintenance.

Methods

Using www.web-of-life.es database, I collated 56 empirical plant-pollinator networks (see table S1 for details and the references). These empirical networks were set up in a spatially-explicit landscape of different sizes of two, five, ten and twenty habitat patches that determined the spatial scale of mutualistic interactions. This spatial scale determined to what extent plant-pollinator interactions were impacted when global changes occur at the scale of the metacommunity. For instance, when changes in climate that drives changes in phenological interactions occur, does spatial scale of mutualistic interactions matter in delaying an abrupt transition to collapse?

These spatially explicit landscape were set up in a two dimensional landscape (Grilli et al., 2015). All habitat patches were connected. Following this, I model the ecological dynamics of mutualistic interactions using generalized Lotka-Volterra equations:

$$\frac{dA_i^k}{dt} = A_i(r_i^k - \sum_j a_{ij}^k A_j + \sum_l \frac{m_{li}\gamma_0 P_l}{1 + h \sum_x m_{xi}\gamma_0 P_x}) + M_i^k - aA_i^k \quad (1)$$

Similarly, the dynamics of plants on a spatially explicit metacommunity can be written as:

$$\frac{dP_i^k}{dt} = P_i(r_i^k - \sum_j a_{ij}^k P_j + \sum_l \frac{m_{li}\gamma_0 A_l}{1 + h \sum_x m_{xi}\gamma_0 A_x}) + M_i^k - aP_i^k \quad (2)$$

where A_i^k, P_i^k represents pollinator and plant abundance for habitat patch k , r_i^k is the species specific growth rate independent of mutualistic interactions at patch k , a_{ij}^k represents interspecific competition within each guild of species at patch k , γ_0 represents the average mutualistic interaction strength when a plant and a pollinator interacts, with m_{li} determining the network structure and is either 0 or 1 depending on whether an interaction exist between a plant and a pollinator, h is the handling time which we fixed at 0.15, M_i^k is the density of species that arrives from all the patches in the metacommunity, and finally a fraction of individuals emigrates from a habitat patch k at the rate a .

157 In our model simulations, we ensured that mutualism was obligate without any loss of gener-
 158 ality. This meant that growth rates of species r_i^k was negative for both the guilds of species
 159 and species persistence totally dependent on mutualistic interactions between species. To
 160 do that we randomly sampled growth rates r_i^k from a random uniform distribution within
 161 the range of $U[-0.05, 0.1]$ for both plants and the pollinators. In addition, we ensured that
 162 intraspecific competition within each guild of species was strictly stronger than interspe-
 163 cific competition. For that we ensured that $a_{ii} = 1$ and we sampled $a_{ij}, i \neq j$ from random
 164 uniform distribution ranging from $U[0.01, 0.05]$. When ensuring that intraspecific compe-
 165 tition to be stronger than interspecific competition, feasibility of mutualistic community
 166 becomes easier provided strength in mutualistic interactions γ_0 was high (Barabás et al.,
 167 2017; Baruah, 2022). Our goal was to finally assess how network properties come into play
 168 at a spatial scale in mitigating the timing of occurrence of abrupt collapses as we change
 169 the strength in mutualistic interactions.

170 Finally, dispersal among patches was constrained by the spatial scale and as well as distance
 171 among patches. Species dispersal among patches decreased exponentially as the distance
 172 among patches increased. Specifically, dispersal of species i from patch k can be written as
 173 (Thompson and Gonzalez, 2017),

$$M_i^k = a \sum_{j \neq k}^n \frac{e^{-y d_{jk}}}{\sum_{f \neq k}^n e^{-y d_{fk}}} N_i^j$$

174 Following Thompson and Gonzalez (2017), more than one dispersal route can be taken
 175 during a particular time step, d_{jk} is the distance between patch j and k and y controls
 176 the rate at which this distance decreases which we fix at 0.5. Fixing it at 0.5 gives global
 177 dispersal, which means that as metacommunity sizes become larger species dispersal does
 178 not necessarily gets constrained locally and species could in principle disperse long distance.
 179 However, the rate at which they disperse would still depend on distance between patches.
 180 Finally, a gives the average rate at which species disperse. Here, when we vary rate of
 181 dispersal we ensure that species dispersal remains same across guilds of species although

182 in nature this might be species-specific. Here, three rates of species dispersal were used, α :
183 0, 0.05, 0.15.

184 Collapse of spatial mutualistic networks

185 Nestedness measured as NODF ranged from as low as 0 to as high as 0.7, while connectance
186 ranged from . Network size also ranged from as low as 8 to as high as 68.

187 By gradually decreasing the average mutualistic strength globally, mutualistic networks were
188 forced to collapse. As mutualism among guilds of species was obligate, decreasing average
189 mutualistic strength, γ_0 , among species would lead to collapses of species. At a specific
190 mutualistic strength (commonly known as threshold strength or tipping point) collapse of
191 the entire mutualistic network would occur. Collapse of mutualistic networks thus was done
192 by gradually decreasing γ_0 from 7 to 0 in steps of 0.25. Globally, across habitat patches
193 this scenario could be linked to changes in the climate such that phenological interaction
194 among plants and pollinators would decrease gradually. For each value of γ_0 I simulated
195 the dynamics of the whole metacommunity till it reached ecological equilibrium. Usually,
196 fluctuations in species density stabilize at around 1000 time points. I discarded the initial
197 transient dynamics and estimated equilibrium plant and animal biomass from the last 1000
198 time points. The extinction threshold of species in such mutualistic networks were fixed at
199 10^{-4} . As the strength of mutualistic interactions decreased, loss of species occurred until
200 the entire meta-mutualistic network collapsed.

201 Next, I determined the point of transition or the mutualistic strength at which a mutualistic
202 network in a habitat patch k transitioned to a collapse state when the total abundance of the
203 network fell below 80 percent of its equilibrium abundance. Once the mutualistic strength at
204 which a network collapsed in a habitat patch k was determined, I evaluated the relationship
205 of the point of transition with network topology such as connectance and network size, and
206 how such a relationship was influenced by spatial scale of interactions.

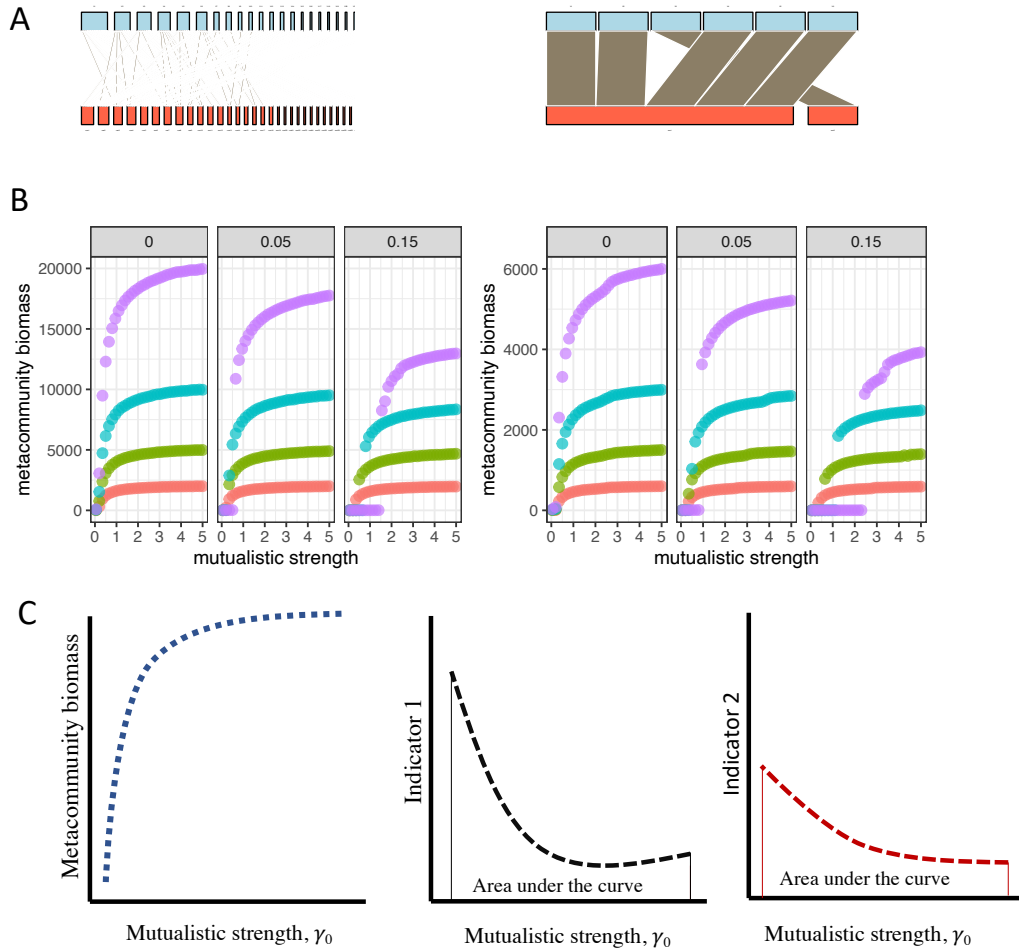
Predictors of temporal and spatial mutualistic network collapses:

I estimated a host of spatial and temporal indicators of collapses at the community level and at the species level. For each mutualistic strength, I estimated spatial variability, regional metacommunity variability, local temporal patch variability. We quantified metacommunity biomass as the sum of all species density across all patches in the metacommunity. I also estimated metacommunity variability defined as the variability in abundance at the metacommunity level (see Wang and Loreau (2014) and Wang et al. (2019) for details) - $\frac{\sqrt{(\sum_{ij} w_{ij})}}{\bar{N}}$, where w_{ij} is the covariance matrix of community biomass $N_i(t)$ at patch i and \bar{N} is the temporal mean of the total metacommunity biomass. Temporal variation or alpha variability was estimated as $\frac{\sqrt{(\sum_i w_{ii})}}{\bar{N}}$ and spatial beta variability was quantified as the variability at spatial level $\frac{\sum_{ij} w_{ij}}{(\sum_i \sqrt{w_{ii}})^2}$ (Wang and Loreau, 2014) for each levels of average dispersal rate, metacommunity size, and for each mutualistic threshold strength.

At the species level, I estimated standard deviation and temporal autocorrelation coefficient of equilibrium species abundance for each level of mutualistic strength, for three different rates of species dispersal and metacommunity sizes. Temporal autocorrelation coefficient at first-lag and standard deviation are the classic phenomenological early warning signals that are suggested to be useful in forecasting critical transitions. Temporal autocorrelation coefficient at first-lag is measured as, $y(N_{t+1}) = \alpha y(N_t) + \sigma \epsilon_n$, where α is the autocorrelation coefficient of the first-order autoregressive (AR(1)) process. α is close to 1 for a red-noise and close to 0 for white noise process. α close to 1 would indicate that the temporal abundance dynamics of a species is highly correlated and 0 would mean uncorrelated. High correlation would indicate that species is closer to a tipping point.

I wanted to evaluate whether statistical metrics measured at the species level or at the level of the community could increase as strength in mutualistic interaction γ_0 decrease, indicating an impending critical transition. So for each level of changes in the mutualistic strength

233 of interaction γ_0 , temporal autocorrelation and standard deviation was measured at the
234 species level, metacommunity variability was measured at the level of the metacommunity,
235 patch variability was measured at the level of a patch, and spatial variability across habitat
236 patches were estimated. To compare whether these metrics performed well, I estimated
237 the area under the curve (AUC). To elaborate on this, as mutualistic strength decreases,
238 one expectation from these statistical metrics is that that the values of these statistical
239 metrics will increase. For instance, as shown in figure 1C, indicator 1 increases steeply as
240 γ_0 decreases, and whether an indicator performs better could be evaluated by calculating
241 the area under the curve of the metric. Stronger the increase, larger would be the AUC of
242 the statistical metric in question.



Indicator 1 has a larger area under the curve and increases steeply as mutualistic strength decreases and metacommunity biomass collapses than indicator 2.

Figure 1: (B) Example equilibrium metacommunity abundance of a mutualistic network as mutualistic strength is decreased gradually for (A) two different networks which vary in the total number of species for different sizes of metacommunity and rate of species dispersal. (Note that in the depiction of mutualistic networks the line thickness describing interactions between plants and animals decreases as network size increases in order to accommodate the increasing number of interactions). C) As metacommunity biomass collapses due to decrease in mutualistic strength, strength in statistical indicator 1 and statistical indicator 2 increases. However, indicator 1 steeply increases in comparison to indicator 2 and this can be compared by calculating the area under the curve of indicator 1 and indicator 2. Clearly in this case, indicator 1 is better as its area under its curve is larger than indicator 2.

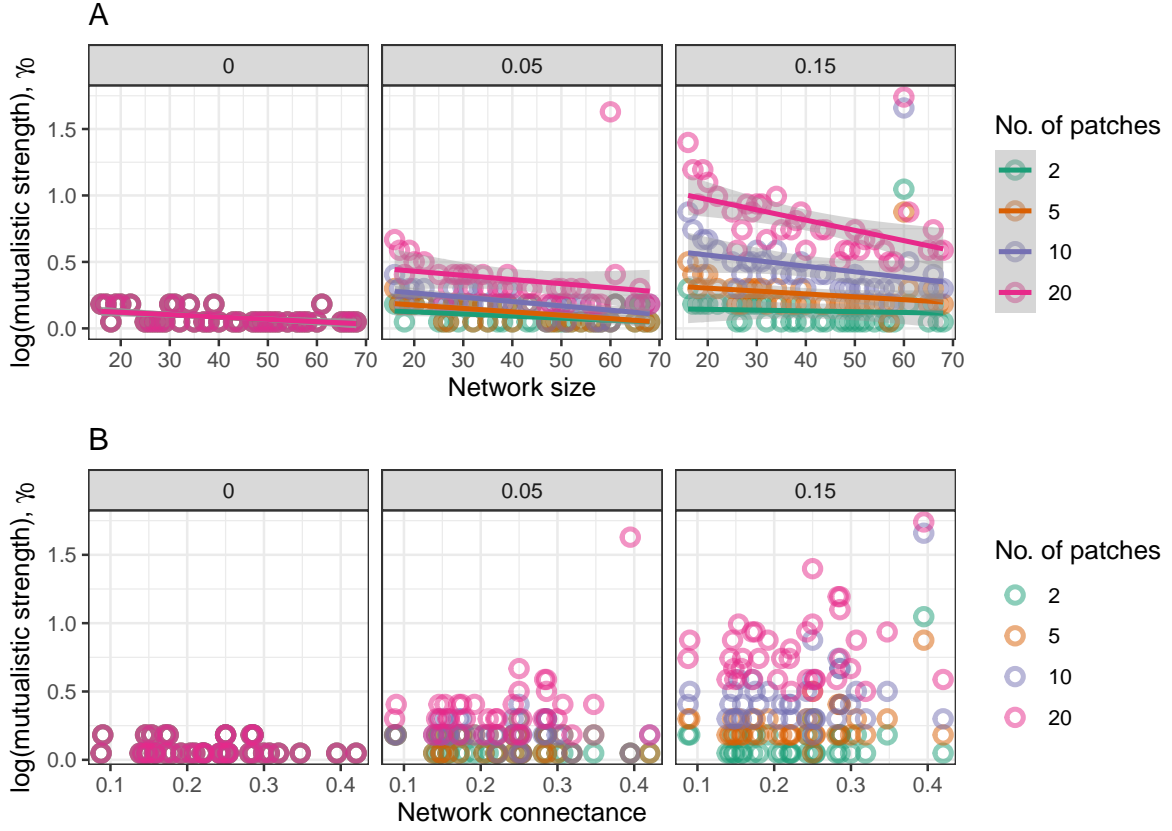


Figure 2: Relationship between the threshold mutualistic strength at which networks collapsed and structural properties of the network namely network size and connectance for different metacommunity sizes (2, 5, 10, 20) and three levels of species dispersal (0, 0.05, 0.15). A) Network size had a significant impact on the strength at which networks collapsed modulated mainly by the number of habitat patches and rate of species dispersal. Networks at larger metacommunities collapsed on average at a higher threshold strength than networks at smaller metacommunities. This indicated that larger metacommunities were more vulnerable to collapses at a much higher mutualistic threshold strength than smaller metacommunities. B) Network connectance didn't have a significant impact on the mutualistic strength at which networks collapsed across a range of dispersal rates and metacommunity sizes.

Results

Point of transition and network properties

Results indicated that the mutualistic strength at which networks collapsed were determined by network size, species dispersal rate, and the size of the metacommunity. Particularly, the relationship between network size and the strength at which networks collapsed becomes negative at the highest dispersal rate modulated by the size of the metacommunity (Fig. 2A). When dispersal rate was zero, the size of metacommunity on the mutualistic strength at which network collapsed remained unaffected. However, at the highest dispersal rate, smaller networks collapsed much earlier than larger networks which became more evident at larger metacommunity sizes. Connectance or nestedness didn't have any significant impacts on the threshold at which mutualistic networks collapsed. This indicated that higher species dispersal might be detrimental as networks could collapse much earlier, particularly when metacommunity sizes were larger.

Indicators of transition and network properties

In an example figure of a mutualistic network (see fig. S1), I show that as metacommunity biomass collapses, indicators such as patch variability, spatial variability, metacommunity variability increases whereas indicators at the species level did not exhibit strong increases as strength in mutualistic interaction decreased. To quantify the strength of such an increased, I measure (as detailed in the methods section) the area under the curve of each of these indicators. Such a measure of AUC would indicate which statistical metric has the strongest increase as the metacommunity collapsed.

Results indicated that when species dispersal was zero, size of mutualistic network had no impact on metacommunity variability. But at higher levels of species dispersal, the relationship between AUC of metacommunity variability and network size becomes negative and was modulated by the metacommunity size (Fig 3A). This indicated that smaller networks

268 at larger metacommunities exhibited stronger metacommunity variability before an abrupt
269 collapse. As metacommunity size decreases, smaller networks exhibited as strong a signal
270 before collapse as larger networks particularly when there were only two habitat patches.
271 Thus, metacommunity variability will increase and could forecast an abrupt transition pro-
272 vided networks are smaller and metacommunity size is larger. Since, network connectance
273 was negatively correlated with network size, the above result remains similar except that the
274 relationship between AUC of metacommunity variability and connectance becomes positive
275 (Fig. S2).

276 In case of spatial variability, when dispersal rate was zero, smaller networks exhibited
277 stronger spatial variability before collapse than larger networks. This result was consistent
278 across metacommunity sizes. But as dispersal increased, which networks exhibited stronger
279 spatial variability before collapse was dependent on the size of the metacommunity. Gener-
280 ally, the relationship between AUC of spatial variability and network size was negative and
281 dependent on the size of the metacommunity. Smaller mutualistic networks embedded in
282 larger metacommunities exhibited stronger spatial variability before collapse than smaller
283 networks in smaller metacommunity sizes (Fig. 3B).

284 Patch variability also known as alpha variability was impacted by size of mutualistic net-
285 works and less impacted by species dispersal and number of habitat patches i.e. metacom-
286 munity size (Fig. 3C). Particularly, larger networks had larger AUC which indicates that
287 such networks exhibited stronger patch variability before an abrupt collapse than smaller
288 networks. At the highest species dispersal, metacommunity size did impact had a slight
289 impact on AUC of patch variability.

290 The strength of mutualistic interaction at which species collapsed as the meta-network col-
291 lapsed was dependent on their degree of interactions. Species which had higher number
292 of interactions i.e., higher degree collapsed later (at a much lower strength of mutualistic
293 strength). This was similar across rate of species dispersal and size of the metacommun-
294 ity. Strength in warning signals such as standard deviation measured at the species-level

295 was related to species degree, rate of species dispersal and less related to the size of the
296 metacommunity. Strength of SD, measured as the AUC of species SD, increased as species
297 degree increased indicating that species which have a larger number of unique interactions
298 will display stronger increases in SD as the network collapses due to changes in the envi-
299 ronment that weakens mutualistic interactions. Strength in autocorrelation, however, did
300 not related to species degree or species dispersal. In addition, autocorrelation at first-lag,
301 or standard deviation measured at the species level was also not impacted by topological
302 properties or species dispersal or size of the metacommunity (Fig. 4A). However, AUC of
303 standard deviation measured at the species level was impacted by topological properties or
304 species dispersal or the size of the metacommunity (Fig. S5).

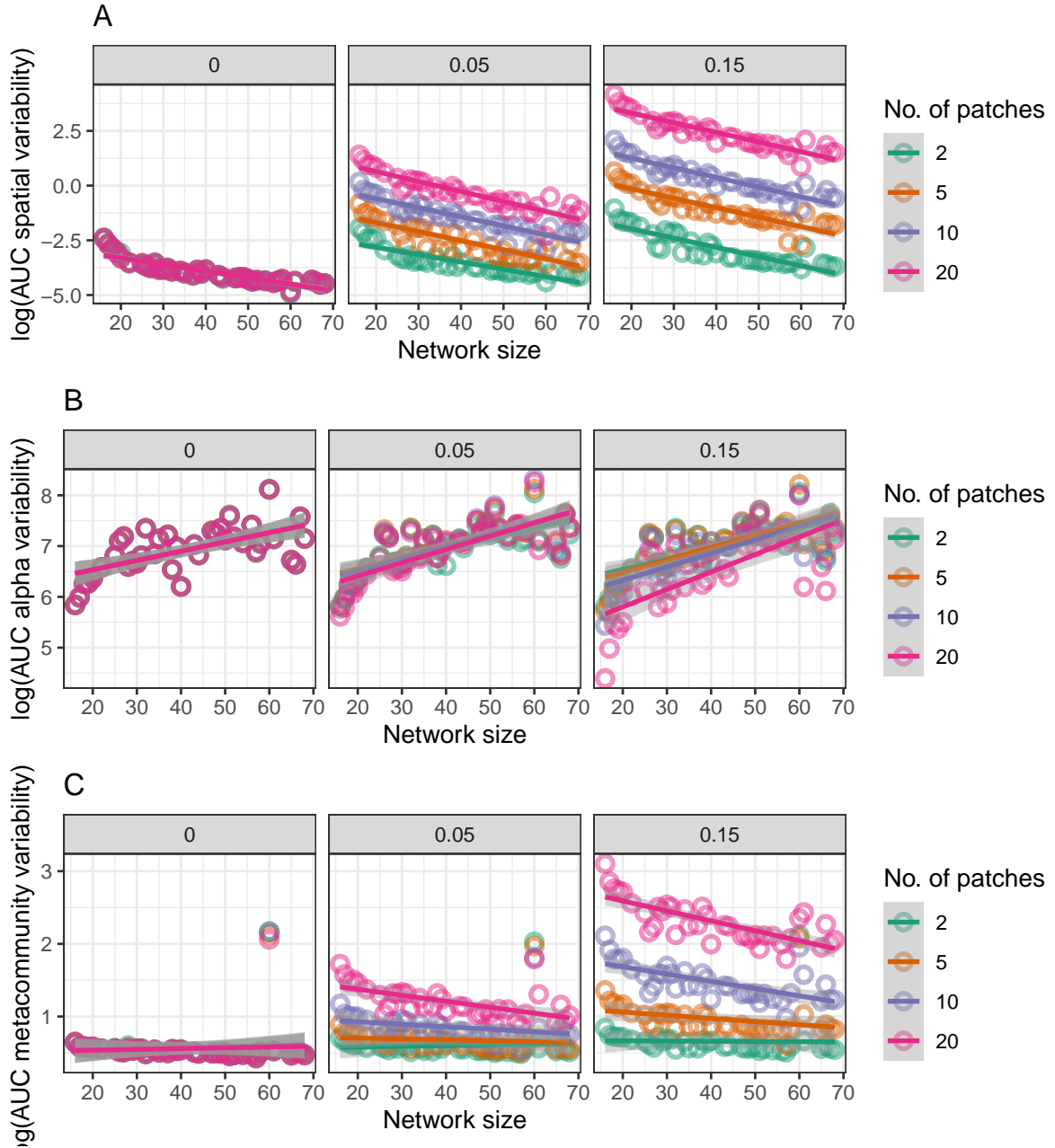


Figure 3: Relationship between network size and AUC of statistical metrics such as A) spatial variability, B) alpha variability, and C) metacommunity variability for three levels of species dispersal (0,0.05,0.15) and four metacommunity sizes (2, 5, 10, 20). Note that the y-axis in all these subplots indicate the strength of increases in these indicators (measured as the AUC of the metric, see figure 1C for description) as a mutualistic metacommunity collapsed. Larger AUC would indicated stronger increases as a mutualistic meta-network collapsed.

305 Alpha variability or patch variability was impacted by network size and less by species dis-
306 persal or metacommunity size. Before an abrupt transition due to decreases in mutualistic
307 strength, larger networks will exhibit stronger patch variability before collapse than smaller
308 networks.

309 Species-level metrics such as species-level autocorrelation and standard deviation were av-
310 eraged over all species in a network before they collapsed as mutualistic strength decreased.
311 Species-level indicators did indicate as networks collapsed but its relationship with network
312 topology such as connectance and network size were not significant (fig. 4A-B).

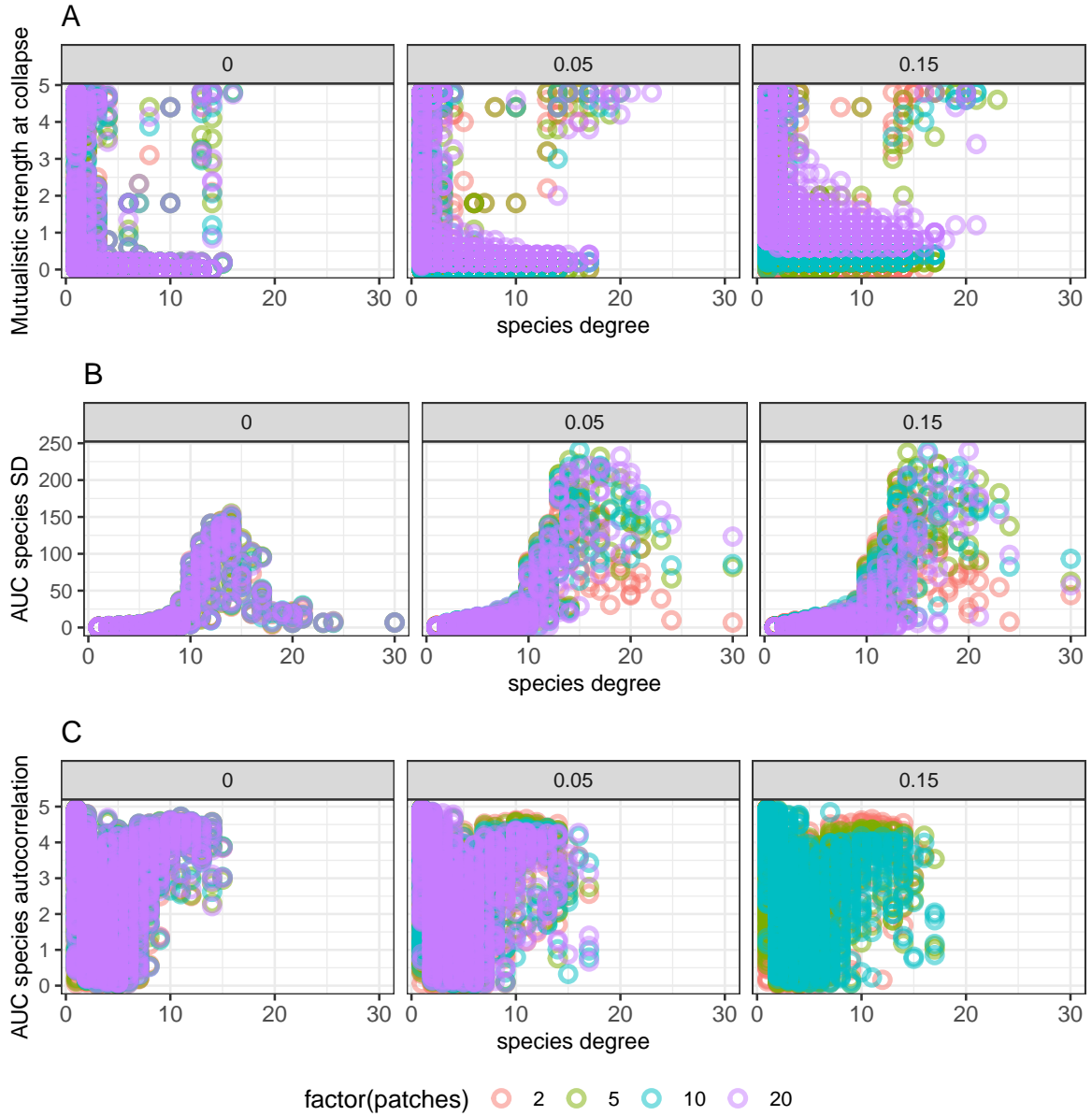


Figure 4: A) Strength of mutualistic interaction at which species in a network collapsed in comparison to its degree. B) Relationship between species degree and AUC of SD (standard deviation) measured at the species-level and C) autocorrelation at first-lag for three levels of dispersal (0,0.05,0.15) and four metacommunity sizes (2, 5, 10, 20). Note that the y-axis in all these subplots indicate the strength of increases in leading indicators (measured as the AUC of the metric, see figure 1C for description) as a mutualistic metacommunity collapsed. Larger AUC would indicated stronger increases as a mutualistic meta-network collapsed.

Discussion

Climate change can cause shifts in interaction strengths that could lead to mismatches in species interactions thereby causing negative impacts on species biomass and diversity (Revilla et al., 2015; Thompson and Gonzalez, 2017). In mutualistic networks, positive interactions between groups of species leads to a positive-feedback mechanism that promotes the occurrence of sudden collapses once environmental change causes interaction strengths to fall below a certain threshold (Baruah, 2022; Kéfi et al., 2016; Lever et al., 2014). Although, studies have tried to understand how such networks are robust to habitat destruction and changes in phenology, little is known about how the architecture of such mutualistic networks at the spatial scale could influence the timing of such collapses. Here, I show that species dispersal rate, size of the metacommunity, and network architecture has significant impacts on the threshold at which a mutualistic meta-network collapses. Furthermore, performance of statistical metrics that could be used to forecast such unwanted collapses, such as metacommunity variability, alpha variability or spatial variability, was not only dependent on the architecture of the mutualistic meta-network but also on species dispersal rate and the size of the metacommunity.

When dispersal rate was zero, all mutualistic networks distributed across a spatial scale could be coalesced to independent local communities. Effectively, metacommunity size i.e., number of habitat patches in the metacommunity, thus, has no impact when a network collapsed. This is obvious as species dispersal is zero and spatial insurance provided by species dispersing across the landscape is effectively negligible (Loreau et al., 2003). As a result, when strength of mutualism decreased, networks collapsed and metacommunity size didn't have any impact when such networks collapsed. There was, however, a slight negative relationship between size of the network and the mutualistic threshold at which such networks collapsed. Particularly, larger networks collapsed later than smaller networks. Earlier studies have indicated that feasibility of mutualistic networks increases as network size or nestedness increases (Baruah, 2022; Lever et al., 2014). This is intuitive as larger

340 networks have larger number of species which effectively increases network biomass and
341 persistence of the network as a whole.

342 As species dispersal increases, the effect of metacommunity size becomes more evident. At
343 high species dispersal, the relationship between network size and the mutualistic strength
344 threshold at which networks collapsed became more negative. Smaller networks collapsed
345 much earlier at higher dispersal rate than larger networks. This particular result was evi-
346 dent at larger metacommunity sizes (Fig. 2A). At smaller metacommunities, for instance
347 a metacommunity with two habitat patches, species were able to easily disperse to the
348 only other habitat and therefore were able to rescue local communities from collapsing at a
349 much earlier mutualistic strength. As such, in smaller metacommunities, smaller networks
350 collapsed at a similar mutualistic strength as larger networks. The relationship between
351 mutualistic strength at which networks collapsed and network size becomes more negative
352 at higher dispersal rates and larger metacommunity sizes. This can be explained as follows.
353 In such mutualistic metacommunities species were modelled to be obligate mutualists, which
354 indicated that species depended solely on mutualistic interactions for maintaining positive
355 growth rate. As species dispersal increased, indicating that a larger chunk of individu-
356 als of a species dispersed from local patches, a stronger average mutualistic interaction
357 was required for a species to maintain an overall positive growth rate locally. As a con-
358 sequence, at very high dispersal rates, species growth rate decreases locally, and hence,
359 a much stronger mutualistic strength on average would be required to maintain positive
360 growth rate. This particular phenomena did not become an issue in smaller metacom-
361 munities, for instance a metacommunity with two habitat patches, as species could easily
362 disperse and compensate for negative growth (Loreau et al., 2003). However, this becomes
363 a problem at larger metacommunities as species now have more than just a few habitats
364 to disperse to. In addition to this, smaller networks, on average, have smaller number of
365 mutualistic interactions when compared with larger networks. As a consequence, smaller
366 networks in larger metacommunities collapsed at a higher mutualistic strength than larger
367 networks in larger metacommunities. Larger networks collapsed later in larger metacom-

368 munities solely because they were able to retain higher biomass due to higher number of
369 mutualistic interactions on average, as well as due to larger number of species. Results,
370 therefore, indicate that in order to preserve biodiversity, it is thus imperative to take into
371 account both the sizes of communities (topological features) as well as the spatial scale of
372 species interactions (Thompson and Gonzalez, 2017).

373 Much work has been done in identifying statistical signals that could forecast unwanted
374 critical transitions. These statistical signals are phenomenological in nature and could be
375 easily identified from state-based timeseries data such as abundance or biomass (Baruah
376 et al., 2019; Clements and Ozgul, 2016; Dakos et al., 2012a, 2012b; Scheffer et al., 2012).
377 However, such signals and their efficacy have been questioned recently both in numerical
378 simulations studies (Baruah et al., 2020; Clements et al., 2015; Hastings and Wysham, 2010)
379 and experimental studies (Baruah et al., 2021; Wilkinson et al., 2018). Their application on
380 multi-species communities (Baruah et al., 2022; Dakos, 2017; Dakos and Bascompte, 2014;
381 Patterson et al., 2021), particularly in the context of a spatial structure has been lack-
382 ing. Here, I evaluated how the efficacy of commonly used statistical signals measured at
383 the species level (autocorrelation at first-lag, standard deviation), community level (patch
384 variability, spatial variability) and at the metacommunity level (temporal regional variabil-
385 ity) in relation to network topology and spatial scale of interactions. Interestingly, species
386 level metrics i.e., standard deviation and autocorrelation at first-lag exhibited increases as
387 strength in mutualistic interaction decreased (AUC greater than 1), however, there was no
388 relationship with network architecture (Fig. S5). Community and metacommunity-based
389 signals such as alpha variability, spatial variability also increased as mutualistic strength
390 decreased. Surprisingly, although smaller networks in larger metacommunities collapsed
391 earlier, however, such networks exhibited stronger increases in spatial variability and meta-
392 community variability particularly at higher species dispersal rates (Fig. 3A-C). This in-
393 dicated smaller networks could exhibit strong statistical signals before collapses which was
394 conditionally dependent on high species dispersal and whether such communities were a
395 part of a large metacommunity. Spatial variability also exhibited a similar pattern. Thus,

when global changes weaken mutualistic interactions thereby leading to loss of biodiversity, indicators measured at the community and metacommunity level could potentially inform instability. Our analysis indicated that these indicators and their performance when estimated at the community or metacommunity level will be dependent on species dispersal, network architecture and how large the metacommunity is.

Changes in the environment can weaken species interactions to the point of biodiversity collapse. Recovering lost ecosystem functions and processes is not easy as demographic information of species are also lost as biodiversity collapses [(Link and Watson, 2019; Scheffer et al., 2009)]. In addition, most ecological systems can exhibit a phenomenon called hysteresis whereby even if the original stable environmental conditions are reverted, the ecological system might still not recover. There are tools that have been thus develop to forecast such unwanted transitions Dakos et al. (2012b). When an ecological network collapses both at the local as well as at the spatial scale, signals of global meta-network instability could also be manifested in species in an ecological community. It is relatively unknown, however, which species could exhibit signals of instability, but see Dakos (2017) , Baruah et al. (2022) or Patterson et al. (2021). Indeed, the species that exhibited strong increases in standard deviation as networks collapsed, were the ones which had on average a larger number of interactions (Fig. 4B). The relationship between species degree and strength of species SD was non-linear, indicating that species with moderate to high number of interactions would show the strongest increase as networks collapsed. Species that had a relatively larger number of mutualistic interactions, benefited from higher positive growth rate which resulted in stronger increases in standard deviation as networks collapsed than those species that had fewer interactions. However, as shown in Dakos and Bascompte (2014), and also here, species that have fewer interactions would collapse earlier and might not exhibit as strong an increase in standard deviation as networks collapsed. This indicates that, although, one could potentially label species that have higher number of interactions as “indicator species,” that, however, would not help in informing instability of “specialist species” as they generally collapsed much earlier (Fig. 4A). Nevertheless, these results indicate that

standard deviation measured at the species level could potentially increase as mutualistic interactions weaken and more so for species with a moderate to high number of interactions. Autocorrelation at first-lag also increased as interactions weakened, but its relation with species degree was unclear.

Our ability to detect an impending transition is dependent on monitoring dynamics at the vicinity of the transition. However, monitoring population dynamics required intense temporal as well as spatial sampling and could potentially impact forecasting of abrupt transitions (Arkilanian et al., 2020; Bruel and White, 2021; Clements et al., 2015) . Many other factors could also impact prediction of such transitions including but not limited to long transients and stochasticity (Hastings et al., 2018; Hastings and Wysham, 2010). There has been quite a debate on the appropriate set of methods or tools that could be used to predict future biodiversity states. Studies have indicated that in addition to monitoring dynamics of species abundance, phenotypic traits should be monitored as well. Including information from phenotypic dynamics such as body size could improve forecasts of biodiversity collapse (Clements and Ozgul, 2016), although such an accurate forecast of biodiversity collapse is dependent on the type of environmental perturbation and the type of interactions prevalent in the community (Baruah et al., 2022, 2019). When changes in the environment impact communities both locally and spatially alike, ecological networks could abruptly collapse. However, when such networks collapses depends on the average rate of species dispersal, with higher species dispersal and larger metacommunities causing meta-networks to collapse at a much higher mutualistic strength. In addition, collapses of mutualistic meta-networks was also dependent largely on the topology of the network, with smaller networks collapsing at a higher mutualistic strength than larger networks. These results are pertinent for conservation efforts particularly because it points to the fact that ecological networks at larger metacommunities are as vulnerable or if not more than meta-networks at a much smaller spatial scale. When assessing whether communities are vulnerable to changes in the environment, the results from this research indicates that it is very pertinent to look at factors beyond species demographic rates, that includes the scale of spatial interactions,

452 and topology of local ecological communities.

453 **Author contributions**

454 GB conceptualized the study, did the analysis and wrote the manuscript.

455 **Data availability**

456 The paper was written in markdown format and files, data, and R scripts to reproduce the
457 paper is located at the repository of [https://github.com/GauravKBaruah/spatial_tipping_](https://github.com/GauravKBaruah/spatial_tipping_points)
458 [points](https://github.com/GauravKBaruah/spatial_tipping_points)

459 **References**

- 460 Arkilanian, A.A., Clements, C.F., Ozgul, A., Baruah, G., 2020. Effect of time series length
461 and resolution on abundance- and trait-based early warning signals of population de-
462 clines. *Ecology* 101, e03040.
- 463 Barabás, G., Michalska-Smith, M.J., Allesina, S., 2017. Self-regulation and the stability of
464 large ecological networks. *Nature Ecology & Evolution* 1, 1870–1875.
- 465 Baruah, G., 2022. The impact of individual variation on abrupt collapses in mutualistic
466 networks. *Ecology Letters* 25, 26–37.
- 467 Baruah, G., Clements, C.F., Guillaume, F., Ozgul, A., 2019. When Do Shifts in Trait
468 Dynamics Precede Population Declines? *The American Naturalist* 193, 633–644.
- 469 Baruah, G., Clements, C.F., Ozgul, A., 2020. Eco-evolutionary processes underlying early
470 warning signals of population declines. *Journal of Animal Ecology* 89, 436–448.
- 471 Baruah, G., Clements, C.F., Ozgul, A., 2021. Effect of habitat quality and phenotypic
472 variation on abundance- and trait-based early warning signals of population collapses.

473 Oikos 130, 850–862.

474 Baruah, G., Ozgul, A., Clements, C.F., 2022. Community structure determines the pre-
475 dictability of population collapse. *bioRxiv*.

476 Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of
477 plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*
478 100, 9383–9387.

479 Bruel, R., White, E.R., 2021. Sampling requirements and approaches to detect ecosystem
480 shifts. *Ecological Indicators* 121, 107096.

481 Clements, C.F., Ozgul, A., 2016. Including trait-based early warning signals helps predict
482 population collapse. *Nature Communications* 7, 1–8.

483 Clements, Drake, J.M., Jason, I.G., Ozgul, A., 2015. Factors Influencing the Detectability
484 of Early Warning Signals of Population Collapse. *The American Naturalist* 186, 50–58.

485 Cunillera-Montcusí, D., Borthagaray, A.I., Boix, D., Gascón, S., Sala, J., Tornero, I., Quin-
486 tana, X.D., Arim, M., 2021. Metacommunity resilience against simulated gradients of
487 wildfire: Disturbance intensity and species dispersal ability determine landscape recover
488 capacity. *Ecography* 44, 1022–1034.

489 Dakos, V., 2017. Identifying best-indicator species for abrupt transitions in multispecies
490 communities. *Ecological Indicators*.

491 Dakos, V., Bascompte, J., 2014. Critical slowing down as early warning for the onset of
492 collapse in mutualistic communities. *Proceedings of the National Academy of Sciences*.

493 Dakos, V., Carpenter, S.R., Brock, W.A., Ellison, A.M., Guttal, V., Ives, A.R., Kéfi, S., Liv-
494 ina, V., Seekell, D.A., Nes, E.H. van, Scheffer, M., 2012a. Methods for Detecting Early
495 Warnings of Critical Transitions in Time Series Illustrated Using Simulated Ecological
496 Data. *PLOS ONE* 7, e41010.

497 Dakos, V., Matthews, B., Hendry, A., Levine, J., Loeuille, N., Norberg, J., Nosil, P., Schef-
498 fer, M., Meester, L.D., 2018. Ecosystem tipping points in an evolving world. *bioRxiv*

499 447227–447227.

500 Dakos, V., Van Nes, E.H., D’odorico, P., Scheffer, M., 2012b. Robustness of variance and
501 autocorrelation as indicators of critical slowing down.

502 Dunne, J.A., Williams, R.J., 2009. Cascading extinctions and community collapse in model
503 food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364,
504 1711–1723.

505 Forrest, J.R.K., 2015. Plant–pollinator interactions and phenological change: What can we
506 learn about climate impacts from experiments and observations? *Oikos* 124, 4–13.

507 Fortuna, M.A., Bascompte, J., 2006. Habitat loss and the structure of plant–animal mutu-
508 alistic networks. *Ecology Letters* 9, 281–286.

509 Grilli, J., Barabás, G., Allesina, S., 2015. Metapopulation Persistence in Random Frag-
510 mented Landscapes. *PLOS Computational Biology* 11, e1004251.

511 Hastings, A., Abbott, K.C., Cuddington, K., Francis, T., Gellner, G., Lai, Y.-C., Morozov,
512 A., Petrovskii, S., Scranton, K., Zeeman, M.L., 2018. Transient phenomena in ecology.
513 *Science* (New York, N.Y.) 361, eaat6412–eaat6412.

514 Hastings, A., Wysham, D.B., 2010. Regime shifts in ecological systems can occur with no
515 warning. *Ecology Letters* 13, 464–472.

516 Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S., Bini, L.M., 2015. Metacomm-
517 unity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes
518 and prospects. *Freshwater Biology* 60, 845–869.

519 Hilker, F.M., 2010. Population collapse to extinction: The catastrophic combination of
520 parasitism and Allee effect. *Journal of Biological Dynamics* 4, 86–101.

521 Hutchings, J.A., Reynolds, J.D., 2004. Marine Fish Population Collapses: Consequences
522 for Recovery and Extinction Risk. *BioScience*.

523 Kéfi, S., Holmgren, M., Scheffer, M., 2016. When can positive interactions cause alternative
524 stable states in ecosystems? *Functional Ecology* 30, 88–97.

525 Kudo, G., Cooper, E.J., 2019. When spring ephemerals fail to meet pollinators: Mechanism
526 of phenological mismatch and its impact on plant reproduction. *Proceedings of the Royal
527 Society B: Biological Sciences* 286, 20190573.

528 Lehman, C.L., Tilman, D., 2000. Biodiversity, Stability, and Productivity in Competitive
529 Communities. *The American Naturalist* 156, 534–552.

530 Lever, J.J., Leemput, I.A. van de, Weinans, E., Quax, R., Dakos, V., Nes, E.H. van,
531 Bascompte, J., Scheffer, M., 2020. Foreseeing the future of mutualistic communities
532 beyond collapse. *Ecology Letters* 23, 2–15.

533 Lever, J.J., Nes, E.H. van, Scheffer, M., Bascompte, J., 2014. The sudden collapse of
534 pollinator communities. *Ecology Letters*.

535 Limberger, R., Pitt, A., Hahn, M.W., Wickham, S.A., 2019. Spatial insurance in multi-
536 trophic metacommunities. *Ecology Letters* 22, 1828–1837.

537 Link, J.S., Watson, R.A., 2019. Global ecosystem overfishing: Clear delineation within real
538 limits to production. *Science Advances* 5, eaav0474.

539 Loreau, M., Mouquet, N., Gonzalez, A., 2003. Biodiversity as spatial insurance in heteroge-
540 neous landscapes. *Proceedings of the National Academy of Sciences* 100, 12765–12770.

541 Morton, E.M., Rafferty, N.E., 2017. Plant–pollinator interactions under climate change:
542 The use of spatial and temporal transplants. *Applications in Plant Sciences* 5, 1600133.

543 Patterson, A.C., Strang, A.G., Abbott, K.C., 2021. When and Where We Can Expect to See
544 Early Warning Signals in Multispecies Systems Approaching Tipping Points: Insights
545 from Theory. *The American Naturalist* 198, E12–E26.

546 Prakash, S., Roos, A.M. de, 2004. Habitat destruction in mutualistic metacommunities.
547 *Theoretical Population Biology* 65, 153–163.

Renner, S.S., Zohner, C.M., 2018. Climate Change and Phenological Mismatch in Trophic Interactions Among Plants, Insects, and Vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49, 165–182.

Revilla, T.A., Encinas-Viso, F., Loreau, M., 2015. Robustness of mutualistic networks under phenological change and habitat destruction. *Oikos* 124, 22–32.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., Nes, E.H. van, Rietkerk, M., Sugihara, G., 2009. Early-warning signals for critical transitions. *Nature* 461, 53–59.

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., Koppel, J. van de, Leemput, I.a. van de, Levin, S.a., Nes, E.H. van, Pascual, M., Vandermeer, J., 2012. Anticipating Critical Transitions. *Science* 338, 344–348.

Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution* 8, 275–279.

Shoemaker, L.G., Melbourne, B.A., 2016. Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology* 97, 2436–2446.

Thompson, P.L., Gonzalez, A., 2017. Dispersal governs the reorganization of ecological networks under environmental change. *Nature Ecology & Evolution* 1, 1–8.

Visser, M.E., Gienapp, P., 2019. Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution* 3, 879–885.

Walter, J.A., Sheppard, L.W., Anderson, T.L., Kastens, J.H., Bjørnstad, O.N., Liebhold, A.M., Reuman, D.C., 2017. The geography of spatial synchrony. *Ecology Letters* 20, 801–814.

Wang, S., Lamy, T., Hallett, L.M., Loreau, M., 2019. Stability and synchrony across ecological hierarchies in heterogeneous metacommunities: Linking theory to data. *Ecography* 42, 1200–1211.

- 573 Wang, S., Loreau, M., 2014. Ecosystem stability in space: A, and variability. *Ecology*
574 *Letters* 17, 891–901.
- 575 Wilkinson, G.M., Carpenter, S.R., Cole, J.J., Pace, M.L., Batt, R.D., Buelo, C.D.,
576 Kurtzweil, J.T., 2018. Early warning signals precede cyanobacterial blooms in multiple
577 whole-lake experiments. *Ecological Monographs* 88, 188–203.
- 578 Wissel, C., 1984. A universal law of the characteristic return time near thresholds. *Oecolo-*
579 *gia* 65, 101–107.

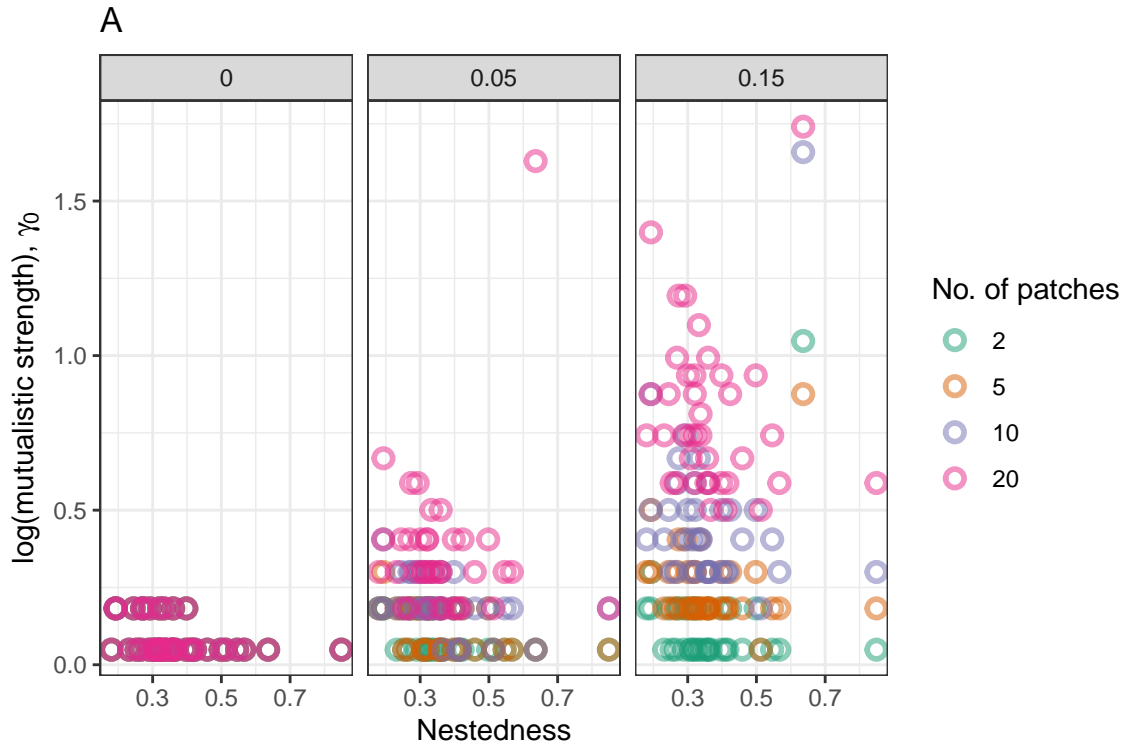


Figure S1: Relationship between the threshold mutualistic strength at which networks collapsed and structural properties of the network namely nestedness (NODF).

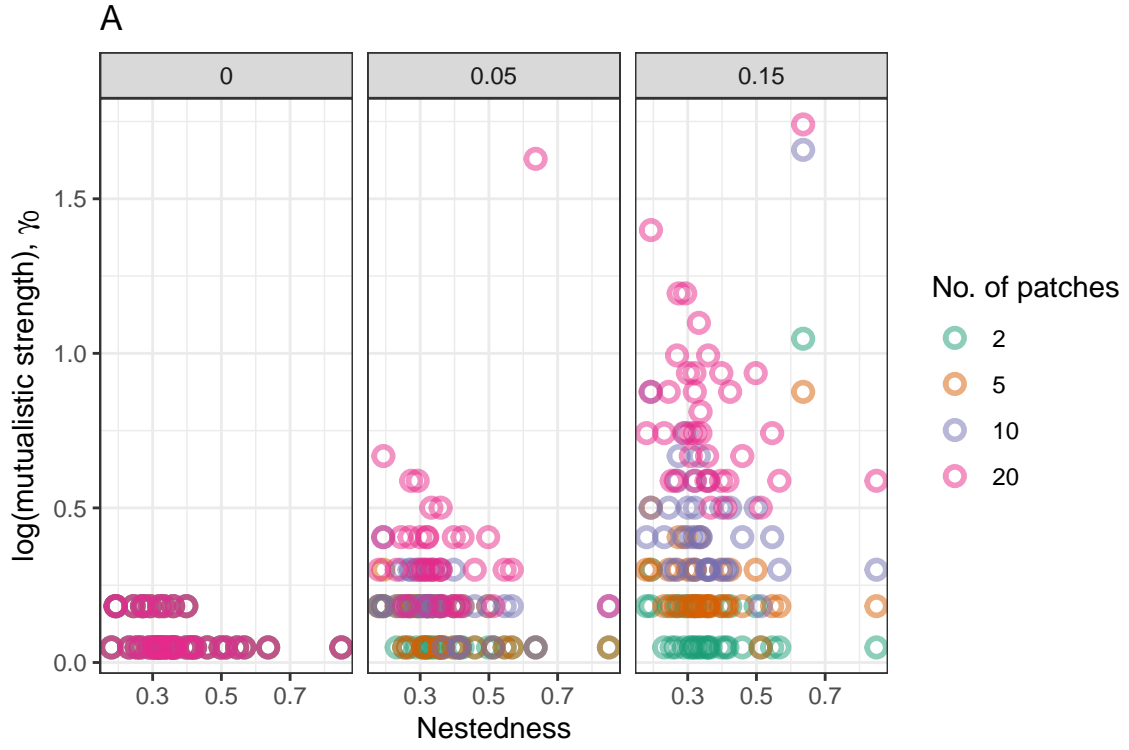


Figure S2: Relationship between the threshold mutualistic strength at which networks collapsed and structural properties of the network namely nestedness (NODF).

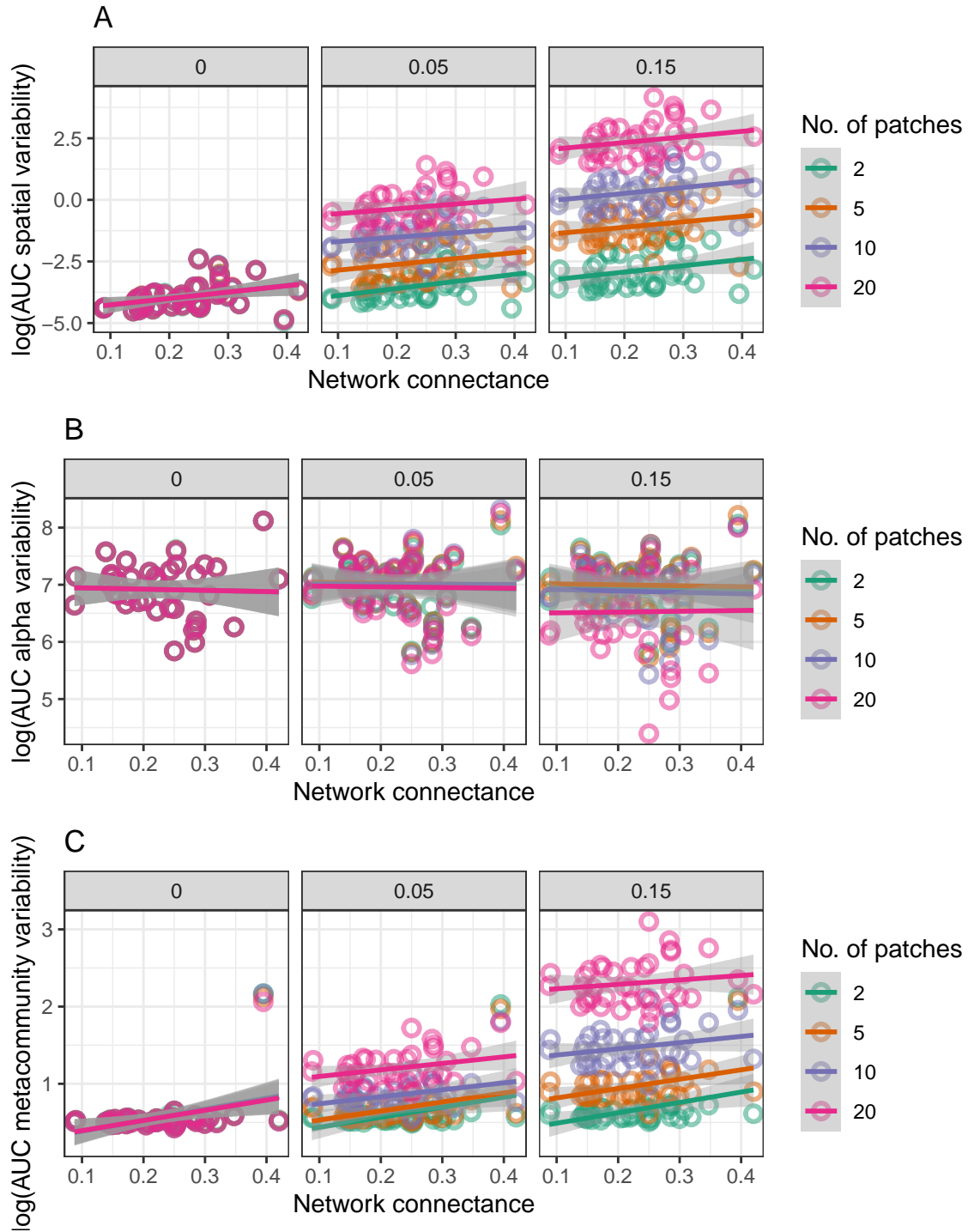


Figure S3: Relationship between network connectance and area under the curve of statistical metrics such as A) spatial variability, B) Alpha variability, and C) metacommunity variability for three levels of species dispersal (0,0.05,0.15) and four metacommunity sizes (2, 5, 10, 20). Note that the y-axis in all these subplots indicate the strength of increases in these indicators (measured as the AUC of the metric, see figure 1C for description) as a mutualistic metacommunity collapsed. Larger AUC would indicated stronger increases as a mutualistic meta-network collapsed.

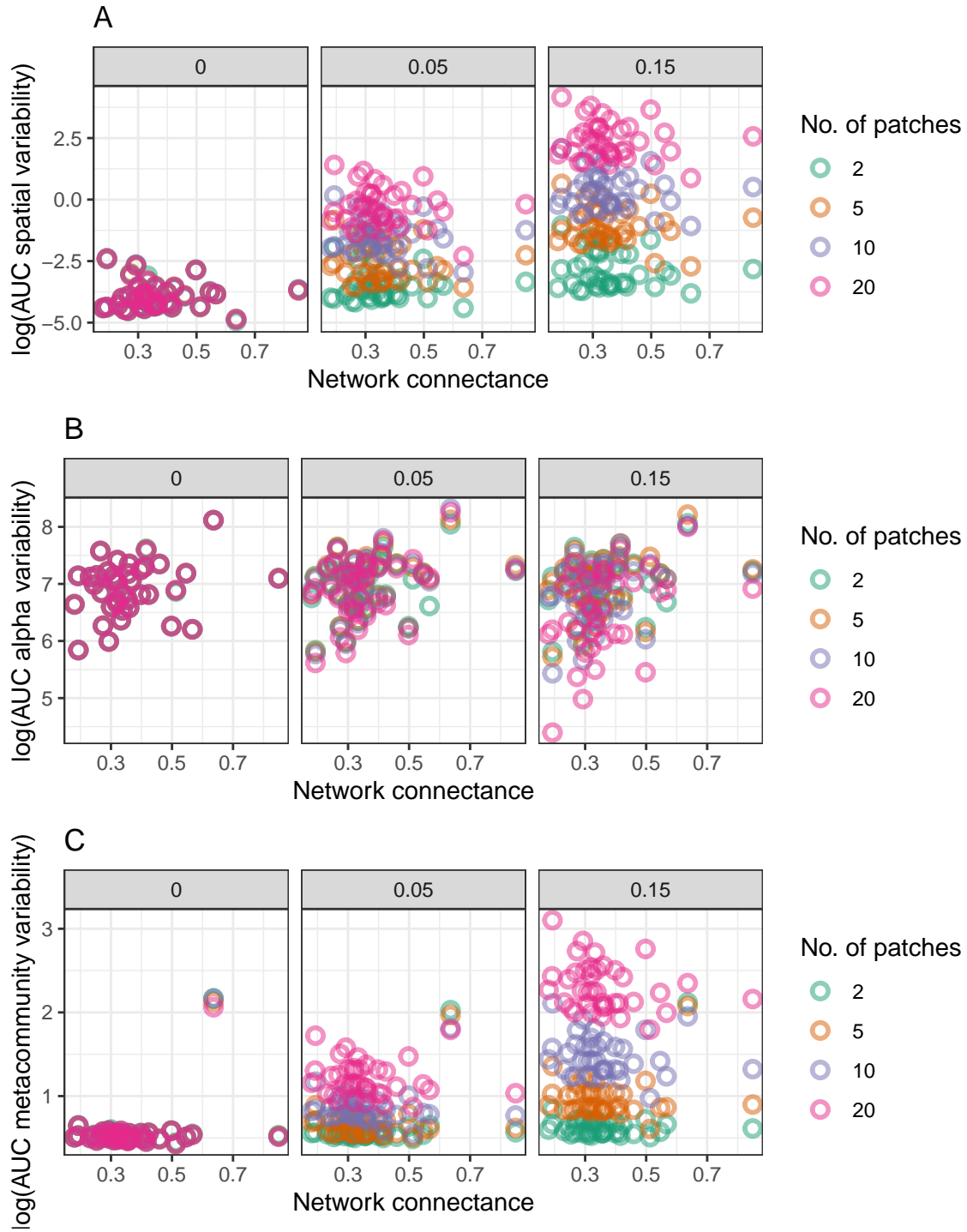


Figure S4: Relationship between network nestedness (NODF) and area under the curve of statistical metrics such as A) spatial variability, B) Alpha variability, and C) metacommunity variability for three levels of species dispersal (0,0.05,0.15) and four metacommunity sizes (2, 5, 10, 20). Note that the y-axis in all these subplots indicate the strength of increases in these indicators (measured as the AUC of the metric, see figure 1C for description) as a mutualistic metacommunity collapsed. Larger AUC would indicated stronger increases as a mutualistic meta-network collapsed.

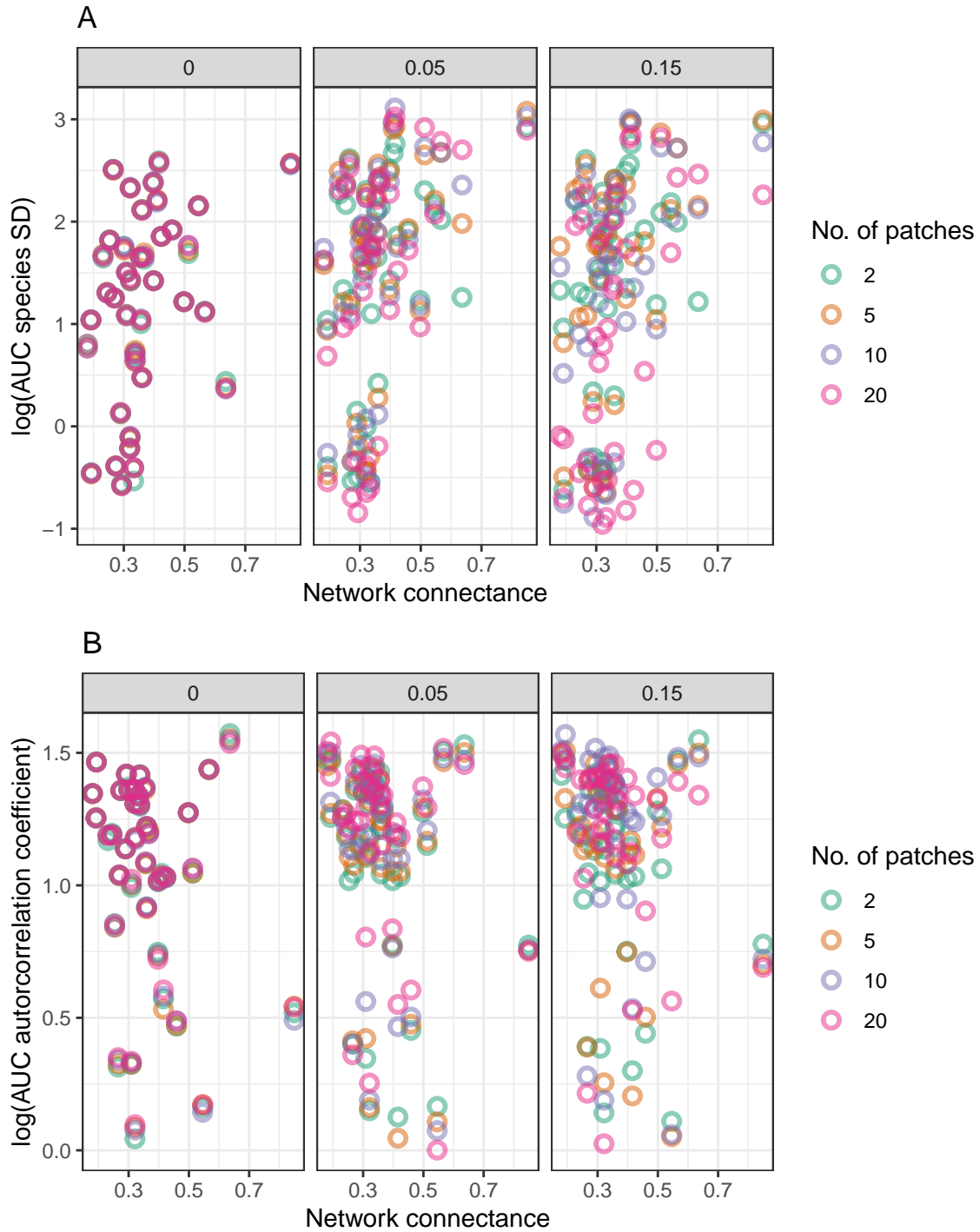


Figure S5: Relationship between network nestedness (NODF) and area under the curve of statistical metrics such as A) species SD, B) Autocorrelation coefficient at first-lag, for three levels of species dispersal (0,0.05,0.15) and four metacommunity sizes (2, 5, 10, 20). Note that the y-axis in all these subplots indicate the strength of increases in these indicators (measured as the AUC of the metric,³⁵ see figure 1C for description) as a mutualistic metacommunity collapsed. Larger AUC would indicated stronger increases as a mutualistic meta-network collapsed.

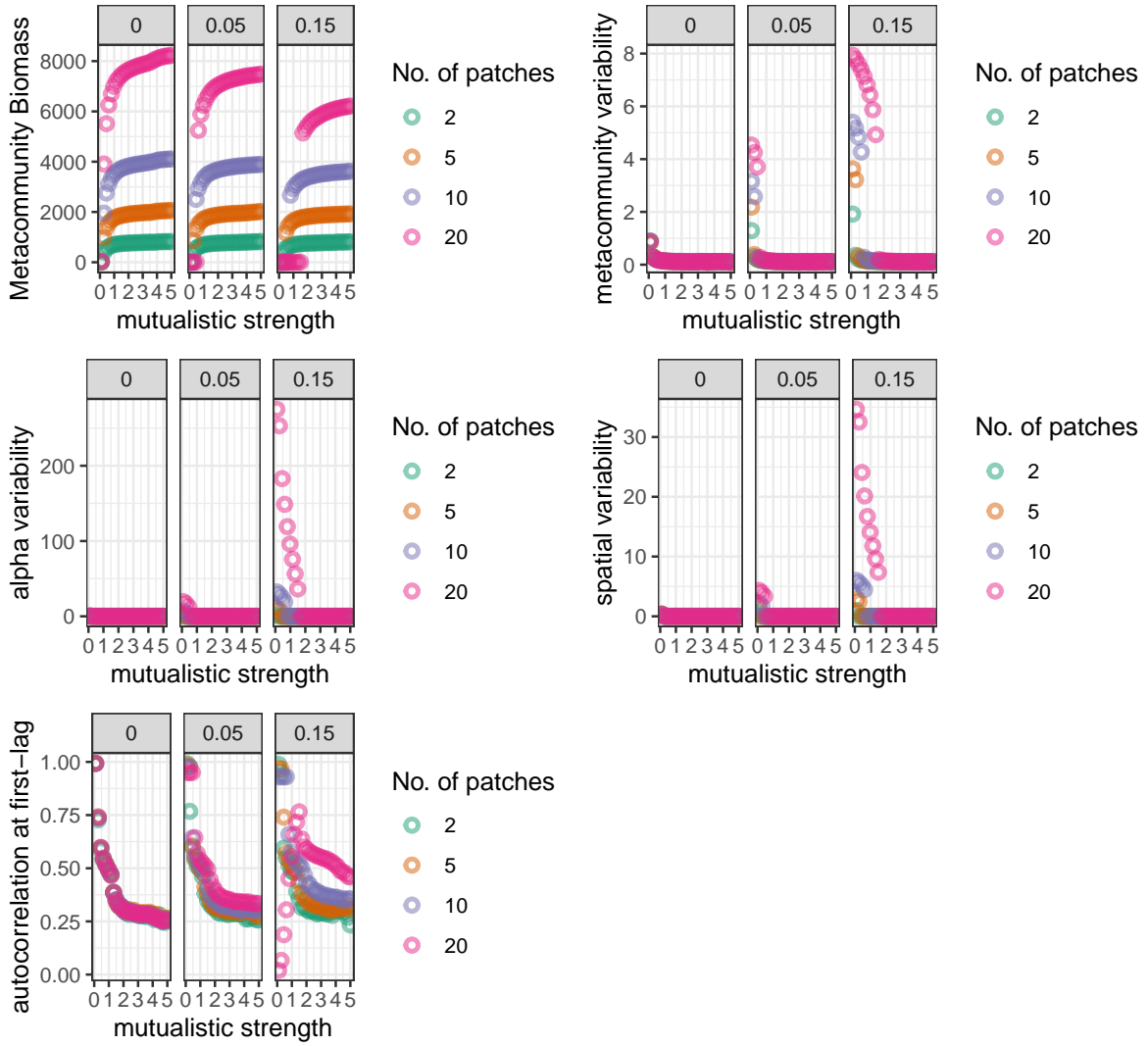


Figure S6: Meta-network collapse and statistical metrics that increased as mutualistic strength decreased for three rates of dispersal, four metacommunity size. A) Example meta-network collapse as mutualistic strength decreased. (B) metacommunity variability as mutualistic strength decreased. (C) alpha variability as mutualistic strength decreased. (D) Spatial variability as mutualistic strength decreased, (E) species autocorrelation as mutualistic strength decreased.