

The spatial synchrony of species richness and its relationship to ecosystem stability

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1 Abstract

1 Synchrony is broadly important to population and community dynamics due to its ubiquity
2 and implications for extinction dynamics, system stability, and species diversity. Investiga-
3 tions of synchrony in community ecology have tended to focus on covariance in the abun-
4 dances of multiple species in a single location. Yet, the importance of regional environmental
5 variation and spatial processes in community dynamics suggests that community properties,
6 such as species richness, could fluctuate synchronously across patches in a metacommunity, in
7 an analog of population spatial synchrony. Here, we test the prevalence of this phenomenon
8 and the conditions under which it may occur using theoretical simulations and empirical
9 data from 20 marine and terrestrial metacommunities. Additionally, given the importance
10 of biodiversity for stability of ecosystem function, we posit that spatial synchrony in species
11 richness is strongly related to stability. Our findings show that that metacommunities often
12 exhibit spatial synchrony in species richness. We also found that richness synchrony can
13 be driven by environmental stochasticity and dispersal, two mechanisms of population spa-
14 tial synchrony. Richness synchrony also depended on community structure, including species
15 evenness and beta diversity. Strikingly, ecosystem stability was more strongly related to rich-
16 ness synchrony than to species richness itself, likely because richness synchrony integrates
17 information about community processes and environmental forcing. Our study highlights a
18 new approach for studying spatiotemporal community dynamics and emphasizes the spatial
19 dimensions of community dynamics and stability.

20 **Key words:** biodiversity, community synchrony, dispersal, ecosystem stability, Moran ef-
21 fect, spatial synchrony

2 Introduction

Synchrony has broad importance in population and community ecology, and recent efforts that integrate perspectives from these sub-disciplines have generated new insights into spatiotemporal population and community dynamics (Wang & Loreau, 2014; Walter *et al.*, 2021; Wilcox *et al.*, 2017; Arribas *et al.*, 2019; Lee *et al.*, 2019). Population spatial synchrony, where temporal fluctuations in abundance are correlated across populations inhabiting multiple locations, is a fundamental feature of population dynamics observed across taxa and over wide-ranging spatial scales (Liebhold *et al.*, 2004; Walter *et al.*, 2017). Mechanisms underlying population spatial synchrony include dispersal, spatially correlated environmental fluctuations driving shared demographic responses (Moran effects), and interactions with a species that itself exhibits spatial synchrony (Moran, 1953; Liebhold *et al.*, 2004). Spatially synchronous populations are at greater risk of regional extirpation or extinction. This is especially true for species of conservation concern, such as stocks of exploited species (Schindler *et al.*, 2015), as simultaneous rarity reduces the population rescue effect of dispersal (Earn *et al.*, 1998; Heino, 1998).

In contrast to population spatial synchrony, community ecology tends to focus on a different kind of synchrony: correlated temporal fluctuations of multiple species' abundances in a single location. This "community synchrony" can alter the stability of its aggregate properties. For example, community synchrony decreases the temporal stability of total abundance or biomass production (Micheli *et al.*, 1999; Loreau & de Mazancourt, 2008), which is commonly equated to ecosystem function (Donohue *et al.*, 2016). Alternatively, stability is maintained when species fluctuate independently and especially if their fluctuations negatively covary. This negative covariance between species, commonly known as compensatory dynamics, reflects heterogeneity in species' responses to environmental drivers, possibly mediated through competitive release (Gonzalez & Loreau, 2009; Hallett *et al.*, 2017).

48 As exemplified via the sustained focus on metacommunity theory over the past decade
49 (Leibold *et al.*, 2004; Leibold & Chase, 2017), there is growing recognition of the importance
50 of spatial scaling and the interplay of local versus regional dynamics on community attributes
51 such as biodiversity (Shoemaker & Melbourne, 2016; De Meester *et al.*, 2016) and stability
52 (Wang & Loreau, 2014; Wang *et al.*, 2019). That many of the factors that are central to
53 population spatial synchrony—including dispersal, temporal environmental variation, and
54 spatial heterogeneity—have also proven important to spatiotemporal community dynamics
55 suggests that we may, *a priori*, expect that biodiversity (e.g., species richness) could exhibit
56 spatial synchrony, at least under some conditions. To date, however, whether biodiversity
57 commonly exhibits spatial synchrony—and if so, why—is unknown. Here, we focus on spa-
58 tial synchrony in species richness and explore potential mechanisms through which richness
59 synchrony could arise, as well as its implications.

60 There are several reasons to investigate synchrony in richness. Biodiversity is often asso-
61 ciated with ecosystem function (Tilman & Downing, 1994; Schulze & Mooney, 2012; Rypel
62 & David, 2017) and stability thereof (Cottingham *et al.*, 2001; de Mazancourt *et al.*, 2013).
63 Species richness is widely used to quantify biodiversity, in part because presence-absence
64 data are more easily obtained than data on abundance, or indices thereof, needed for other
65 measures. Furthermore, studying synchrony in numbers of species bears quantitative simi-
66 larity to studying synchrony in numbers of individuals, as in population spatial synchrony,
67 even though the generating processes are more complex.

68 Here, we consider how spatial synchrony in species richness might arise mechanistically.
69 In a given location (e.g., a patch in a metacommunity), fluctuations in richness reflect local
70 colonization and extinction events. Species richness could therefore exhibit spatial synchrony
71 if colonization and extinction dynamics are themselves spatially correlated, for example due
72 to dispersal. Dispersal could in principle produce synchronous fluctuations in species rich-
73 ness even in a competitively neutral, homogeneous environment. Additionally, environmental

74 fluctuations could themselves cause or enhance richness synchrony (Harrison & Quinn, 1989),
75 especially in settings where local extinctions are possible. Spatially correlated environmen-
76 tal fluctuations could also synchronize patch-level richness by altering available niche space
77 (Shoemaker & Melbourne, 2016) or shifting the suite of species favored under current con-
78 ditions (Pitt & Heady, 1978). We expect that Moran effects on species richness are likely
79 given that biodiversity can fluctuate in response to climatic variation (Peco *et al.*, 1998), and
80 that Moran effects on populations comprising the community—which are common (Liebhold
81 *et al.*, 2004)—may manifest in community metrics.

82 Drawing on the implications of spatial synchrony for population stability, and the impli-
83 cations of diversity and community synchrony for stability, we predict that spatial synchrony
84 in richness will relate strongly to stability of ecosystem function at the landscape scale. More
85 biodiverse systems may be more stable in the sense of tending to have lower tempo-
86 ral variance in ecosystem function (Cottingham *et al.*, 2001). Synchrony is destabilizing in
87 the same sense because shared fluctuations reinforce each other and thereby total to large
88 variations in the aggregate, while asynchronous fluctuations cancel out (Hallett *et al.*, 2014;
89 Anderson *et al.*, 2021).

90 This study integrates insights from a theoretical metacommunity model with a synthesis
91 of 20 empirical metacommunities from terrestrial grassland and coastal marine biomes to
92 examine the prevalence of spatial synchrony in species richness, the ecological factors that
93 can promote or diminish it, and how it can provide insight into the stability of ecosystem
94 function. Specifically, we address the following research questions: 1) Do local fluctuations
95 in species richness exhibit spatial synchrony across metacommunity patches? 2) Are the
96 well-documented drivers of population spatial synchrony (i.e., Moran effects and dispersal)
97 also key drivers of spatial synchrony in richness? 3) Does a community’s strength of spatial
98 synchrony of richness relate to ecosystem stability and how does this compare to relationships
99 between richness and stability? Overall, our study demonstrates the commonness of spatial

100 synchrony in species richness, identifies key abiotic and biotic factors that alter the degree
101 of richness synchrony, and explores how the spatial synchrony of richness may be strongly
102 related to the temporal stability of ecosystem function.

103 **3 Methods**

104 **3.1 Quantifying synchrony in community properties**

105 Although spatial synchrony has mainly been quantified for population variables, spatial
106 synchrony can, in principle, be quantified for any time-varying quantity with measurements
107 taken through time in different places. We measured spatial synchrony of species richness
108 as follows. We began with data consisting of species' abundances at P locations (hereafter,
109 patches) through time. We measured species richness of each patch at each time step to
110 compute richness, $R_{p,t}$, where p is the patch and t is the time-step. We then linearly detrended
111 the time series, standardized variances of each time series to one, and computed the matrix
112 of Spearman correlations for fluctuations in richness through time between all patch pairs.
113 Finally, the lower triangle (excluding the diagonal) of the correlation matrix was averaged to
114 produce one representative value for each site (metacommunity), as commonly occurs when
115 examining community synchrony (Hallett *et al.*, 2014; Kent *et al.*, 2007), and allows us to
116 compare across metacommunities.

117 **3.2 Theoretical modelling**

118 To examine when we expect to observe spatial synchrony of richness and what mechanisms
119 most alter it, we applied the above workflow to simulated metacommunities. Coupling a
120 theoretical model that incorporates known underlying mechanisms with a statistical analy-
121 sis of the spatial synchrony of richness provides insight into the behavior of synchrony under

122 different ecological mechanisms. In brief, our metacommunity model connects local patch-
123 level dynamics to regional dynamics via dispersal. Growth, competition, and environmental
124 effects occur within a patch, environmental conditions of each patch vary both through space
125 and time, and patches are connected via dispersal of individuals. Within-patch dynamics
126 follow a multispecies, metacommunity extension of the model of Loreau and de Mazancourt
127 (2013), which is a discrete-time modification of classic Lotka-Volterra competition dynam-
128 ics that incorporates both demographic and environmental stochasticity and disentangles
129 species' carrying capacities from their competitive effects (Loreau & de Mazancourt, 2008;
130 Loreau, 2010).

131 First, prior to local population dynamics, dispersal between patches occurs. We model
132 dispersal as both local and global (global results are presented in Appendix S1). Abundance
133 N of each species s in a given patch p after dispersal, but before population growth, is
134 indexed as time step $t + \delta$, and is modeled as:

$$N_{s,p,t+\delta} = N_{s,p,t} - E_{s,p,t} + I_{s,p,t} \quad (1)$$

135 where $E_{s,p,t}$ denotes emmigration of species s from patch p while $I_{s,p,t}$ denotes immigraiton.
136 For global dispersal, $E_{s,p,t} = -d_s N_{s,p,t}$ and $I_{s,p,t} = d_s \sum_{x \neq p} \frac{N_{s,x,t}}{P-1}$ where P denotes the total
137 number of patches in the metacommunity, and d is the across-patch stochastic dispersal prob-
138 ability, where propagule dispersal is binomially distributed with the probability of success
139 equal to d (Shoemaker & Melbourne, 2016). Alternatively, for local dispersal, propogules
140 disperse only to their nearest neighbor patches, and the landscape is modeled as a square
141 lattice with wrap-around boundaries (Kerr *et al.*, 2002).

142 Following dispersal, within a patch, p , the abundance of each species changes through

143 time t according to:

$$N_{s,p,t+1} = N_{s,p,t+\delta} \exp\left[r_s \left(1 - \frac{N_{s,p,t+\delta}}{K_s} - \sum_{j \neq s} \frac{\beta_{s,j} N_{j,p,t+\delta}}{K_j}\right) + \sigma_{e,s} \mu_{e,p,t} + \frac{\sigma_{d,s} \mu_{d,s,p,t}}{\sqrt{N_{s,p,t+\delta}}}\right], \quad (2)$$

144 In the above equation, r is a species' intrinsic (density-independent growth rate), K is its
145 carrying capacity in a patch, and $\beta_{s,j}$ is the competition coefficient of species j on species s .
146 Compared to a classic Lotka-Volterra model, here we separate species' interspecific competi-
147 tive effects ($\beta_{s,j}$) from their carrying capacities (K_s). This formalization is related to the α
148 coefficients of Lotka-Volterra dynamics where $\beta_{s,j} = \alpha_{s,j} K_j / K_s$ (Loreau & de Mazancourt,
149 2013). Model parameters and their values are given in Table 1.

150 Demographic stochasticity is incorporated as a traditional first-order normal approxima-
151 tion, and represents inherent variation between individuals in birth and death rates (Lande
152 *et al.*, 2003). Here, $\sigma_{d,s}$ is the susceptibility of species s to demographic fluctuations and
153 $\mu_{d,s,p,t}$ are independent, identically distributed normal variables with mean zero and variance
154 one representing fluctuations through time for each species in each patch.

155 Environmental stochasticity is similarly incorporated through $\mu_{e,p,t}$, which represents
156 environmental variation in each patch through time and $\sigma_{e,s}$, which quantifies the impact of
157 environmental variation on each species s . While Loreau and de Mazancourt (2013) restricted
158 $\mu_{e,p,t}$ to be uncorrelated, here we extend their model to allow for temporal autocorrelation in
159 environmental conditions and variation across patches. To do so, we follow the formulation
160 from Ripa and Lundberg (1996), where we first create a time series of regional climate
161 conditions, c :

$$c_{t+1} = ac_t + b\phi_t. \quad (3)$$

162 We set the initial condition $c_0 = 0$. In eqn 3, a controls the temporal autocorrelation of the

163 climate where $a = 0$ represents uncorrelated, white noise. When $a > 0$, successive events
164 are more likely to be similar to other events that occur closely in time (Ripa & Lundberg,
165 1996). Stochastic noise $\phi_t \sim Normal(0, 1)$ is scaled by the magnitude of its effect, b . Fol-
166 lowing Ripa and Lundberg 1996, $b = (1 - a^2)^{0.5}$, which restricts $var(c)$ to be the same for all
167 autocorrelation (a values) considered. From the time series of regional climactic conditions,
168 we create between-patch variation that represents the degree of microhabitat variation, as-
169 suming that spatial heterogeneity is less than temporal variation to match the spatial scale
170 of our empirical metacommunities (Ford *et al.*, 2013; Gómez-Aparicio *et al.*, 2005). To cre-
171 ate microhabitat variation, $\mu_{e,p,t} \sim Normal(c_t, h)$ where h controls the variability between
172 patches.

173 Using the above model, we examine the relative effects of multiple abiotic and biotic
174 factors on the spatial synchrony of richness. We simulated metacommunities that differed
175 in: richness of the regional species pool (S ; matching the empirically observed range), number
176 of patches (P ; again matching the empirically observed range), spatial heterogeneity in patch
177 quality (h), temporal autocorrelation of the regional climate conditions (a), species' responses
178 to environmental fluctuations ($\sigma_{e,s}$), species' growth rates (r), species' competitive strengths
179 ($\beta_{s,j}$), and dispersal rates (d). All variable parameters were drawn independently from the
180 distributions in Table 1, which also includes values for non-focal parameters (e.g. $\mu_{d,s}$, K_s).
181 We began each simulation with species' abundances set to their carrying capacities, K_s ,
182 and as the model quickly settles on its steady-state distribution, we simulated our model
183 for 100 time steps. We used the first 50 time steps as a "burn-in" period to remove any
184 effect of initial conditions on our analyses. The last 50 time steps were used for calculating
185 spatial synchrony of species richness, creating time series for each simulation with length on
186 the same order as those from our empirical analyses. We ran a total of 2500 simulations
187 and calculated spatial synchrony in species richness and the coefficient of variation in total
188 abundance in all simulations.

189 **3.3 Empirical datasets**

190 We paired our theoretical model with a study of 20 empirical metacommunities encompassing
191 both grassland and coastal marine habitats, primarily drawing from the United States Long
192 Term Ecological Research Network. All datasets consisted of regularly sampled observations
193 of species' abundance in a community for at least 6 plots and 10 years (Table 2). All datasets
194 focused on primary producer taxa in unmanipulated plots. Plots in empirical datasets were
195 taken to be equivalent to patches and for consistency are called patches henceforth. At some
196 sites, up to three distinct metacommunities were considered separately. Metacommunities
197 were considered distinct on the basis of diverging habitat such as soil type or disturbance
198 frequency, dissimilarity in species present, and the opinion of investigators familiar with these
199 sites. Additional description of dataset properties and provenance is provided in Appendix
200 S1: Section 1. We included all species having non-zero abundance in at least 5% of patch-
201 by-time combinations in order to minimize any potential bias of observational error on our
202 results. Preliminary analyses using different thresholds from 0% (no threshold) to 10%
203 indicated that measured spatial synchrony of richness was robust to our 5% threshold choice.

204 **3.4 Analyses of empirical and theoretical communities**

205 We applied parallel analyses to our model simulations and empirical data to address our
206 research questions. We first asked whether species richness exhibits spatial synchrony (Q1).
207 To address this question using theoretical simulations, we computed the mean richness syn-
208 chrony for all 2500 simulated metacommunities and examined the distribution of theoretical
209 richness synchrony measures. To address this question empirically, we computed the mean
210 spatial synchrony of richness for all 20 focal metacommunity datasets and tested the statisti-
211 cal significance of spatial synchrony of richness for each. Significance testing was performed
212 by comparing empirical values to surrogate values from simulated data generated under a null

213 hypothesis of no spatial synchrony, while preserving the temporal autocorrelation structures
214 of the empirical data. Surrogate datasets were generated by taking the amplitude-adjusted
215 Fourier transform of input species richness time series, randomizing the phases of the Fourier
216 components so that any remaining spatial synchrony is due to chance alone, inverse trans-
217 forming the data, and measuring the synchrony of the surrogates (Schreiber & Schmitz,
218 2000). We generated 1,000 surrogates for each dataset, and considered richness synchrony
219 statistically significant when the empirical value exceeded 95% of surrogates.

220 To determine the key drivers of spatial synchrony in richness (Q2), we used multiple
221 linear regression to measure the combined effects of multiple predictors on the synchrony of
222 richness. Predictors were re-scaled to have a mean of zero and standard deviation of 1 so
223 that regression coefficients corresponded to effect sizes. In our theoretical simulations, we ex-
224 amined the effects of key parameters that fall into three general categories: abiotic temporal
225 factors, abiotic spatial factors, and demographic factors. Abiotic temporal factors included
226 in our regression are the effect of environmental variation on species (env_{sd} , the variability
227 of environmental driver σ_e), and temporal autocorrelation in environmental variation (a)
228 (Table 1). Abiotic spatial factors include the total number of patches (P) and the amount of
229 patch heterogeneity (h). Finally, we examined the effect of demographic variation, specifi-
230 cally in the parameters: average species' density-independent growth rates (r_{avg}), maximum
231 competitive strength (β_{max}), and species' dispersal rates (d_s).

232 To answer Q2 for empirical metacommunities, we considered the following predictor
233 variables: biome (terrestrial or marine), metacommunity extent (maximum distance between
234 patches), species richness, evenness, beta diversity, and species turnover rate. To facilitate
235 model-data comparisons, we also examined the effects of species richness, evenness, beta
236 diversity, and turnover rate in simulated metacommunities. Species richness and evenness
237 were the mean richness and evenness of individual patches, averaged across time. Spatial
238 beta diversity was the mean Jaccard similarity (Hallett *et al.*, 2016) among patches, with

239 the species list for each patch inclusive of all years in the time series (after removing species
240 present in less than 5% of patch-years). Turnover rate was the average patch-level temporal
241 turnover in species composition (Hallett *et al.*, 2016), and metacommunity extent was the
242 maximum distance between patches, measured in kilometers.

243 To address whether the strength of synchrony in richness predicts ecosystem stability
244 (Q3), we measured the temporal stability of ecosystem function as $-1 \times$ the coefficient of
245 variation (CV) over time of metacommunity total biomass/cover as a measure of ecosystem
246 stability. That is, $-1 \times \frac{\hat{\sigma}}{\hat{\mu}}$, where $\hat{\mu}$ is the sample mean and $\hat{\sigma}$ is the sample standard deviation.
247 We multiplied values by -1 so that increases in the statistic corresponded to increases in
248 stability. Other studies have used $1/\text{CV}$, but in our data this created skewed distributions.
249 We examined how richness synchrony predicts ecosystem stability using linear regression, and
250 compared the strength of this relationship to the relationship between ecosystem stability
251 and: species richness, evenness, beta diversity, and turnover rate. We focus primarily on the
252 often-studied relationship between richness and ecosystem stability (e.g. Tilman & Downing
253 (1994); García-Palacios *et al.* (2018)). Here, species richness is the average richness over all
254 patches and time steps (years).

255 4 Results

256 In both our theoretical model and across 20 empirical metacommunities, spatial synchrony in
257 species richness varied widely among communities, spanning nearly the entire plausible range
258 of the statistic (Figure 1). The distributions of theoretical and empirical richness synchrony
259 were qualitatively similar (Figure 1a,b). Coastal marine metacommunities tended to exhibit
260 less richness synchrony than terrestrial grasslands, but also tended to have the larger spatial
261 extents (Table 2). The magnitudes of spatial synchrony in richness tended to be significantly
262 greater than surrogates representing a null hypothesis of no synchrony, suggesting that spatial

263 synchrony of richness is a common phenomenon across ecosystems (Appendix S1: Section
264 2); in all empirical metacommunities, $p < 0.05$, with the exception of Dry Tortugas (Florida
265 Keys) corals (DRT; $p = 0.18$) and Maui, Hawaii corals (MAU; $p = 0.052$).

266 When examining which parameters predominantly alter the synchrony of richness in
267 our model, we found that temporal abiotic variation had the strongest effect, followed by
268 demographic rates. Specifically, the effect sizes indicated that the strength of temporal envi-
269 ronmental variation (env_{sd}) and the degree of autocorrelation in the temporal environmental
270 fluctuations (a) had the strongest effects on richness synchrony (Fig. 2). Dispersal (d)
271 and competitive strength (β_{max}) had smaller, but still positive effect on richness synchrony.
272 The positive effect of dispersal was consistent with our expectations from population syn-
273 chrony, where increasing dispersal increases population synchrony. Surprisingly, however,
274 spatial heterogeneity in environmental variation had essentially no effect on richness syn-
275 chrony. This combination of predictors explained 25% of variation in richness synchrony
276 across 2,500 simulations.

277 In empirical metacommunities, biome (i.e. marine versus grassland ecosystems) was
278 strongly related to richness synchrony, but with a large standard error (Figure 3). Because
279 both the degree of spatial autocorrelation in environmental conditions and the rate of dis-
280 persal between patches typically decrease as the distance between them grows, we expected
281 that extent would have a negative effect on richness synchrony, consistent with dispersal and
282 Moran effects acting as key drivers of richness synchrony. Consistent with our prediction,
283 metacommunity extent was negatively related to synchrony in richness, however with a large
284 standard error (Figure 3).

285 As some underlying biological and abiotic factors were impossible to measure in observa-
286 tional studies, we examined potential covariates of richness synchrony that were calculated
287 for both theoretical models and observational data. There was a strong positive relationship
288 between species turnover on richness synchrony across both theoretical and empirical meta-

289 communities (Figure 3). This is consistent with the fact that changes in species richness
290 imply turnover, but also highlights how community structure and environmental perturba-
291 tions also likely shaped the spatial synchrony of richness since these factors influence turnover
292 rates (Kraft *et al.*, 2011; Myers *et al.*, 2015). Given that some communities may be more
293 prone to turnover than others when faced with environmental variation, communities may
294 vary in the magnitude of spatial synchrony of richness. In empirical communities, richness
295 synchrony was positively related to the average richness of the metacommunity, but the stan-
296 dard error was large; in theoretical metacommunities, the effect had a similar magnitude but
297 was negative (Figure 3). In both theoretical and empirical metacommunities there was no
298 substantial effect of beta diversity on richness synchrony. For theoretical metacommunities
299 only, we further examined the importance of beta diversity using the decomposition method
300 of Baselga & Orme (2012) into components associated with change in species number ver-
301 sus species replacement between communities. The component associated with change in
302 species number had a positive effect on richness synchrony and the component associated
303 with species replacement had a negative effect on richness synchrony. We did not examine
304 this for empirical metacommunities because of the much lower sample size. Neither model
305 nor data show a notable effect of evenness on richness synchrony. In our simulations, these
306 possible explanatory variables were emergent properties of underlying community assembly
307 mechanisms, not directly controlled. This combination of predictors explained 69% of vari-
308 ability in richness synchrony in empirical metacommunities, and 5% of variability in richness
309 synchrony in simulated metacommunities.

310 Importantly, spatial synchrony of richness was negatively related to the stability of ecosys-
311 tem function in both theoretical and empirical metacommunities, and exhibited a stronger
312 relationship with stability than species richness itself (Figure 4). Both theoretical and em-
313 pirical relationships between the spatial synchrony of richness and community stability were
314 relatively strong ($R^2 = 0.22$ and $R^2 = 0.42$, respectively), compared to the relationship be-

315 tween diversity and stability ($R^2 = 0.08$ and $R^2 = 0.13$, respectively). As such, across meta-
316 communities and underlying mechanisms—as manipulated in our simulation modeling—the
317 spatial synchrony of richness emerged as the stronger predictor of stability. Additionally, the
318 spatial synchrony of richness was generally more strongly related to stability than evenness,
319 beta diversity, turnover rate, although the relationship with turnover had an approximately
320 equal R^2 as for richness synchrony (Appendix S1: Section 3).

321 Theoretical simulations using global versus local dispersal yielded consistent results (Ap-
322 pendix S1: Section 4).

323 5 Discussion

324 Metacommunities often exhibit spatially synchronous fluctuations in species richness (Q1)
325 that are driven in part by Moran effects and dispersal (Q2), two canonical drivers of popu-
326 lation spatial synchrony (Liebhold *et al.*, 2004; Moran, 1953; Walter *et al.*, 2017). In both
327 mathematical models and observational data spanning marine and terrestrial metacommun-
328 ities, spatial synchrony of richness was negatively correlated with ecosystem stability, and
329 showed a stronger correlation than species richness itself (Q3). These findings integrate
330 perspectives on spatial synchrony from population ecology with biodiversity’s implications
331 for ecosystem stability and function, and reinforce the importance of spatial dimensions of
332 stability (Wang & Loreau, 2014; Wilcox *et al.*, 2017; Lamy *et al.*, 2019; Gonzalez *et al.*, 2020;
333 Wang *et al.*, 2019).

334 Spatial synchrony in species richness appears to be a common phenomenon. Across 20
335 empirical metacommunities in grassland and coastal marine habitats, spatial synchrony in
336 richness varied substantially, but in 90% of cases was greater than expected under a null
337 hypothesis of no spatial synchrony. In addition, spatial synchrony in species richness has
338 been documented in two recent studies (Barringer *et al.*, 2020; Arribas *et al.*, 2019), but

339 these studies considered only a few empirical metacommunities. In our study, terrestrial
340 ecosystems tended to exhibit higher spatial synchrony in species richness. Marine metacom-
341 munities tended to have larger spatial extents (Table 2), which may partially explain this
342 pattern due to the potential for decreased dispersal and environmental spatial correlation
343 with increasing spatial extent. The biomes also tended to differ in the typical lifespans of in-
344 dividuals in the community (e.g. long-lived corals vs. a mix of annual and perennial plants),
345 possibly affecting the sensitivity of the community to interannual environmental variability.

346 The variability in the degree of spatial synchrony of richness exhibited by a metacom-
347 munity was influenced by attributes of the environment, especially the degree of temporal
348 variability in environmental conditions, and by the structure of the community. Fluctua-
349 tions in species richness imply year-to-year species turnover, and some communities will be
350 more prone to turnover than others due to underlying environmental conditions, disturbance
351 events (Worm & Duffy, 2003; Myers *et al.*, 2015), and the demography of constituent species
352 (Ripa & Lundberg, 1996; Adler & Drake, 2008). How demography alters richness synchrony
353 likely interacts with the nature of environmental fluctuations. Some communities with many
354 rare, extinction-prone species could exhibit little richness synchrony if extinctions are spa-
355 tiotemporally random, e.g. if they arise more so from demographic stochasticity than from
356 environmental forcing. By contrast, a community with lower turnover might exhibit greater
357 synchrony in richness if turnover is closely tied to large, spatially synchronous environmental
358 perturbations that locally extirpate, or facilitate the emergence of, multiple species simulta-
359 neously.

360 In fact, the dependence of richness synchrony on both environmental variation and com-
361 munity structure seems to explain small discrepancies between our theoretical and empirical
362 results. In particular, species richness had opposing relationships with richness synchrony in
363 empirical versus theoretical cases (Figure 3). In empirical metacommunities, turnover was
364 higher than simulated communities, and richness and evenness were positively correlated,

365 suggesting that as we added more species the aggregated community-level carrying capac-
366 ity was partitioned among more species; this lowered abundances on average, making more
367 species susceptible to environmental perturbation and leading to synchronous fluctuations in
368 richness. Meanwhile, in our simulated metacommunities, turnover rates were low and even-
369 ness was high but negatively correlated with richness. In this case, higher richness yielded
370 more rare species that tended to stochastically and asynchronously become locally extinct
371 and/or colonize new patches.

372 The relationship between biodiversity and stability of ecosystem function has generated a
373 great deal of interest in ecology over multiple decades of research (Tilman & Downing, 1994;
374 Schulze & Mooney, 2012; Cottingham *et al.*, 2001; de Mazancourt *et al.*, 2013). We found
375 that spatial synchrony in richness was more strongly related to stability of total biomass
376 production than was species richness itself (Figure 4). The negative relationship between
377 richness synchrony and ecosystem stability was expected due to the known destabilizing
378 effects of synchrony in population spatial (Anderson *et al.*, 2021) and community (Hallett
379 *et al.*, 2014; de Mazancourt *et al.*, 2013) synchrony. However, it remains noteworthy since
380 the relationship between synchrony in species number and aggregate abundance (as in this
381 study) is less direct than the relationship between abundances in component units and
382 aggregate abundance (as in population spatial and community synchrony studies). The
383 relative success of the spatial synchrony of richness in predicting ecosystem stability seems
384 to arise primarily because it is a metric that simultaneously reflects information both about
385 community structure and both spatial and temporal environmental variability. For example,
386 greater stability and lower richness synchrony in marine metacommunities, which tended to
387 have larger extents in our study, could reflect spatial insurance effects (Wang & Loreau, 2014;
388 Lamy *et al.*, 2019). Our study suggests that richness synchrony may generally be closely
389 related to ecosystem stability and function, providing additional insight into the relationship
390 between biodiversity, synchrony, and stability.

391 Studying the spatial synchrony of species richness represents a promising approach for
392 investigating drivers of community variability and their consequences for stability of ecosys-
393 tem function. Although the causes of spatial synchrony in species richness appear complex
394 and remain only partly understood, richness synchrony appears to be an effective integrator
395 of several processes linking biodiversity and stability. While investigations of the spatial
396 synchrony of community variables are uncommon now, the growing availability of long-term,
397 spatially replicated community datasets enables broader application of this approach. Re-
398 gardless of whether this approach ultimately earns widespread use, the apparent commonness
399 of richness synchrony and its relationship to stability underscore the importance of spatial
400 structure and spatial scale to ecological stability and biodiversity-ecosystem function rela-
401 tionships (Chase & Ryberg, 2004; Wang & Loreau, 2014; Gonzalez *et al.*, 2020; Downing
402 *et al.*, 2008).

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Table 1: Model parameters, description, and ranges used in generating simulations.

Parameter	Description	Value/Range
S	number of species in the regional species pool	Sample(min= 15, max= 55)
P	number of patches in the metacommunity	Sample(min= 9, max= 49)
h	spatial heterogeneity between patches	Uniform(min= 0, max= 0.5)
a	temporal autocorrelation in climate	Uniform(min= 0, max= 0.75)
b	magnitude of the effect of climate	$(1 - a^2)^{0.5}$
$\mu_{e,p,t}$	environmental fluctuations in each patch	Normal(mean= c_t , sd= h)
env_{sd}	standard deviation of effect of env. variation	Uniform(min= 0.05, max= 0.5)
$\sigma_{e,s}$	response of each species to env. variation	Normal(mean= 0, sd= env_{sd})
$\mu_{d,s,p,t}$	demographic fluctuations	Normal(mean= 0, sd= 1)
$\sigma_{d,s}$	effect of demographic fluctuations	Uniform(min= 0, max= 0.75)
r_{avg}	scaled average growth rate	Uniform(min= 0, max= 0.25)
r_i	species-specific growth rate	Uniform(min= $0.5 - r_{avg}$, max= $0.5 + r_{avg}$)
β_{max}	maximum competition coefficient	Uniform(min= 0, max= 0.5)
$\beta_{s,j}$	competition coefficient of species j on species s	Uniform(min= 0, max= β_{max})
d	dispersal rate	Uniform(min= 0, max= 0.2)
K_s	carrying capacity	Lognormal(logmean= 3, Logsd= 1)

Table 2: Empirical datasets. Dataset codes correspond to, respectively: DRT, Dry Tortugas, FL; HAY, Hayes, KS; JRG, Jasper Ridge, CA; JRN_BASN, Jornada LTER Basin; JRN_IBPE Jornada LTER International Biological Program enclosure; JRN_SUMM Jornada LTER Mount Summerford; KNZ_UP, Konza Prairie upland; KNZ_LOW, Konza Prairie lowland; LOK, Lower Florida Keys; MAU, Maui, HI; MCR_BACK, Moorea Coral Reef LTER Backreef; MCR_FRNG, Moorea Coral Reef LTER fringing reef; MCR_OUT, Moorea Coral Reef outer reef; MDK, Middle Florida Keys; SBC, Santa Barbara Coastal LTER; SEV_B, Sevilleta LTER blue gramma; SEV_C, Sevilleta LTER creosotebush; SEV_G, Sevilleta LTER black gramma; UPK, Upper Florida Keys; USVI, US Virgin Islands LTER. *Year* corresponds to the initial year of the time series. *Extent* gives the maximum inter-patch distance, in km. N_{taxa} gives the total number of taxa (i.e., γ -diversity) of the metacommunity.

Dataset	Year	Length	N_{plots}	Extent	Biome	N_{taxa}	Variable	Plot size
DRT	2005	11	6	16.5	marine	25	% cover	$0.25m^2$
HAY	1943	30	13	0.05	grassland	16	% cover	$1m^2$
JRG	1983	34	12	0.03	grassland	25	% cover	$1m^2$
JRN_BASN	1989	24	49	0.09	grassland	44	biomass	$1m^2$
JRN_IBPE	1989	24	49	0.08	grassland	51	biomass	$1m^2$
JRN_SUMM	1989	24	49	0.09	grassland	53	biomass	$1m^2$
KNZ_UP	1983	33	20	0.17	grassland	47	% cover	$10m^2$
KNZ_LOW	1983	33	20	0.23	grassland	44	% cover	$10m^2$
LOK	1996	20	14	49.0	marine	28	% cover	$0.25m^2$
MAU	2001	16	9	50.4	marine	21	% cover	$0.25m^2$
MCR_BACK	2006	10	30	16.65	marine	15	% cover	$0.25m^2$
MCR_FRNG	2006	10	30	15.67	marine	28	% cover	$0.25m^2$
MCR_OUT	2006	10	30	17.29	marine	25	% cover	$0.25m^2$
MDK	1996	20	8	55.4	marine	24	% cover	$0.25m^2$
SBC	2001	18	34	73.38	marine	30	biomass	$80m^2$
SEV_B	2002	13	30	0.70	grassland	42	biomass	$1m^2$
SEV_C	1999	16	30	1.33	grassland	29	biomass	$1m^2$
SEV_G	1999	16	22	0.81	grassland	27	biomass	$1m^2$
UPK	1996	20	10	44.7	marine	23	% cover	$0.25m^2$
USVI	1992	26	6	1.38	marine	17	% cover	$0.25m^2$

7 Figure Captions

Figure 1: Spatial synchrony in species richness in (A) 2500 simulated and (B, C) 20 empirical metacommunities.

Figure 2: Effect sizes of variation in model parameters on the degree of spatial synchrony of richness in simulated metacommunities. Effect sizes are linear regression coefficients on standardized predictors. Error bars indicate 1 standard error.

Figure 3: Effect sizes of variation in attributes of empirical and theoretical metacommunities on spatial synchrony of richness. Effect sizes are linear regression coefficients on standardized predictors. There is no direct analog of biome or extent in our theoretical simulations, so no bar is drawn. Error bars indicate 1 standard error.

Figure 4: Richness synchrony is related to stability of ecosystem function in theoretical (A) and empirical (C) metacommunities, and more strongly so than species richness itself in both theoretical (B) and empirical (D) metacommunities. Stability is measured, for simulations, as the $-1 \times$ the coefficient of variation (CV) of total abundance, and for empirical datasets as that of total biomass or total cover, depending on units of the underlying data (Table 2).

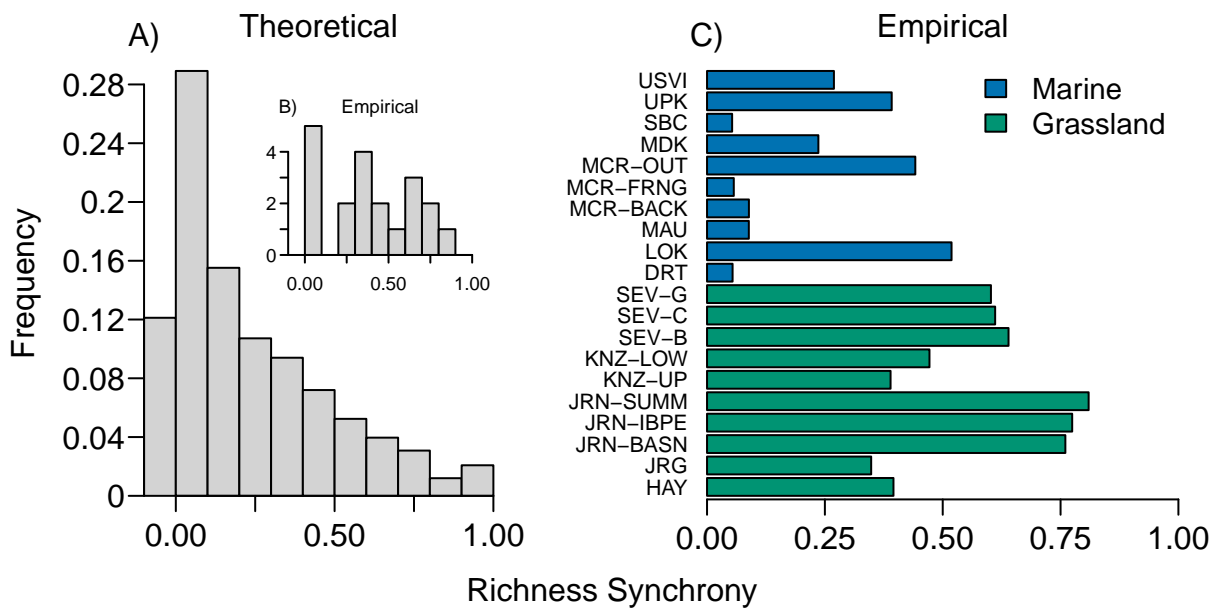


Figure 1: Spatial synchrony in species richness in (A) 2500 simulated and (B, C) 20 empirical metacommunities.

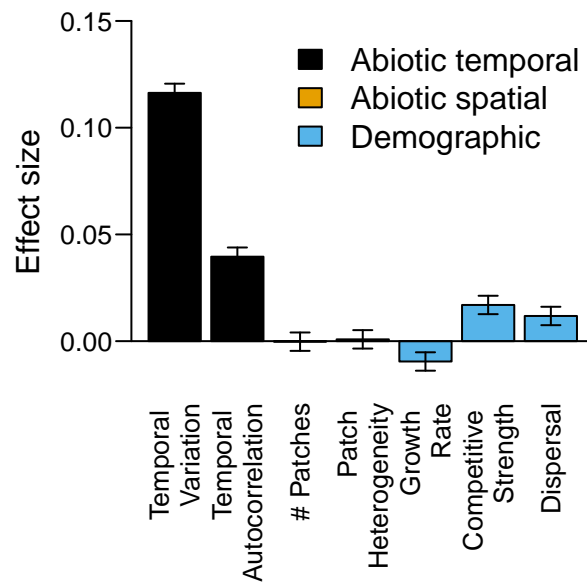


Figure 2: Effect sizes of variation in model parameters on the degree of spatial synchrony of richness in simulated metacommunities. Effect sizes are linear regression coefficients on standardized predictors. Error bars indicate 1 standard error.

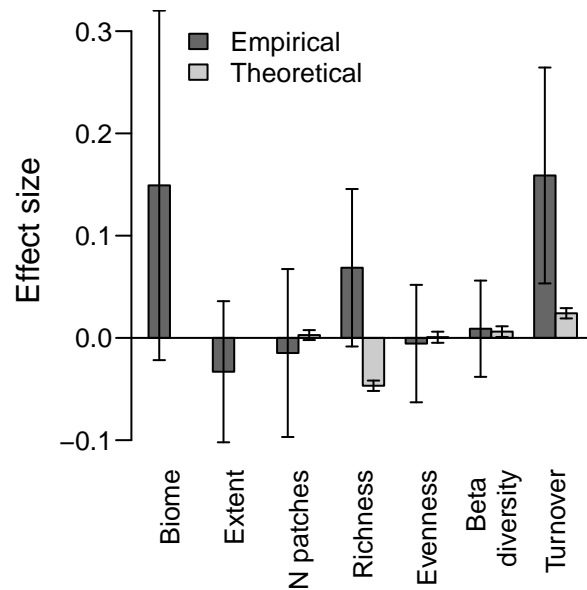


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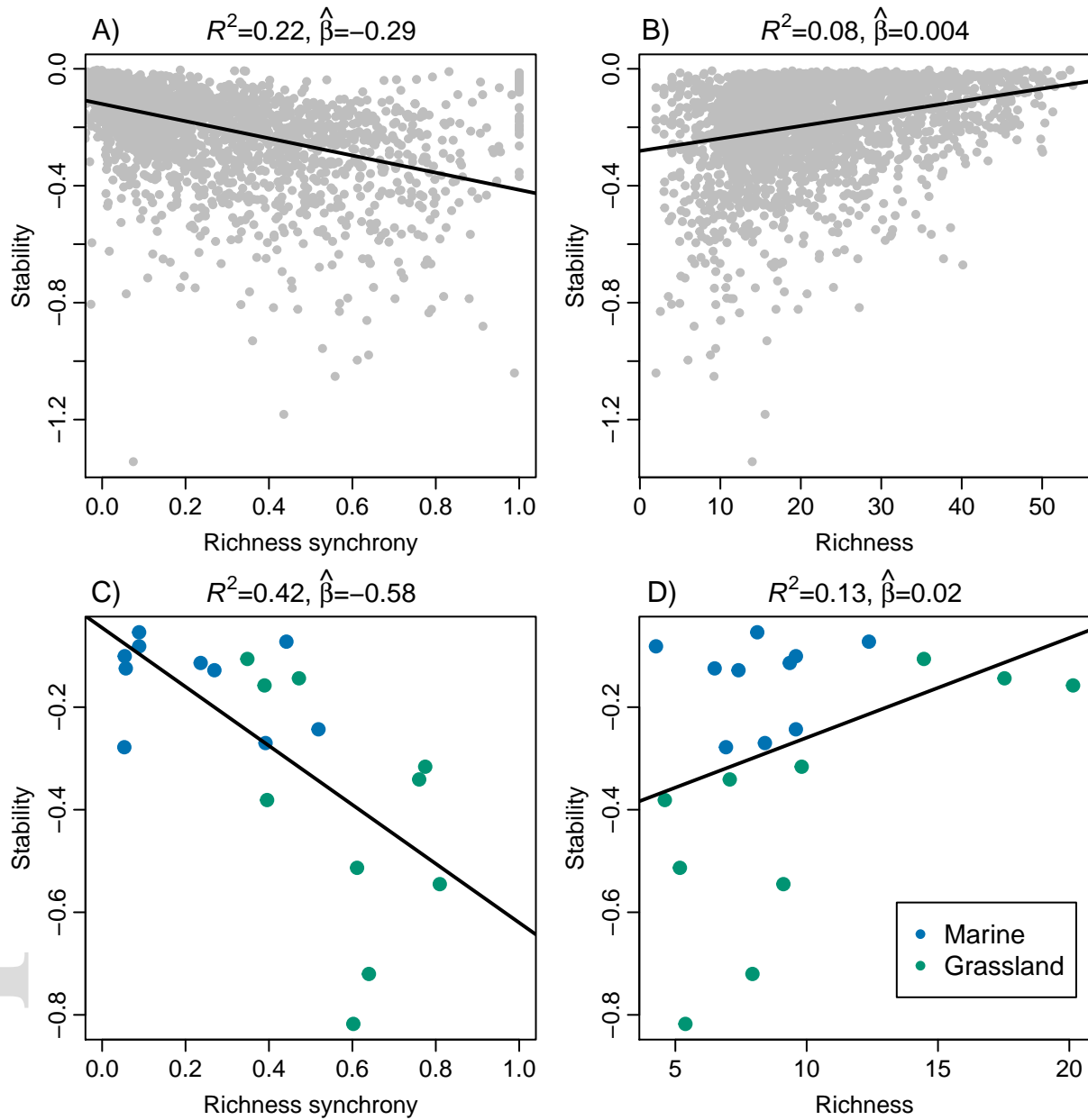


Figure 4: Richness synchrony is related to stability of ecosystem function in theoretical (A) and empirical (C) metacommunities, and more strongly so than species richness itself in both theoretical (B) and empirical (D) metacommunities. Stability is measured, for simulations, as the $-1 \times$ the coefficient of variation (CV) of total abundance, and for empirical datasets as that of total biomass or total cover, depending on units of the underlying data (Table 2).