

# Unveiling the temporal signatures of demographic stochasticity from populations to metacommunities

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**Abstract:** The temporal stability of ecological properties tends to increase with spatial scale and levels of biological organization, which is mostly associated with deterministic processes. However, random fluctuations caused by demographic stochasticity in small populations might extend to communities and metacommunities, potentially affecting stability propagation across biological levels and spatial scales. Here, we tested this hypothesis by combining process-based simulations and statistical modeling of 468 sites distributed across 39 regions, sampled from 1981 to 2019, to investigate how fish communities and metacommunities changed over time at local and regional scales. We found that more communities with more species and in more seasonal environments were more variable. However, the major driver of compositional temporal variability was community size. Communities comprising smaller populations were more temporally variable than those comprising larger populations. This relationship was weaker at the regional scale, suggesting a dampening effect at the metacommunity level. Our results suggest that the potential effects of demographic stochasticity, which are undoubtedly stronger in small populations, might extend beyond populations, leaving different signals in the temporal variability of ecological properties. These effects appear to be stronger and consistent within small communities and weaker in metacommunities. Our study advances the knowledge of how

25 populational-demographic stochasticity might affect biodiversity temporal dynamics across  
26 scales.

27 **KEYWORDS:** random demography; community size; compositional variability; environmental  
28 variability; spatial scale; temporal variability

## 29 **Introduction**

30           Theoretical and observational research posit that the temporal variability of ecological  
31 properties (e.g., coefficient of variation of biomass) decreases with the increase of spatial scale,  
32 levels of biological organization, and trophic levels (Kéfi et al. 2019; Wang et al. 2019;  
33 Hammond et al. 2020; Siqueira et al. 2024). The explanations for these relationships are mainly  
34 based on deterministic processes, such as compensatory dynamics (Gonzalez and Loreau 2009,  
35 Brown et al. 2016), the role of mobile predators (McCann et al. 2005), and the Moran effect  
36 (Steiner et al. 2013). Small populations experience high temporal variability due to random  
37 demographic events (Reed and Hobbs 2004; Melbourne and Hastings 2008). Thus, as a process  
38 that unfolds over time, could demographic stochasticity increase the temporal variability of  
39 communities and metacommunities? Or do its effects also weaken from populations to  
40 metacommunities? Understanding how random demographic events may affect biodiversity  
41 temporal variability at larger scales is important to better forecast how ecosystems will respond  
42 to global changes.

43           Demographic stochastic events such as birth, death, and emigration are inherent elements  
44 of population dynamics (Lande 1988; 1993; Otto and Whitlock 1997; Whitlock 2004; Willi, van  
45 Buskirk, and Hoffmann 2006; Melbourne and Hastings 2008). While various forces influence  
46 population demography, their impacts are consolidated into population size. Small populations  
47 are more susceptible to the effects of random events, making them more temporally variable than  
48 larger populations (Otto and Whitlock 1997; Reed and Hobbs 2004; Whitlock 2004). Expanding  
49 on this understanding, recent research suggests that the effects of local demographic stochastic  
50 events might extend to larger spatial scales and levels of biological organization. For example,  
51 there is mounting evidence indicating that demographic stochasticity increases spatial beta

52 diversity among local communities comprised of small populations (small communities; (Orrock  
53 and Watling 2010; Gilbert and Levine 2017; Siqueira et al. 2020) and weakens community-  
54 environment relationships (Jacobi and Siqueira 2023).

55         Although there is limited research about the effects of demographic stochasticity on the  
56 temporal variability of multispecies communities, most studies suggest that small communities  
57 tend to exhibit greater temporal variability (temporal beta diversity) compared to larger ones  
58 because small populations have few individuals to buffer against random fluctuations in their  
59 demography (Orrock and Fletcher 2005; Pedruski, Fussmann, and Gonzalez 2015; Gilbert and  
60 Levine 2017; Legault, Fox, and Melbourne 2019). One possible explanation for such relationship  
61 is that when demographic stochasticity plays a strong role in community assembly, niche  
62 differences become less important, as the likelihood of any demographic event happening is  
63 similar for all individuals, regardless of their fitness differences (Orrock and Watling 2010,  
64 Legault et al. 2019). For this reason, it is reasonable to expect that small local communities  
65 should have higher temporal variability in their species composition (i.e. high temporal beta  
66 diversity) than large communities. However, stochastic variability in species composition might  
67 be also caused by an interaction between trait-diversity, dispersal and population size (Arim et al.  
68 2023). Thus, further empirical research still needed to understand the effects of demographic  
69 stochasticity in the temporal assembly of ecological communities.

70         Considering that small communities may experience high temporal variability in species  
71 composition, it is possible that metacommunities formed by small communities may also be  
72 highly variable in time. Simulations and experiments analyzing biodiversity variability have  
73 found that metacommunity size is a key factor shaping species composition temporal variability  
74 (LeCraw, Srivastava, and Romero 2014; Suzuki and Economo 2024). Thus, large temporal

75 fluctuations in species composition within the metacommunity should happen if random  
76 extinctions (or abundance changes) of species occur independently across different sites within  
77 the metacommunity. Alternatively, if demographic stochasticity is not widespread within the  
78 metacommunity, its effects might be negligible compared to the influence of deterministic  
79 processes like compensatory dynamics (Andrew Gonzalez and Loreau 2009; Loreau 2010;  
80 Brown, Downing, and Leibold 2016).

81         In light of the ongoing declines in population sizes and the elevated rates of species  
82 extinction (McCallum 2015; He et al. 2019; Almond, Grooten, and Petersen 2020), we ask  
83 whether the effects of population-level demographic stochasticity propagate to higher levels of  
84 biological organization and influence biodiversity temporal dynamics at larger spatial scales. To  
85 do so, we analyzed how temporal variability in species composition was related to the size of  
86 communities at local and regional scales. If small communities are more variable than large ones  
87 simply due to their size, this would indicate a stronger influence of demographic stochasticity on  
88 these communities. However, analyzing this relationship is challenging as, aside from the need  
89 for a significant amount of independent temporally and spatially replicated data across a gradient  
90 of community size, it is crucial that the metrics used to quantify temporal variation in species  
91 composition are not inherently affected by differences in community size. Thus, we first used a  
92 process-based simulation model to test if metrics commonly used to quantify variation in species  
93 composition could indicate the effects of demographic stochasticity via their relationship with  
94 community size. We then applied these metrics to time-series observational data and statistical  
95 models to understand the relationships of temporal variability in species composition at both the  
96 community and metacommunity levels with community size and other potential predictors,

97 including temporal variation in environmental conditions, time series length, the number of  
98 samples in the time series, and species richness.

99         We expected to find a negative relationship between temporal variability in species  
100 composition within local communities and community size, suggesting that local species  
101 composition vary more over time within small communities. At the metacommunity level, we  
102 had two competitive expectations: (1) either a negative relationship between temporal variability  
103 in spatial beta-diversity and regional community size (2) or no relationship between temporal  
104 variability in spatial beta-diversity and regional community size. Evidence supporting the latter  
105 would indicate that the effects of local demographic stochasticity are weakened over time at the  
106 regional scale.

107

## 108 **Material and methods**

### 109 **Data**

110         We ran our empirical analyses using data from two large databases. From RivFishTIME  
111 (Comte et al. 2021), we obtained time series count data of riverine fish. TerraClimate  
112 (Abatzoglou et al. 2018) provided high-resolution monthly data for environmental variables,  
113 from which we calculated annual averages for precipitation, maximum air temperature, and  
114 minimum air temperature (a good proxy for water temperature; Stefan and Preud'homme 1993).

115         We defined a metacommunity as the set of sites within basin delineations (HydroBASINS  
116 level 7 – Lehner and Grill 2013) and assigned a Strahler stream order for each sampled site using  
117 information from the HydroRIVERS network (Lehner and Grill 2013). After that, we selected  
118 metacommunities that met the following criteria: (1) were composed of at least five communities  
119 in first to third-order streams, (2) were sampled at least four times in different years, and (3) had

120 at least five species. When dealing with metacommunity data comprising multiple sampling  
121 events per year, we selected the sampling date with the highest number of sampled sites. These  
122 steps resulted in 468 communities distributed within 39 metacommunities, sampled from 1981 to  
123 2019, located in the Australasia (12), Nearctic (12), and Palearctic (15) biogeographical realms  
124 (Figure S1). These metacommunities are composed on average of 12 communities (standard  
125 deviation = 9) sampled, on average, 11 times in the time-series (standard deviation = 5) with an  
126 average temporal extent of 14 years (standard deviation = 5). All data selection and manipulation  
127 were made in R v. 4.2.1 ([www.r-project.org](http://www.r-project.org)) using the packages `ncdf4` (Pierce 2023), `mapview`  
128 (Appelhans et al. 2022) `raster` (Hijmans 2023), `sf` (Pebesma 2018; Pebesma and Bivand 2023), `sp`  
129 (Pebesma and Bivand 2005, Bivand et al. 2013), `tidyverse` (Wickham et al. 2019).

130

### 131 **Representing the signature of demographic stochasticity**

132 Because the effects of demographic stochasticity are negatively correlated with  
133 population size, we used the median of community size over time as a proxy to represent the  
134 signature of demographic stochasticity. We measured the size of each community as the median  
135 number of individuals over time (local community size), considering that communities composed  
136 of fewer individuals are also composed, on average, of smaller populations than communities  
137 with more individuals. Finally, to represent the signature of demographic stochasticity at the  
138 regional scale, we measured the size of each metacommunity as the median community size  
139 within each metacommunity over time (regional community size).

140

141

### 142 **Metrics of temporal variability**

143 A major challenge involved in the use of community size as a proxy for the signature of  
144 demographic stochasticity is that many community metrics can be mathematically related to  
145 sample size regardless of the underlying assembly process (Beck, Holloway, and Schwanghart  
146 2013; Chase and Knight 2013; Barwell, Isaac, and Kunin 2015; Cao et al. 2021). Thus, to select  
147 appropriate metrics of temporal variability that could be modelled against community size, we  
148 first developed a process-based simulation model according to the following steps.

149 We first simulated a purely neutral dynamics in 39 metacommunities of varying sizes  
150 over 1000-time steps with the mcbnet package (Terui and Pomeranz 2023). These simulations  
151 were performed using different levels of dispersal within the metacommunities, which mirrored  
152 the empirical dataset in terms of community and species numbers. Given that the assembly of the  
153 simulated metacommunities was entirely neutral, there should be no relationship between  
154 temporal variability in species composition and community size. If any metric of temporal  
155 variability was related with size, we understood it as unsuitable for our objective. Secondly, we  
156 selected 10 time steps and measured temporal variability at both local (within each community)  
157 and regional (among communities) scales using different metrics: (i) temporal variability in  
158 species abundance measuring the coefficient of variation of abundance at each organizational  
159 level based on the partitioning framework developed by Wang et al. (2019); (ii) temporal  
160 variability in species composition at the local and regional scales employing the metric proposed  
161 by Lamy et al. (2021) and implemented with the ltmc package (Sokol & Lamy 2022); (iii)  
162 temporal beta diversity as the median of species rank changes (Avolio et al. 2019) within each  
163 community over time, using the RAC\_change function from the codyn package (Hallett et al.  
164 2020). Additionally, we used codyn to assess spatial beta diversity at the metacommunity level  
165 via the RAC\_difference function. The median difference in species rank among communities



166 was calculated at each time step. Finally, we regressed all these metrics of temporal variability  
167 described above against the median community size over time and compared the outcomes. The  
168 performance of each metric is informed in the Results section. Further details on the process-  
169 based simulation are available in the supplementary information.

170

### 171 **Predictors of temporal variability in species composition**

172 We measured several metrics that are expected to play a role in explaining temporal  
173 variability in species composition. This included assessing the number of samples collected over  
174 time (number of samples) and the temporal extent of each sampling (time series length) for each  
175 community and metacommunity. We also measured the coefficient of variation (CV) of  
176 maximum (CV tmax) and minimum (CV tmin) temperature and of precipitation (CV ppt) as  
177 potential predictors of community variability over time. These metrics were measured by  
178 dividing the standard deviation of temperature and precipitation values at each site over time by  
179 the mean of these values. We also estimated the median asymptotic richness of each community  
180 over time to be included as a predictor of community variability. Asymptotic richness was  
181 estimated with the iNEXT package (Hsieh et al. 2022), which combines extrapolation and  
182 interpolation techniques. At the metacommunity level, we also measured environmental  
183 synchrony as a proxy for the Moran effect (Siqueira et al. 2024). We measured environmental  
184 synchrony within metacommunities by calculating the correlation of each environmental variable  
185 (syn tmax, syn tmin, syn ppt) between communities over time. A high correlation or  
186 environmental synchrony would indicate that the environmental conditions being analyzed  
187 changed similarly across sites, while a low synchrony indicates that environmental conditions  
188 vary more independently across sites. Finally, we measured the spatial connectivity within each

189 metacommunity by calculating the mean Euclidean distance, in meters, between the central point  
190 of each metacommunity and its respective communities. The smaller the mean distance between  
191 communities, the greater the proximity centrality between them (Erős et al. 2012). We used the  
192 geosphere package to perform this calculation (Hijmans 2022).

193

## 194 **Statistical analysis**

195 To investigate how temporal variability in the species composition of local communities  
196 was related to community size, we fitted a Generalized Linear Mixed Model (GLMM) with  
197 metacommunity identity as a random effect. We modeled temporal variability in the species  
198 composition as the response variable and included as fixed-effects the median of local  
199 community size over time, estimated species richness (median of estimated species richness over  
200 time), the coefficients of variation of local environmental variables over time (CV tmax, CV  
201 tmin, CV ppt), the number of samples and the time series length of each community. All  
202 variables were log transformed and we assumed a Gaussian distribution. We used the lme4  
203 package (Bates et al. 2015) to fit this GLMM model and estimated the marginal (due to fixed  
204 effects) and the conditional (due to fixed and random effects)  $R^2$  values with the MuMIn package  
205 (Bartoń 2023). We also estimated p-values associated with the fixed effects using Wald chi-  
206 square tests with the Anova function in the car package (Fox and Weisberg 2019).

207 To investigate whether temporal variability in species composition within  
208 metacommunities was related to regional community size, we used a Generalized Linear Model  
209 (GLM). We included regional community size (median community size within each  
210 metacommunity over time), spatial connectivity, environmental synchrony (syn tmax, syn tmin,  
211 syn ppt), number of metacommunity samples over time, and the time series length of each

212 metacommunity as predictors. This model was also described by a Gaussian distribution and the  
213 variables were not log transformed. Model assumptions were examined via a visual assessment,  
214 utilizing the `check_model` function from the performance package (Lüdecke et al. 2021), and the  
215 `simulateResiduals` function from the DHARMA package (Hartig 2022). All analyses were  
216 performed in R version 4.2.1 ([www.r-project.org](http://www.r-project.org)). Data and codes used in this research are  
217 available at Zenodo (Jacobi 2024).

218

## 219 **Results**

### 220 **Metrics of temporal variability in simulated metacommunities**

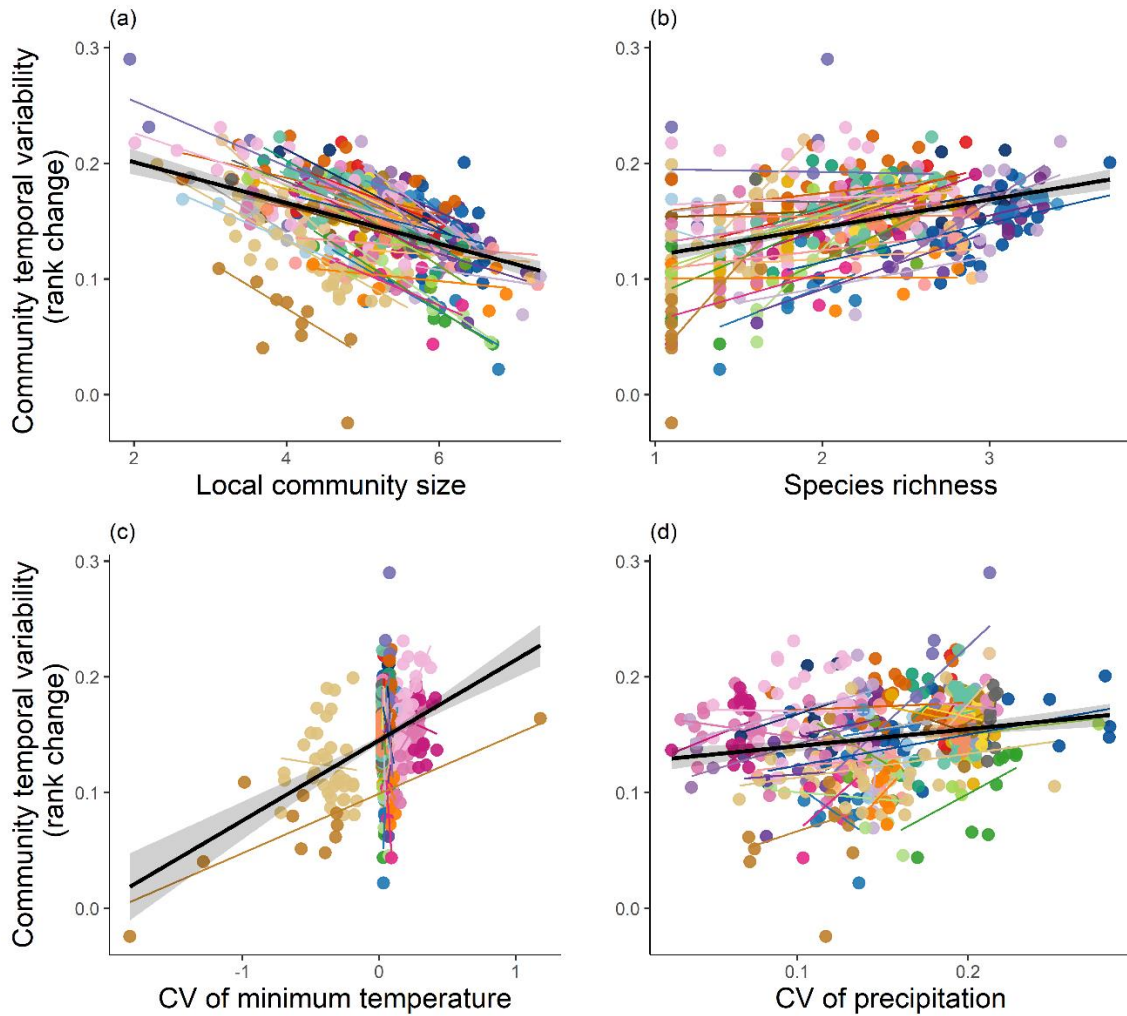
221 Our process-based simulation models indicated that while the temporal variability (CV)  
222 in abundance had a consistent negative relationship with community size both at the local and  
223 regional scales, the LTMC metric exhibited a negative relationship with community size at the  
224 local scale (Table S1). Thus, these metrics of temporal variability were not adequate to be used  
225 in our study. The species rank change metric was the only metric that was not related to  
226 community size at the local scale (Table S1). The species rank difference was positively related  
227 to community size in most simulations at the regional scale; however, the explanatory power of  
228 the models ( $R^2$ ) was consistently low across all simulation scenarios (mean  $R^2 = 0.03$ ; Table S1).  
229 Conversely, the LTMC metric had a negative relationship with regional community size in some  
230 simulations, while in others, no such relationship was observed (Table S1). However, when a  
231 relationship was present, it exhibited a higher explanatory power compared to the metric based in  
232 species rank differences.

233 Thus, considering that the metrics based on change in species rank yielded the most  
234 robust results regarding community size variations in a neutral scenario, we used them to analyze

235 the empirical data. More specifically, to represent temporal variability in species composition for  
236 each community, we used the species rank change metric. To represent temporal variability in  
237 species composition in metacommunities we used the coefficient of variation (CV) of the rank  
238 difference of each year over time.

### 239 **Relationships in the empirical dataset**

240 Despite a small violation of model assumptions (residuals slightly deviated from the  
241 model predicted values; Figure S2; S3), the model describing temporal variability in species  
242 composition at the local scale explained 34% of the variation in community turnover (fixed  
243 effects = 29%, random effects = 5%). Temporal variability in community composition was  
244 negatively related to local community size (Wald  $X^2_{[1, 458]} = 112.4725$ , p-value =  $2.2e-16$ , Figure  
245 1a), indicating that species change more in rank position over time in smaller communities. Such  
246 result was not observed in the null model, which reinforces the significance of observing this  
247 relationship in the real dataset. Compositional variability also increased with the increase of  
248 species richness (Wald  $X^2_{[1, 458]} = 93.2697$ , p-value =  $2.2e-16$ , Figure 1b), CV of the minimum  
249 temperature (Wald  $X^2_{[1, 458]} = 9.3190$ , p-value = 0.002, Figure 1c), and of the CV of precipitation  
250 (Wald  $X^2_{[1, 458]} = 7.8240$ , p-value = 0.005, Figure 1d). These relationships indicate that more  
251 diverse communities in more variable environments were also more temporally variable in their  
252 species composition.



253

254 Figure 1. Relationship between temporal variability in species composition of local communities

255 (rank change) and (a) local community size, (b) species richness, (c) coefficient of variation of

256 minimum temperature (CV  $t_{min}$ ), and (d) coefficient of variation of precipitation (CV ppt).

257 Points represent local communities; colors represent the metacommunity to which the local

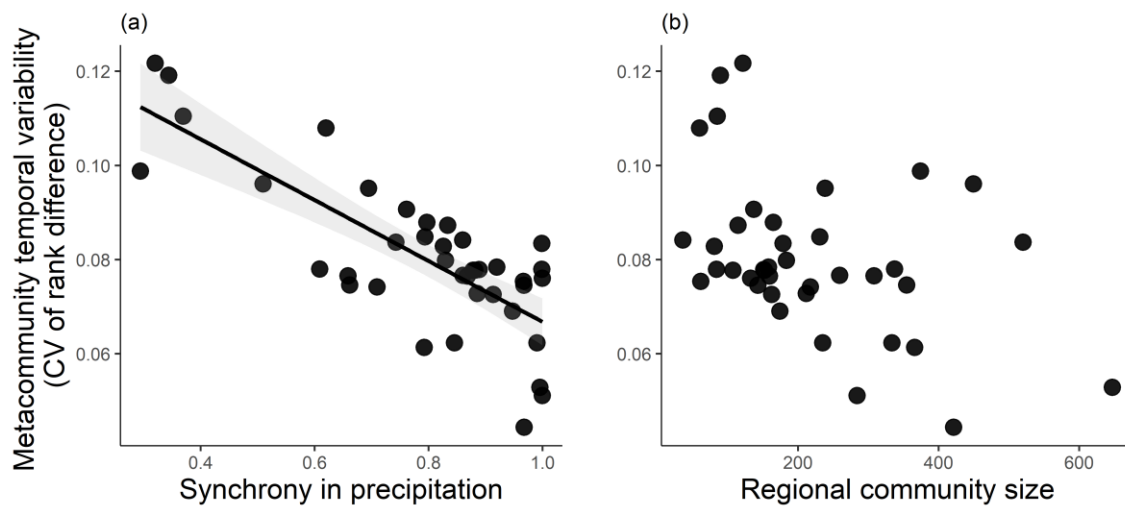
258 communities belong to. All variables are in log scale. Grey bands represent the 95% confidence

259 interval.

260 The model describing temporal variability in species composition at the regional scale

261 exhibited high collinearity among the predictors of environmental synchrony. To address this

262 issue, we refitted the model by including only one environmental synchrony variable at a time  
263 and then selected the model with the lowest Akaike information criterion value corrected for  
264 small sample size ( $AIC_c$ ). The selected model was the one that included synchrony of  
265 precipitation as a predictor of environmental synchrony (Table S2). Following this adjustment,  
266 the model showed no issues with assumptions (Figure S4) and explained 16% of temporal  
267 variability in species composition. The only predictor variable associated with  $p$ -value  $< 0.05$  in  
268 the model was syn ppt ( $\beta = 0.0820$ ; std. error = 0.0367;  $t$ -value<sub>[38, 33]</sub> = -2.232;  $p = 0.0324$ ; Figure  
269 2a; Table S3), indicating that greater synchronicity in precipitation across communities reduces  
270 the temporal variability in regional species composition. While no relationship was found  
271 between temporal variability and regional community size, the data exhibited a slight negative  
272 trend (Figure 2b; Table S3), which may suggest that a negative relationship could emerge with a  
273 larger sample. In summary, our results indicate that the relationship between temporal variability  
274 in species composition and size was statistically strong only for the local scale.



275

276 Figure 2. Relationship between temporal variability in species composition in metacommunities  
277 (CV of rank difference) and (a) synchrony in precipitation among localities, and (b) regional  
278 community size. Grey bands represent the 95% confidence interval.

279

## 280 **Discussion**

281 Our research investigated the potential for random fluctuations driven by demographic  
282 stochasticity to extend beyond the population level and influence the dynamics of higher  
283 organizational levels of biological organization, such as communities and metacommunities.  
284 Agreeing with our predictions, we found a consistent negative relationship between temporal  
285 variability in species composition and community size, but mainly at the local scale. Although  
286 statistically weak, there was also a negative trend between temporal variability in species  
287 composition and community size at the regional scale. Together, our results suggest that the  
288 potential effects of demographic stochasticity, which are undoubtedly stronger in small  
289 populations, might leave different signals in the temporal variability of ecological properties,  
290 being stronger and consistent within small communities and weaker in metacommunities.

291 Populations comprising few individuals tend to fluctuate more over time because  
292 independent random demographic events can cause substantial changes in both their mean size  
293 and variance compared to populations with many individuals (Lande 1993; Legendre et al. 1999;  
294 Melbourne and Hastings 2008; Fauvergue et al. 2012). In line with this knowledge, our finding  
295 of a negative relationship between temporal variability in species composition and community  
296 size suggests that communities comprised of small populations are also more likely to vary in  
297 time. This means that species abundances within these communities change more over time than  
298 within larger communities, relatively to their size and number of species. This result provides

299 empirical support to previous theoretical and experimental findings that indicated how random  
300 demographic events in small populations can lead to temporal changes in the compositional  
301 turnover of individual communities (Gilbert and Levine 2017; Legault, Fox, and Melbourne  
302 2019). These studies suggest that communities comprising small populations undergo more  
303 pronounced demographic fluctuations, preventing any species from maintaining a constant  
304 competitive advantage over others (Orrock and Fletcher 2005). Consequently, the smaller the  
305 community, the more the effects of demographic stochasticity increase community variability  
306 over time.

307         Our results also indicated that the influence of demographic stochasticity on community  
308 composition weakens or even disappears over time as we move from the local to the regional  
309 scale. While at the local scale stochastic events are likely to cause major shifts in the species  
310 composition of small communities, at the regional scale they are likely to be counterbalanced by  
311 other factors such as the dispersal of individuals among patches and population spatial  
312 asynchrony (Wang and Loreau 2016; Thompson et al. 2020). To influence regional species  
313 composition, random demographic events that influence the species composition of local  
314 communities would need to occur concurrently and similarly in different communities, resulting  
315 in the loss (or change in the abundance) of the same species across the entire metacommunity.  
316 However, due to the inherently random nature of demographic stochasticity (Hubbell 2001;  
317 Lande, Engen, and Sæther 2003), its impact is unlikely to be uniform across communities. Even  
318 if demographic stochasticity were widespread within the metacommunities we studied, its effects  
319 on local communities would have been asynchronous, meaning that the species affected by its  
320 effects would vary from one community to another, thus keeping regional species composition  
321 relatively stable.



322           Although our analyses did not indicate a statistical relationship between temporal  
323    variability in species composition at the regional scale with metacommunity size, a visual  
324    inspection of the scatter plot suggested a negative trend between these variables. As the first  
325    study of its kind, we caution that our analyses, derived from a limited sample size (39  
326    metacommunities), should be approached with care before dismissing the potential propagation  
327    of the effects of random demography to the metacommunity level. Further studies comprising  
328    more metacommunities, longer time-series, and different response and predictor variables might  
329    clarify this potential relationship. For example, Suzuki and Economo (2024) found that  
330    increasing the number of patches in simulated metacommunities led to less temporal variability,  
331    implying that larger metacommunities could be more temporally stable.

332           Beyond community size, multiple abiotic and biotic factors can influence the temporal  
333    variability of multispecies communities (Dunson and Travis 1991; Araújo and Luoto 2007;  
334    Valencia et al. 2020). After adjusting for the effect of community size, we found that  
335    communities with more species were also the ones with more compositional variability over  
336    time. Although this finding contrasts with the exiting research on the temporal stability of  
337    ecological properties, it can be explained by the type of variability being used here. The temporal  
338    variability of aggregate ecological properties, such as total biomass or abundance, is expected to  
339    decrease with the increase in the number of species due to the statistical averaging of fluctuations  
340    in species abundances (Doak et al. 1998; Xu et al. 2021). But our analyses were based on the  
341    temporal variability of species composition (rank of species abundances). As found recently by  
342    Arim et al. (2023), high functional and taxonomic diversity allows for a wider array of responses  
343    to environmental fluctuations, potentially resulting in varying levels of success for different  
344    species over time or under different conditions. Differential responses of species to stochastic

345 fluctuations in the environment can lead to changes in species dominance over time and increase  
346 the variability in species rank abundance (A. Gonzalez and Descamps-Julien 2004). This is likely  
347 the reason why we found that the coefficient of variation (CV) of both minimum temperature and  
348 precipitation were positively related to the temporal variability in species composition of local  
349 communities.

350 Demographic stochastic events are a natural component of population dynamics (Otto  
351 and Whitlock 1997, Whitlock 2004, Willi et al. 2006). Our research indicates that such  
352 population-level events can have consequences for the temporal dynamics of local communities  
353 and potentially to metacommunities. So far, most previous research on this topic highlighted the  
354 effects of demographic stochasticity on either population temporal dynamics or community  
355 spatial dynamics (Lande 1993; Legendre et al. 1999; Vindenes and Engen 2017; Siqueira et al.  
356 2020; Feng et al. 2022; Jacobi and Siqueira 2023). We extend previous findings here by showing  
357 with empirical data that demographic stochasticity can also generate greater temporal variability  
358 in species composition, but mainly at the local scale. We thus suggest that the effects of  
359 demographic stochasticity are scale-dependent, being strongest at the local scale and decreasing  
360 in intensity with the increase of spatial scale or level of biological organization.

361

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588

## 589 **Supplementary Information**

### 590 **Process-based simulation model**

591 To select temporal variability metrics that could be used to investigate the role of  
592 demographic stochasticity, we simulated neutral temporal dynamics in metacommunities of  
593 varying sizes and examined the relationship between temporal variability metrics and community  
594 size. By simulating neutral metacommunities, we eliminated niche selection effects on species  
595 composition. As communities were assembled under neutral dynamics, any relationship between  
596 temporal variability and community size would suggest that a given variability metric was not  
597 appropriate.

598 Initially, we simulated random branching networks using the function `brnet` from the  
599 `mcbnet` package (Terui & Pomeranz, 2023). The branching networks were then employed in the  
600 `mcsim` function of the `mcbnet` package to simulate our metacommunities. We generated 39  
601 metacommunities comprising the same range of community (5-30) and species (5-48) numbers  
602 as observed in the datasets used for statistical modeling. Given that we were interested in  
603 simulating a neutral dynamic, we excluded environmental variation and niche differences from  
604 the simulation. We randomly varied the number of species among the metacommunities to  
605 generate a gradient of metacommunity sizes. We also incorporated a species carrying capacity  
606 value within communities to restrict growth and prevent excessive size increase over time. The  
607 carrying capacity of each population was consistent within communities of a given  
608 metacommunity but varied randomly among metacommunities (ranging from 50 to 150  
609 individuals). We also introduced variability in species abundance within communities by  
610 simulating a disturbance. To achieve this, we set the disturbance probability to 1 and the intensity  
611 to 0.43 for all metacommunities. We arrived at this disturbance value by adjusting it to match

612 metacommunity sizes similar to those in real datasets. Additionally, we conducted simulations  
613 considering different dispersal values within metacommunities (0.1, 0.5, and 1) to observe if this  
614 could impact the relationships with size. Then, we ran each simulation for a total of 1000 time  
615 steps. We selected the time-steps 100, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 as our  
616 temporal samples to calculate metrics related to the temporal variability in species composition.

617         We started measuring the temporal variability in species abundance at both the  
618 community and metacommunity levels to subsequently relate them to the median community  
619 size. We assessed temporal variability in species abundance by measuring the temporal  
620 variability of aggregate abundance at each biological level based on the framework proposed by  
621 Wang et al. (2019). However, we excluded this metric from our future analyses as it  
622 demonstrated a negative relationship with community size, both at the local and regional scales  
623 (Table. S1). Then, we decided to test some metrics for temporal variability in species  
624 composition. We measured both community and metacommunity variability using the approach  
625 proposed by Lamy et al. (2021) with the *ltmc* package. We also assessed temporal variability in  
626 the rank of species (Avolio et al. 2019), measuring the rank change within each community over  
627 time and the rank difference between communities at each time point. This was done using the  
628 *codyn* package (Hallett et al.) Considering multiple simulations conducted with various dispersal  
629 rates and different seeds, we observed that both at the local and regional scales, the metrics of  
630 species rank variability were less influenced by community size compared to the *ltmc* metrics  
631 (Table S1). When the metrics of species rank variability showed an association with size, the  
632 relationship exhibited low explanatory power. In contrast, the local *ltmc* metric consistently  
633 showed a negative relationship with community size, while the regional *ltmc* demonstrated  
634 higher explanatory power when related to community size.

635

636 Table S1. Statistics obtained in the process-based simulation model by relating the metrics of  
 637 temporal variability in species composition with the median community size. Simulations were  
 638 conducted using different seeds and dispersal rates. The p-value represents the significance of  
 639 each relationship, and the explanatory power was measured by R<sup>2</sup>.

Temporal variability metric	set.seed	Dispersal	Slope	p-value	R <sup>2</sup>	Adjusted R <sup>2</sup>
Local abundance (CV)	1234	0.1	-1.7E-04	2.5E-14	0.7958	0.7903
Regional abundance (CV)	1234	0.1	-4.1E-05	0.0002	0.3084	0.2897
LTMC local	1234	0.1	-1.2E-04	0.0055	0.1901	0.1683
LTMC regional	1234	0.1	-6.4E-06	0.0985	0.0721	0.0470
Rank change	1234	0.1	1.0E-06	0.8411	6.3E-05	-0.0015
Rank difference	1234	0.1	1.1E-05	0.0017	0.0252	0.0227
Local abundance (CV)	1234	0.5	-1.3E-04	5.2E-15	0.8123	0.8072
Regional abundance (CV)	1234	0.5	-4.4E-05	0.0006	0.2777	0.2581
LTMC local	1234	0.5	-3.8E-05	0.0132	0.1549	0.1321
LTMC regional	1234	0.5	-1.2E-06	0.6211	0.0067	-0.0202
Rank change	1234	0.5	8.6E-06	0.0364	0.0069	0.0053
Rank difference	1234	0.5	4.2E-06	0.301	0.0028	0.0002
Local abundance (CV)	1234	1	1.1E-01	2.7E-13	0.7682	0.7619
Regional abundance (CV)	1234	1	-5.1E-02	7.7E-05	0.3482	0.3306
LTMC local	1234	1	-3.7E-05	0.0108	0.1632	0.1406
LTMC regional	1234	1	-2.3E-06	0.405	0.0188	-0.0077
Rank change	1234	1	5.0E-07	0.9071	2.2E-05	-0.0016
Rank difference	1234	1	1.2E-05	0.0091	0.0174	0.0149
Local abundance (CV)	111	0.1	-1.9E-04	4.0E-11	0.6967	0.6885
Regional abundance (CV)	111	0.1	-6.0E-05	3.6E-05	0.3736	0.3567
LTMC local	111	0.1	-1.3E-04	0.0001	0.328	0.3098
LTMC regional	111	0.1	-9.0E-06	0.0021	0.2274	0.2065
Rank change	111	0.1	-2.3E-07	0.9565	4.8E-06	-0.0016
Rank difference	111	0.1	1.4E-05	1.5E-06	0.0580	0.0556
Local abundance (CV)	111	0.5	-1.4E-04	9.5E-12	0.7192	0.7116
Regional abundance (CV)	111	0.5	-4.8E-05	6.8E-06	0.4258	0.4103
LTMC local	111	0.5	-4.6E-05	0.0003	0.3016	0.2827
LTMC regional	111	0.5	-6.7E-06	0.0060	0.1868	0.1648
Rank change	111	0.5	6.3E-06	0.1187	0.0039	0.0023
Rank difference	111	0.5	2.1E-05	2.1E-08	0.0778	0.0754

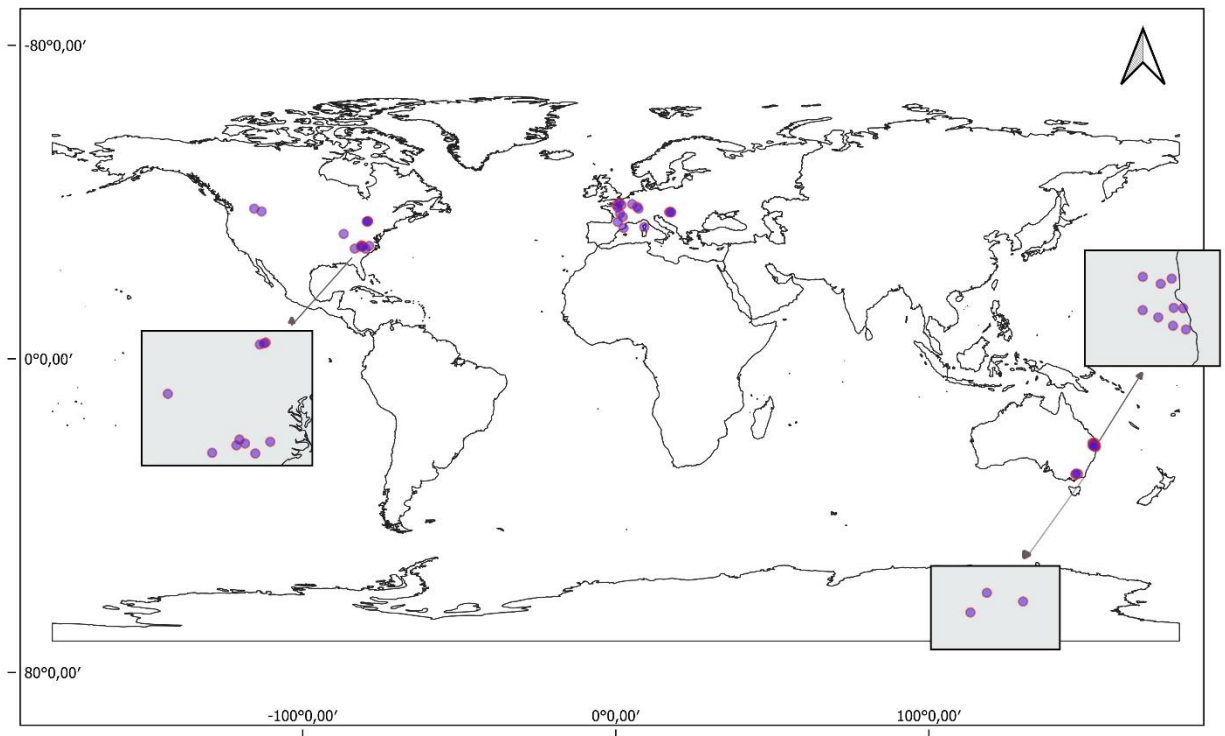
Temporal variability metric	set.seed	Dispersal	Slope	p-value	R <sup>2</sup>	Adjusted R <sup>2</sup>
Local abundance (CV)	111	1	-1.4E-04	2.7E-11	0.7028	0.6948
Regional abundance (CV)	111	1	-4.7E-05	1.3E-07	0.5329	0.5203
LTMC local	111	1	-4.3E-05	0.0003	0.3063	0.2875
LTMC regional	111	1	-5.5E-06	0.0255	0.1278	0.1042
Rank change	111	1	-4.8E-07	0.9029	2.4E-05	-0.0016
Rank difference	111	1	1.7E-05	1.4E-05	0.0476	0.0451

640

641



642 **Supplementary Figures**

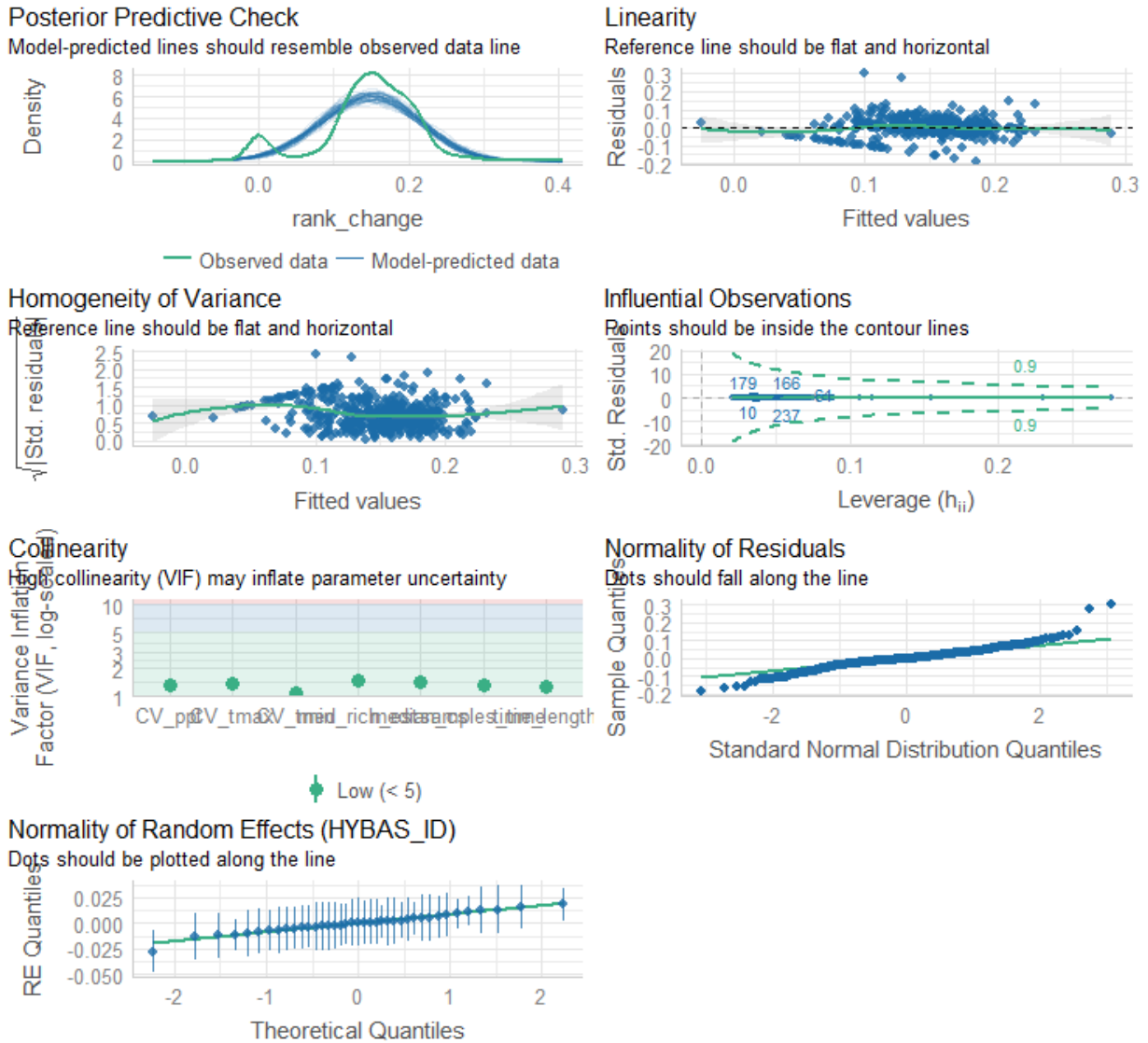


643

644 Figure S1. Geographic distribution of the 39 metacommunities selected in our study, located in

645 Australasia (12), Nearctic (12), and Palearctic (15) biogeographical realms.

646

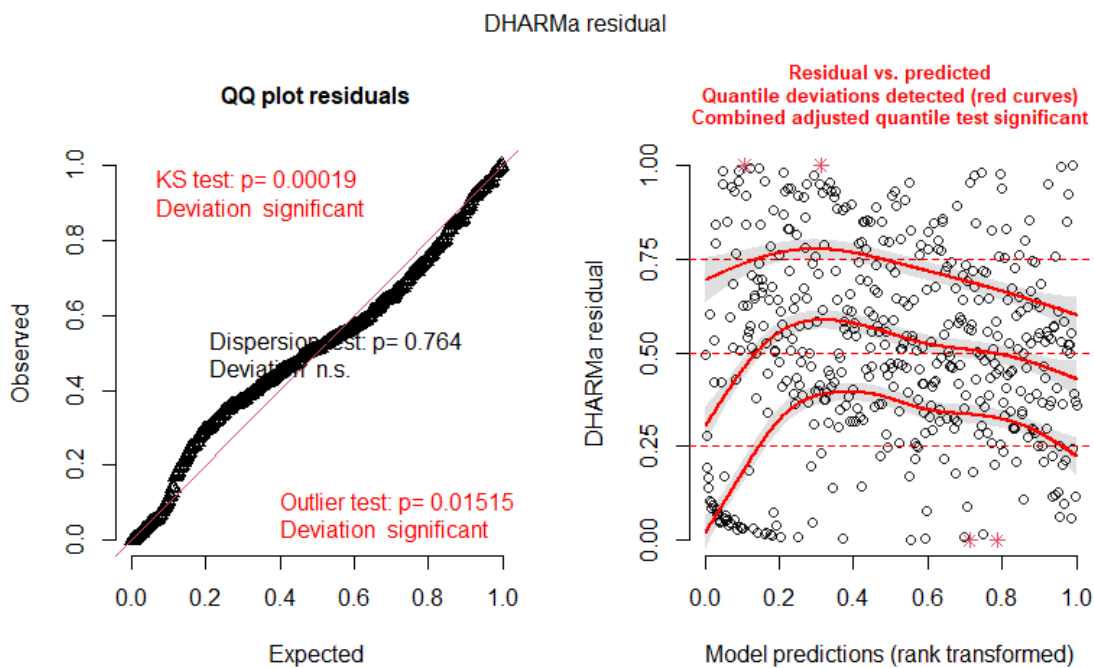


647

648 Figure S2 – Visual check of various assumptions of the model explaining temporal variability in  
 649 species composition in local communities.

650 An alternative way to assess a GLMM is by examining the residuals from the fitted  
 651 model, a process that can be done with simulateResiduals function from the DHARMA package  
 652 (Hartig, 2022). This function generates a qq-plot (Fig. S3 - left panel) to identify overall  
 653 deviations from the expected distribution, typically including tests for distribution correctness

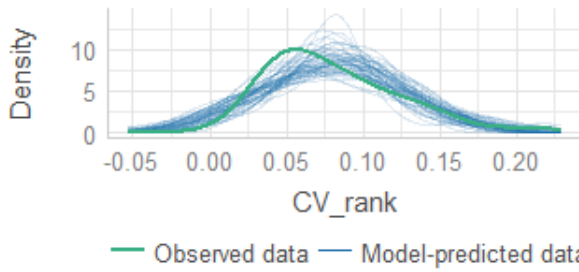
654 (KS test), dispersion, and outliers. Additionally, it produces the plotResiduals (Fig. S3 - right  
 655 panel), which generates a plot of residuals against predicted values, aiding in visualizing  
 656 deviations from uniformity. We observed that the residuals deviated slightly from the model's  
 657 predictions (Fig. S3; the closer the solid line to the dashed line, the better the fit). However, a  
 658 residual pattern does not suggest the model is unsuitable (Hartig, 2022). With a considerable  
 659 number of data points, residual diagnostics are likely to show significance, as achieving a  
 660 perfectly fitting model is improbable (Hartig, 2022).



661  
 662 Figure S3 – Output from the simulateResiduals function of the DHARMA package, providing a  
 663 visual aid in detecting deviations from uniformity for the model that explains the temporal  
 664 variability in species composition in local communities (model one). Red stars represent  
 665 simulation outliers.

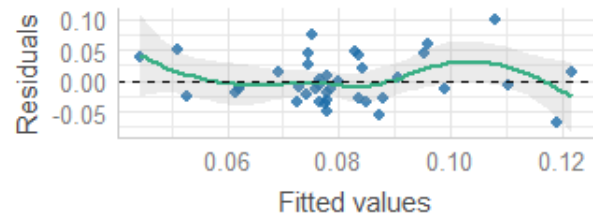
### Posterior Predictive Check

Model-predicted lines should resemble observed data line



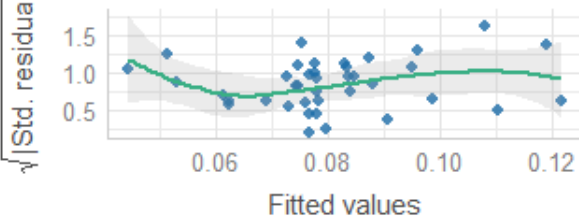
### Linearity

Reference line should be flat and horizontal



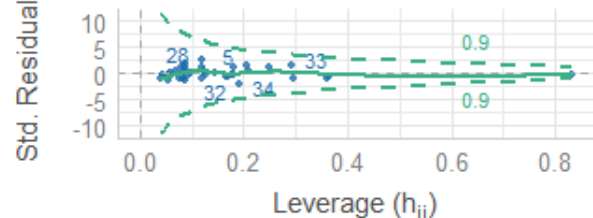
### Homogeneity of Variance

Reference line should be flat and horizontal



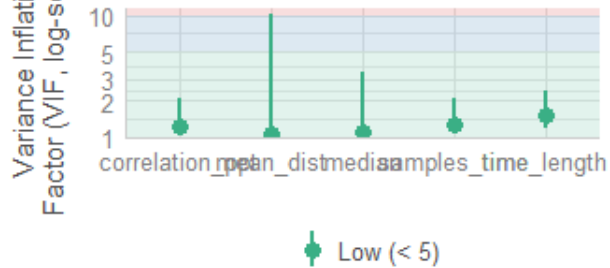
### Influential Observations

Points should be inside the contour lines



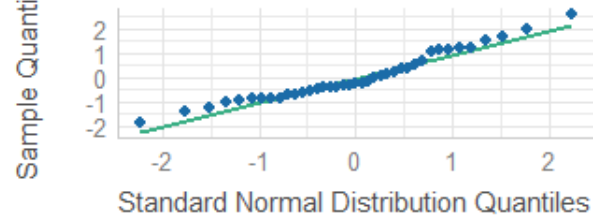
### Collinearity

High collinearity (VIF) may inflate parameter uncertainty



### Normality of Residuals

Dots should fall along the line



666

667 Figure S4 – Visual check of various assumptions from the model that explains the temporal  
668 variability in species composition in metacommunities.

669

670 **Supplementary Tables**

671 Table S2. Model selection for generalized linear model of temporal variability in species  
 672 composition at the regional scale (CV of rank difference) as a function of regional community  
 673 size (Reg. size), spatial connectivity (Connectivity), number of metacommunity samples over  
 674 time (Number of samples), time series length of each metacommunity (Time series length),  
 675 synchrony in precipitation (Syn ppt), synchrony in maximum temperature (Syn tmax) and  
 676 synchrony in minimum temperature (Syn tmin). AICs is Akaike's Information Criterion  
 677 corrected for small sample sizes,  $\Delta AIC_c$  indicates the difference between a model's  $AIC_c$  value  
 678 and the  $AIC_c$  value for the best-fitting model.

Model	Reg. size	Connectivity	Number of samples	Time series length	Syn ppt	Syn tmax	Syn tmin	$AIC_c$	$\Delta AIC_c$
M1	x	x	x	x	x			-128.6	0
M2	x	x	x	x			x	-128.28	0.32
M3	x	x	x	x		x		-128.02	0.58

679

680 Table S3. Model statistics summary for the metacommunity GLM. Here, the response variable  
 681 was the temporal variability in species composition at the regional scale (CV of rank difference).  
 682 Model coefficients (and their standard errors), t-values, and p-values are reported for each  
 683 predictor variable and the intercept.

	Estimate	Std. Error	t-value	p-value
Intercept	1.769e-01	4.538e-02	3.899	0.000447
Regional size	-4.074e-05	5.001e-05	-0.815	0.421058
Connectivity	-1.387e-09	1.438e-07	-0.010	0.992362
Syn ppt	-8.202e-02	3.674e-02	-2.232	0.032488
Number of samples	3.278e-04	1.521e-03	0.216	0.830645
Time series length	-1.865e-03	1.720e-03	-1.085	0.285962

684

685

686           **References**

687

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