

# Null models for community dynamics: Beware of the cyclic shift algorithm

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**Biosketch:** Michael Kalyuzhny performed the study as a PhD student in the Hebrew University of Jerusalem. He is interested in understanding the processes that shape species diversity and ecological dynamics, changes and stability.

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Null models for community dynamics:

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Beware of the cyclic shift algorithm

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Running title: Beware of the cyclic shift algorithm

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**Abstract**

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**Aim**

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Temporal patterns of community dynamics are drawing increasing interest due to their

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potential to shed light on assembly processes and anthropogenic effects. However, interpreting

22 such patterns considerably benefits from comparing observed dynamics to the reference of a null  
23 model. For that aim, the cyclic shift permutations algorithm, which generates randomized null  
24 communities based on empirically observed time series, has recently been proposed. This  
25 algorithm, borrowed from the spatial analysis literature, shifts each species time series randomly  
26 in time, which is claimed to preserve the temporal autocorrelation of single species. Hence it has  
27 been used to test the significance of various community patterns, in particular excessive  
28 compositional changes, biodiversity trends and community stability.

## 29 **Innovation**

30 Here I critically study the properties of the cyclic shift algorithm for the first time. I show  
31 that, unlike previously suggested, this algorithm does not preserve temporal autocorrelation due  
32 to the need to “wrap” the time series and assign the last observations to the first years. Moreover,  
33 this algorithm scrambles the initial state of the community, making any dynamics that results  
34 from deviations from equilibrium seem excessive. I exemplify that these two issues lead to a  
35 highly elevated type I error rate in tests for excessive compositional changes and richness trends.

## 36 **Conclusions**

37 Caution is needed when using the cyclic shift permutation algorithm and interpreting results  
38 obtained using it. Interpretation is further complicated because the algorithm removes all  
39 correlations between species. I suggest guidelines for using this method and discuss several  
40 possible alternative approaches. The non-preservation of autocorrelation also raises questions  
41 regarding the use of the analogous spatial null model, the torus-translation.

42  
43 **Keywords:** null models, community dynamics, statistical ecology, richness trends,  
44 compositional changes, species richness, cyclic shift, permutations, randomization methods,  
45 torus-translation.

## 47 **Introduction**

48 One of the main approaches for the study of community ecology is documenting patterns of  
49 variation in ecological communities and underpinning the mechanistic basis for these patterns

50 (Rosenzweig, 1995). Some of the most commonly studied patterns are species-area relationships  
51 (e.g. Preston, 1960; Rosindell & Cornell, 2007), latitudinal diversity gradients (e.g. Hillebrand,  
52 2004; Usinowicz et al., 2017) and productivity-diversity relationships (e.g. Kondoh, 2001;  
53 Tilman & Pacala, 1993). Multiple explanations have been suggested for these patterns and  
54 studying them has shed light on the mechanisms determining species diversity in ecological  
55 communities (e.g. DeMalach, Zaady, & Kadmon, 2017; Usinowicz et al., 2017).

56 However, all the aforementioned patterns have a thing in common: they are static,  
57 representing “snapshots” or time averages of ecological communities, without any temporal  
58 dimension. While interest in these patterns continues, in recent years there is growing interest in  
59 understanding temporal patterns in communities (Dornelas et al., 2013; Loreau & de  
60 Mazancourt, 2013; Magurran, 2016; McGill, Dornelas, Gotelli, & Magurran, 2015). It is  
61 believed that some of these patterns, that represent community dynamics and assembly “in  
62 action”, may reveal new insights on the processes shaping ecological communities (Chisholm et  
63 al., 2014; Kalyuzhny, Seri, et al., 2014). For example, studies on the scaling of the magnitude of  
64 population fluctuations with abundance revealed the central role of temporal environmental  
65 variability in shaping ecological communities (Chisholm et al., 2014; Jabot & Lohier, 2016;  
66 Kalyuzhny, Schreiber, et al., 2014; Kalyuzhny, Kadmon, & Shnerb, 2015), and studies focusing  
67 on long-term changes in abundance and diversity revealed that population-level regulation is  
68 often weak (Kalyuzhny, Seri, et al., 2014; Knape & de Valpine, 2012; Ziebarth, Abbott, & Ives,  
69 2010), while total-abundance and species diversity are indeed regulated (Brown, Ernest, Parody,  
70 & Haskell, 2001; Goheen, White, Ernest, & Brown, 2005; Gotelli et al., 2017; Magurran &  
71 Henderson, 2018). Moreover, in recent years there is an increasing interest in understanding  
72 richness trends and compositional turnover, partly motivated by concerns over the effect of  
73 anthropogenic activities on ecological communities (Elahi et al., 2015; Magurran et al., 2018;  
74 McGill et al., 2015; Vellend et al., 2013). Several studies have shown that while some local  
75 communities show richness trends, negative and positive changes may cancel out in multiple  
76 communities worldwide (Dornelas et al., 2014; Vellend et al., 2013). On the other hand, many  
77 ecological communities show large compositional turnover (Dornelas et al., 2014; Magurran et  
78 al., 2018).

79 This immediately raises the question: what qualifies as a “large” change in richness or  
80 composition? Stochastic community models generally predict that ecological communities would  
81 undergo constant changes at steady state (Lande, Engen, & Saether, 2003), and so do some  
82 deterministic models of nonlinear dynamics (May, 1976). Importantly, these models also predict  
83 that community properties, such as species richness, will have considerable temporal-auto  
84 correlation, which may generate spurious “trends” on decadal time-scales (see Figure 1a,b for an  
85 example). This is true even for the simplest and most minimalistic models of community  
86 dynamics such as the Neutral Theory and Dynamic Equilibrium theory (Hubbell, 2001).  
87 Consequently, and in analogy to null models of community patterns in space, temporal patterns  
88 should be compared to some null model to evaluate whether they deviate from the expectations  
89 under a minimalistic set of mechanisms (Gotelli & Graves, 1996; Gotelli & McCabe, 2002).  
90 Such null models preserve some aspects of the data and randomize others.

91 A recent suggestion for a null model of community dynamics is the cyclic shift permutations  
92 algorithm (Hallett et al., 2014), originally proposed for spatial analysis (Harms, Condit, Hubbell,  
93 & Foster, 2001). This algorithm gets as an input a matrix of the abundance, presence/absence or  
94 biomass of species by years (or other temporal units). In each realization of the algorithm, the  
95 time series of every species is shifted forwards in time a random number of years  $y$ ,  
96 independently of other species. The last  $y$  data points are then assigned to the first  $y$  years, hence  
97 “wrapping” the time series like a loop. For example, two possible resamples of the time series [1  
98 2 3 4 5] could be [5 1 2 3 4] or [3 4 5 1 2] with equal probability. This approach has been  
99 claimed to preserve the autocorrelation structure and the abundance distribution of each species  
100 time series (Hallett et al., 2014; Lamy et al., 2019; Magurran et al., 2018), which results from the  
101 ecological dynamics of this species, while removing all correlations between species. Hence, the  
102 cyclic shift algorithm was designed to test whether patterns of community dynamics differ from  
103 the expectation of an independent-species, temporally-autocorrelated process.

104 Cyclic shift permutations have been used as a null model for richness and compositional  
105 changes (Demars et al., 2014; Magurran et al., 2018), changes in dominance (Jones & Magurran,  
106 2018), and compensatory dynamics and stability of species diversity and total biomass (Gotelli et  
107 al., 2017; Hallett et al., 2014; Lamy et al., 2019; Magurran & Henderson, 2018). The application

108 of the cyclic shift null model is greatly facilitated by the available implementation of this  
109 algorithm within the open source R package Codyn (Hallett et al., 2016).

110 Here I would like to point out two important issues with the use of cyclic shift permutations  
111 and investigate their implications for statistical tests of temporal patterns. I claim that a) Cyclic  
112 shift permutations do not preserve the autocorrelation structure of single species time series,  
113 especially on the time scales of the length of the time series; and b) cyclic shift permutations  
114 scramble the initial state of the community, making any dynamics that result from initial  
115 deviations from equilibrium seem excessive. See Figure 1 for examples of such deviations and  
116 for the effect of cyclic shifts on them. I show that these two properties lead to seriously inflated  
117 type I error rates when testing for excessive compositional changes and richness trends.

118 For that aim, I generate synthetic community time series using a flexible multispecies  
119 Ricker model (Kalyuzhny & Shnerb, 2017; Kilpatrick & Ives, 2003) in multiple parameter  
120 regimes under three scenarios assuming that species a) are independent; b) compete neutrally  
121 (i.e. all species are identical) and c) compete and are different. See Figure 2 for examples of  
122 simulated time series. For these synthetic time series, richness trends and compositional changes  
123 are compared to the predictions of cyclic shift permutations. If the cyclic-shift algorithm works  
124 properly, it should generate patterns similar to those of the independent species model (since the  
125 algorithm break intra-specific correlations), and more variable than the model of non-neutral  
126 competition due to its stabilizing processes. While this could lead to acceptable or even reduced  
127 levels of type I errors, the aforementioned methodological issues are prevalent..

128 I conclude by discussing the possible applications of the cyclic shift algorithm and other  
129 community null models.

### 130 Do cyclic shift permutations preserve temporal autocorrelation?

131 The most important argument raised for using the cyclic shift permutations algorithm is that  
132 it preserves the temporal autocorrelation of the data (Hallett et al., 2014; Lamy et al., 2019;  
133 Magurran et al., 2018). While this argument is highly intuitive, it ignores a crucial aspect of the  
134 algorithm – the “wrapping” procedure, where the last  $y$  data points (where  $y$  is the number of  
135 years that the time series has been shifted) are assigned to the first  $y$  years.

136 Consider the first and last year data points in the resampled time-series. It is highly likely  
137 that in the original time series, those were consecutive years, now maximally separated by the  
138 “wrapping” of the time series. Assuming the original time series had positive short-term  
139 temporal autocorrelation, this results in the last data point in the resample resembling  
140 considerably the first data point. This is generalizable, to some degree, to the first several data  
141 points resembling the final several data points. Moreover, the wrapping “attaches” a pair of years  
142 that were originally maximally separated in time, also distorting autocorrelation at short time-  
143 scales.

144 Given data that were generated by some process, the goal of bootstrap resampling is  
145 generating more data that should resemble new data that would have been generated by repeating  
146 that process. Many ecological models, and the Ricker (for parameter regimes where the  
147 nonlinear effects do not take place) in particular, predict that consecutive time points would be  
148 relatively similar, and as time passes dissimilarity would monotonously increase (Kalyuzhny et  
149 al. 2015). Figure 3 exemplifies this for communities of independent species (Figure 3a), species  
150 that compete neutrally (Figure 3b) and non-neutrally (Figure 3c). In all three cases, time series  
151 resampled using the cyclic shift permutations show a unimodal pattern of Bray-Curtis  
152 dissimilarity, very different from the original time series. Dissimilarity indeed initially increases,  
153 but then, after half the time series duration, begins to symmetrically decrease, so that the last  
154 time-points are quite similar in composition to the first time points. For the first time-points in  
155 the resamples, dissimilarity increases too fast, due to the “attachment” of maximally separated  
156 years. Other parameter regimes and the Jaccard dissimilarity index show similar behaviors  
157 (Figures S1-S2), emphasizing that this is a general issue not limited to a narrow set of conditions  
158 and models. See methods for details about the simulations and the parameter regimes.

159 I conclude that the “wrapping” of the time series inherently distorts the temporal  
160 autocorrelation structure of ecological processes. This effect is dramatic on time scales that are  
161 on the order of the length of the time series, and less dramatic for shorter time scales. This raises  
162 the question – what are the implications of this, and of the “scrambling” of the initial state that  
163 was mentioned earlier, for the performance of statistical tests?

## 164 Type I errors of richness trends and excessive turnover

165 I exemplify the consequences of these properties for the testing of two fundamental patterns  
166 of community dynamics – temporal trends in diversity and compositional turnover. These are  
167 quantified by calculating the linear regression slope of a) species richness and b) the dissimilarity  
168 of species composition of each year w.r.t the initial year; both versus time. These patterns have  
169 been studied in various communities and compared to the expectations under cyclic shift  
170 permutations to test for significance (Demars et al., 2014; Magurran et al., 2018). To examine the  
171 performance of the cyclic shift permutations null model I generated  $10^4$  synthetic communities  
172 under several parameter regimes using the Ricker model, assuming one of three modes of inter-  
173 specific interactions: a) no interactions; b) neutral competition and c) non-neutral competition. I  
174 then applied the cyclic shift algorithm 500 times to each community and compared the observed  
175 compositional and richness slopes in the time series generated by the model to the distribution of  
176 slopes under the cyclic shift algorithm. This allows me to calculate the significance of the  
177 observed slopes for each community.

178 Since simulations began at steady state, and since the parameters of the simulations remain  
179 fixed, there are no real trends in species richness (beyond the spurious trends generated by  
180 temporal autocorrelation, see Figure 1a,b). For this reason, detected trends are false-positive  
181 results (type I errors), and their percent should be close to 0.05 if the null model is appropriate.  
182 This is particularly true for the non-interacting species case, since the breaking of correlations  
183 imposed by cyclic shift permutations should have no effect. However, I found that for both  
184 models and under all parameter regimes, type I errors were considerably inflated (Figure 4).

185 Type I errors for compositional changes were very high (0.15 – 1) under all parameter  
186 regimes, interaction types and using either the Jaccard or Bray-Curtis indices (yellow and blue,  
187 respectively, in Figure 4a). These results are the consequences of the unimodal pattern of  
188 dissimilarity with time that is generated by cyclic-shift permutations (Figure 3). The distribution  
189 of linear slopes fitted to this unimodal pattern is very different from the slope of the actual data,  
190 leading inevitably to a strong inflation of type I errors. In several cases it appears that type I  
191 errors increase with the number of species, leading to communities with more immigration and  
192 less environmental stochasticity having less errors. However, this also depends on the shape of  
193 the dissimilarity vs. time curve, which is more complex.



194 Regarding richness trends, communities starting at the equilibrium species richness had  
195 elevated type I errors (0.08 - 0.14, Figure 4b). However, the most pronounced result is that  
196 communities whose richness in the first year deviated from equilibrium, even by a few species,  
197 had a much higher type I error probability, reaching 0.3 – 0.7 in some parameter regimes.  
198 Moreover, type I error probabilities increased sharply with the magnitude of the initial deviation  
199 from equilibrium. It is important to emphasize that I did not intentionally initiate the  
200 communities at a deviation from equilibrium richness. Rather, deviations were a result merely of  
201 stochastic dynamics at steady state. These results hold under all parameter regimes and  
202 interaction modes, implying that such deviations, and the resulting inflation in type I errors, are  
203 to be expected in natural ecological communities.

204 The sharp increase in type I error rate as initial community richness moves away from  
205 equilibrium is a result of the “scrambling” of the initial state. Fairly generally for communities in  
206 steady state, if some community property (richness, in this case, but without loss of generality)  
207 has an equilibrium value, and we find it initially at a different value, it is expected to return to  
208 that equilibrium. However, the cyclic-shift permutation eliminates the initial state of the  
209 community, and as a result any trend towards equilibrium would seem excessive. Figure 1 shows  
210 how the spurious trends that result from the autocorrelation and from beginning not at  
211 equilibrium (Figure 1b) are eliminated by the cyclic shift randomization (Figure 1c).

## 212 Discussion

213 The cyclic shift algorithm is a generalistic and easy to apply null model, making it an  
214 appealing approach for testing a variety of different patterns. However, as I have shown, this  
215 approach has two fundamental undesired properties. First, it distorts the autocorrelation structure  
216 so that the end of the resampled time series for each species closely resembles its beginning. The  
217 short-term autocorrelation (for the first several years, less than half the length of the time series)  
218 is also affected, but to a lesser degree. Moreover, the cyclic shift randomization “scrambles” the  
219 initial state of the community, making any dynamics that results from properties of this initial  
220 state seem unlikely. I have further exemplified that these fundamental limitations have severe  
221 consequences for type I error rates in tests for trends in species richness and excessive  
222 compositional changes under a broad set of parameters, emphasizing the generality of the results.  
223 I believe that the fundamental nature of the issues with the cyclic shift null model would have

224 negative consequences for tests that may be developed for other patterns as well. For this reason,  
225 I recommend using this null model with extra caution.

226 Another aspect that must be considered carefully before using the cyclic shift algorithm is  
227 the implications of removing the correlations between species. If the goal of the analysis is  
228 testing for the significance of such correlations (e.g. Hallett et al., 2014) then using a null with no  
229 correlations definitely makes sense. However, other aspects of the dynamics, such as temporal  
230 changes in diversity, composition and dominance, may very well be affected by correlations  
231 between species. These correlations could be caused by biotic interactions or responses to  
232 environmental changes, and the interpretation of finding excessive changes compared to such a  
233 null of independent species should be carefully considered. Even more so, one should be  
234 cautious about using cyclic-shift permutations on data that is available at a resolution of less than  
235 a year (e.g. Magurran et al., 2018; Magurran & Henderson, 2018). In such data, correlation  
236 between species may be the result of seasonality, and randomly shifting each species  
237 independently of other species removes its effect. Consequently, the likely strong effects of  
238 seasonality on community composition will be detected as excessive changes.

239 These issues do not lessen, however, the need that led to the development of the cyclic shift  
240 algorithm. Indeed, I believe that the interest in temporal patterns will continue to grow, along  
241 with the need for a null model to serve as reference for them. I would like to suggest several  
242 possible directions for addressing this need.

243 An alternative approach that has been suggested as a null model for community dynamics is  
244 neutral models (Dornelas et al., 2014; Gotelli & McGill, 2006; Hubbell, 2001), whose predicted  
245 dynamics has been compared to observed dynamical patterns on decadal (e.g. Dornelas et al.,  
246 2014; Kalyuzhny et al. 2015) or paleobiological time scales (e.g. Clark & McLachlan, 2003;  
247 McGill, Hadly & Maurer, 2005). However, the dynamic predictions of neutral models are quite  
248 sensitive to the level of immigration (e.g. Hubbell 1997; Dornelas et al. 2014) and temporal  
249 resolution (Tomasovych & Kidwell, 2010; Kalyuzhny et al. 2015), which are often unknown.  
250 Furthermore, it has been shown that neutral models where stochastic events affect individuals  
251 independently (known as “demographic stochasticity” or “ecological drift”), such as the classical  
252 Unified Neutral Theory of Biodiversity and Biogeography (Hubbell, 2001), predict considerably  
253 smaller changes than observed in multiple communities (Dornelas et al., 2014; Kalyuzhny,

254 Schreiber, et al., 2014; Kalyuzhny, Seri, et al., 2014). It has been shown that this is the result of  
255 ignoring environmental fluctuations, which affect the growth rate of entire populations  
256 synchronously (Chisholm et al., 2014; Fung, O'Dwyer, Rahman, Fletcher, & Chisholm, 2016;  
257 Jabot & Lohier, 2016; Kalyuzhny et al., 2015). Hence, a neutral model with environmental  
258 fluctuations would be a much more appropriate null (Jabot & Lohier, 2016; Kalyuzhny et al.,  
259 2015). Furthermore, neutral theories impose compensatory dynamics, or negative correlations,  
260 between species, which stem from the zero-sum assumption. This makes them not necessarily  
261 the best choice as a null model (Gotelli & McGill, 2006). Overall, using neutral theories as a  
262 dynamic null model involves multiple non-trivial challenges. Another alternative would be to try  
263 to fit multispecies autoregressive models (Ives, Dennis, Cottingham, & Carpenter, 2003). This  
264 framework is more flexible, and one may decide to preserve (or not to preserve) multiple  
265 properties such as the autocorrelation structure of the data, the magnitude of fluctuations, the  
266 correlations between species and the initial state of the community. This approach has not been  
267 studied much as a null model to this day.

268 Finally, a null model for presence-absence data named Presence-Absence Resampling  
269 within periods (PARIS) has recently been suggested as a methodology to generate synthetic  
270 communities where each species independently undergoes colonization and extinction dynamics  
271 at fixed rates (Kalyuzhny, Flather, Shnerb & Kadmon, 2019). While this approach imposes the  
272 autocorrelation structure of a Poisson process and species independence, it preserves the initial  
273 state of the community and has recently been shown to have excellent statistical properties:  
274 acceptable type I error rates, robustness to problems in the data and statistical power under  
275 alternative assumptions (Kalyuzhny et al., 2019). PARIS is also very easy to apply to ecological  
276 time series because, like the cyclic-shift algorithm, it is a randomization-based methodology with  
277 publicly available code.

278 It is noteworthy that the cyclic shift algorithm was initially borrowed from the literature on  
279 spatial analysis (Harms et al., 2001, named “torus-translation”), where the preservation of  
280 autocorrelation argument was initially raised. Since its proposition, tests based on this torus-  
281 translation have been published in dozens of works (e.g. Hall, McKenna, Ashton & Gregoire,  
282 2004; Yamada et al., 2007; Lan et al., 2012). The finding that the temporal analogue, the cyclic  
283 shift algorithm, does not preserve temporal autocorrelation, implies that the torus-translation

284 does not preserve spatial autocorrelation as well. This casts doubt on the justification for the  
285 torus-translation. I hope future works will examine the implications of this non-preservation of  
286 autocorrelation to the performance of statistical tests using the torus-translation as a spatial null  
287 model.

288 Overall, I believe that studying temporal patterns has great promise to shed light on the  
289 processes shaping ecological communities. This promise is amplified by the increasing  
290 availability of extensive datasets of temporal community dynamics (Dornelas et al., 2018).  
291 However, more research is required on how to appropriately analyze such data, and in particular  
292 on the best practices for applying null models of community dynamics. I hope this work will  
293 reduce the improper application of such null models and help guide the use and development of  
294 more appropriate null models for temporal community dynamics.

## 295 Methods

### 296 Models

297 I have studied the statistical performance of the cyclic shift permutations algorithm by  
298 applying it to synthetic time series generated using a discrete-time multispecies Ricker model (  
299 Kalyuzhny & Shnerb, 2017; Kilpatrick & Ives, 2003), whose flexibility allows generating  
300 a variety of dynamic regimes.

301 In the multispecies Ricker model, the expected population of species  $i$  at time  $t+1$ ,  $N_{i,t+1}$ , in  
302 the absence of immigration is:

$$303 \quad (\text{eq. 1}) \quad E(N_{i,t+1}) = N_{i,t} \exp \left( r_i \frac{K_i - N_{i,t} - \sum_{j \neq i} \alpha_{ij} N_{j,t}}{K_i} + \varepsilon_{i,t} \right),$$

304 where  $r_i$  and  $K_i$  are the growth rate and carrying capacity of species  $i$ , respectively,  $\alpha_{ij}$  is the  
305 per capita effect of an individual of species  $j$  on the growth of species  $i$ , representing inter-  
306 specific interactions, and  $\varepsilon_{i,t}$  represents stochastic fluctuations in growth rate due to  
307 environmental changes.  $\varepsilon_{i,t}$  is normally distributed with a mean of 0 and variance of  $\sigma_e^2$ .

308 While eq. 1 represents the expected population of species  $i$  at time  $t$ , the actual population  
309 size is drawn from a Poisson distribution:  $N_{i,t+1} \sim \text{Poisson}(E(N_{i,t+1}))$ . This introduces  
310 demographic stochasticity, that is, random variation between individuals in demography, as well  
311 as the discreteness of individual, which allows species to go stochastically extinct. Finally, after

312 the local demography step described above, A Poisson distributed number of immigrants (with  
313 mean  $I$ , representing immigration rate) are introduced and are chosen uniformly from the  $S_{\text{reg}}$   
314 species available in the species pool.

315 The flexibility of the Ricker model allows considering multiple parameter regimes and  
316 modes of interspecific interactions. I have used three such general modes of interactions: First, to  
317 be as consistent as possible with the properties of the cyclic shift algorithm, I considered  
318 communities of non-interacting species by setting all  $\alpha_{ij}$ s to zero. I further assumed that the  $K_i$ s  
319 of species are lognormally distributed with mean of 1000 and SD of 2000, the  $r_i$ s are  
320 exponentially distributed with mean 0.1. To resemble neutral models, which are also used as null  
321 models, I have assumed all  $\alpha_{ij} = 1$ , all  $K_i = 1000$  and all  $r_i = 0.1$ . In this case, all the species are  
322 identical, subject to one community-wide carrying capacity  $K = K_i$  and to demographic and  
323 possibly environmental stochasticity. Hence, this model is analogous to classic neutral theory,  
324 but with the community carrying capacity subject to fluctuations rather than being a fixed  
325 number. Finally, to generate more complex and realistic dynamics I considered non-neutrally  
326 competing species. In this case, I assumed that the  $\alpha_{ij}$ s are gamma distributed with mean and SD  
327 of 0.1, and the  $K_i$ s and  $r_i$ s are distributed similarly to the case of independent species.

328 In all three modes of interactions, I considered five parameter regimes. Under the baseline  
329 regime,  $I = 1$  and  $\sigma_e = 0.2$ . Under the high immigration and low immigration regimes,  $I$  was set  
330 to 0.2 and 10, respectively, and under the low stochasticity and high stochasticity  $\sigma_e$  was set to 0  
331 and 0.5, respectively. Communities were initiated with each species at its carrying capacity  $K_i$ ,  
332 or at  $K_i/S_{\text{reg}}$  in the neutral interactions regime and were given  $20 * S_{\text{reg}}/I$  time steps to equilibrate  
333 before being recorded for 20 time steps (unless otherwise presented). This approach comes to  
334 allow 20 immigration events (on average) for each species before I consider the community as at  
335 steady state.

336 For all models, I considered two levels of  $S_{\text{reg}}$ , 20 and 100 species. The results were  
337 qualitatively similar but more pronounced for the 100 species (because there are more changes  
338 overall), so I present the result for  $S_{\text{reg}} = 100$  in all cases. Examples of time-series generated  
339 under the models in the three interaction modes are given in Figure 1

340 **Statistical tests**

341 I am interested in examining the performance of tests for excessive compositional turnover  
342 and richness trends. For compositional turnover, I computed the Jaccard and Bray-Curtis  
343 dissimilarity indices of every year with respect to the initial year (as in Figure 3) and used the  
344 linear slope of dissimilarity vs. time as the test statistic. For richness trends, I computed the slope  
345 of the regression of richness vs. time. For every synthetic community generated by the  
346 multispecies Ricker model I calculated these two test statistics, generated 500 resampled  
347 communities by applying cyclic shift permutations to the original data, and then compared the  
348 observed statistics to their distribution in the resampled communities using a two-sided test. This  
349 gave the P value of both statistics for every community. This procedure is in line with the  
350 approach of Magurran et al. (2018).

351 To evaluate the performance of the statistics, I calculated the proportion of cases falling in  
352 the tails (using  $\alpha = 0.05$ ). Since I expect no excessive changes, this proportion can be thought of  
353 as type I error rate, which should not exceed  $\alpha$ . For examining the tests of compositional change  
354 (Figure 4a), the proportion was calculated over all  $10^4$  synthetic communities in a given  
355 parameter regime. For examining the tests of richness trends, I first assigned the communities to  
356 bins according to their initial deviation from equilibrium richness. Equilibrium richness was  
357 calculated as the average richness in the 20 year data for the sake of simplicity and resemblance  
358 to empirical analyses, where the real equilibrium is unknown. The bins that were used were  $D \leq -$   
359  $7, -7 < D \leq -4, -4 < D \leq -2, -2 < D \leq -1, -1 < D \leq 1, 1 < D \leq 2, 2 < D \leq 4, 4 < D \leq 7, 7 < D,$   
360 where D is initial deviation from richness equilibrium. In each bin, I calculated the average D  
361 (presented on the X axis), and the proportion of false positive results among the communities in  
362 the bin (presented on the Y axis). Bins with less than 10 communities were discarded.

363 All analyses were performed in Matlab 2016a with the full code supplied in supporting  
364 information S2.

365

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515

## 516 Data accessibility statement

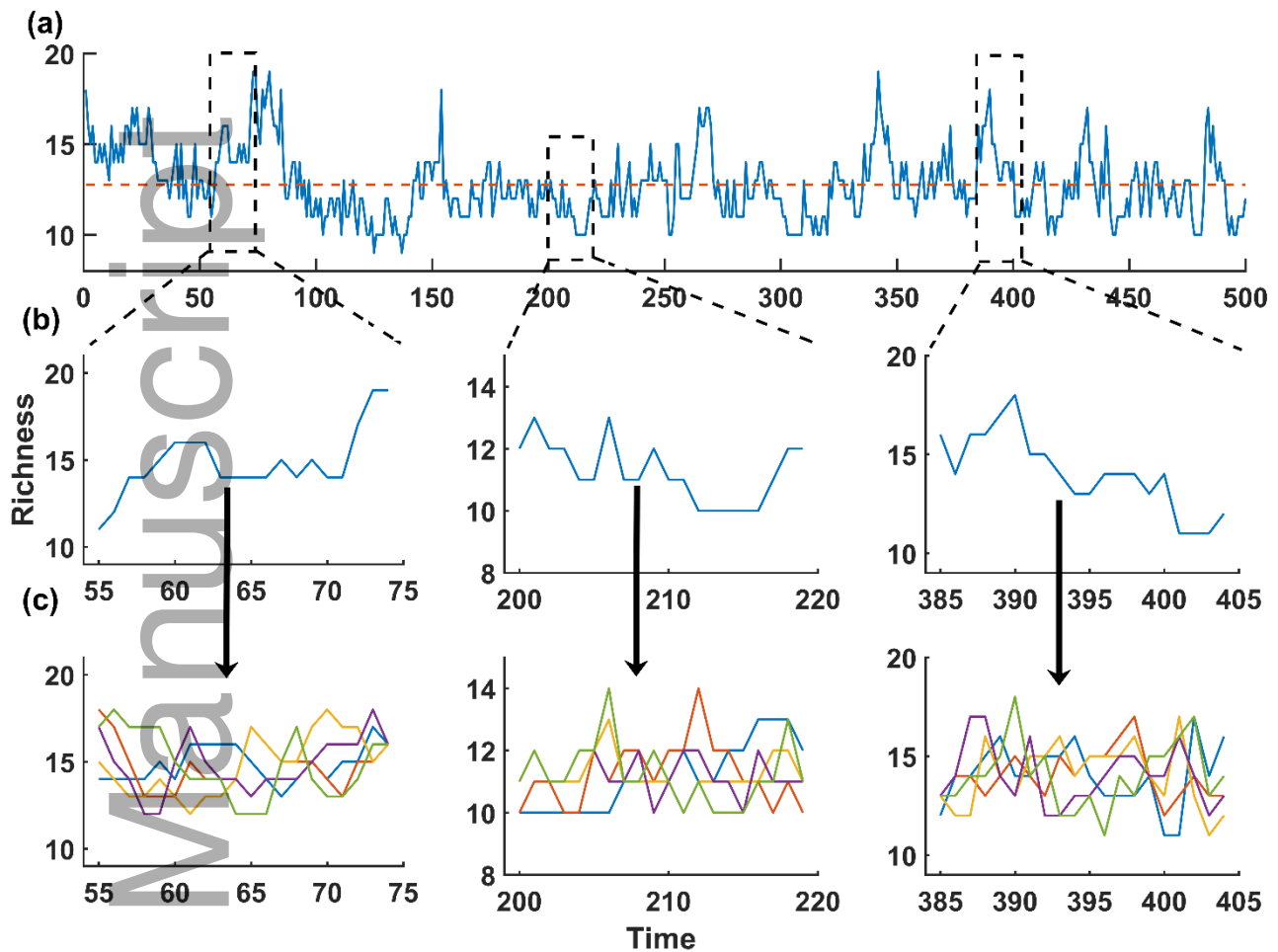
517 The manuscript does not use data. All the code is available in the supporting information.

518

## 519 Figures and legends

520

521 Figure 1:

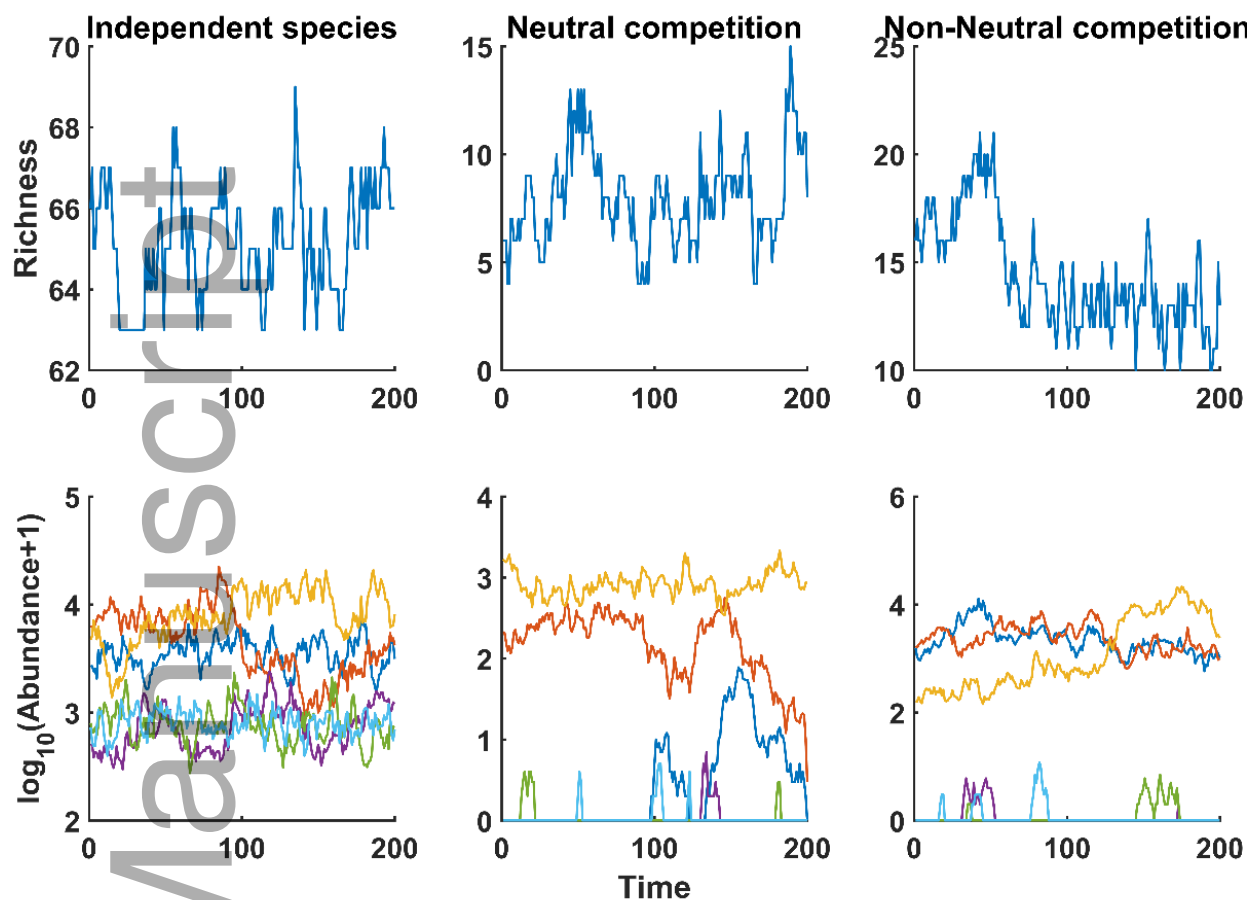


522

523 **Figure 1** – The challenges in analyzing community time series, as exemplified with species  
524 richness through time. In (a), richness in 500 time steps of a Ricker model at steady state in the  
525 default non-neutral competition regime is presented (blue), along with the long-term average  
526 (red). Note the “noisiness”, the degree of temporal autocorrelation and the observation that the  
527 system can stay away from the equilibrium richness for long times. Zooming in on three sections  
528 (b), it is noticeable that some may show spurious “trends”, which are solely a result of this  
529 autocorrelation, as the system is in steady state with fixed parameters. However, time series  
530 produced by applying the cyclic-shift null model to these short time-series (five resamples for  
531 each time series, presented in c) would lack these “trends” and make them seem excessive.

532

533 Figure 2:

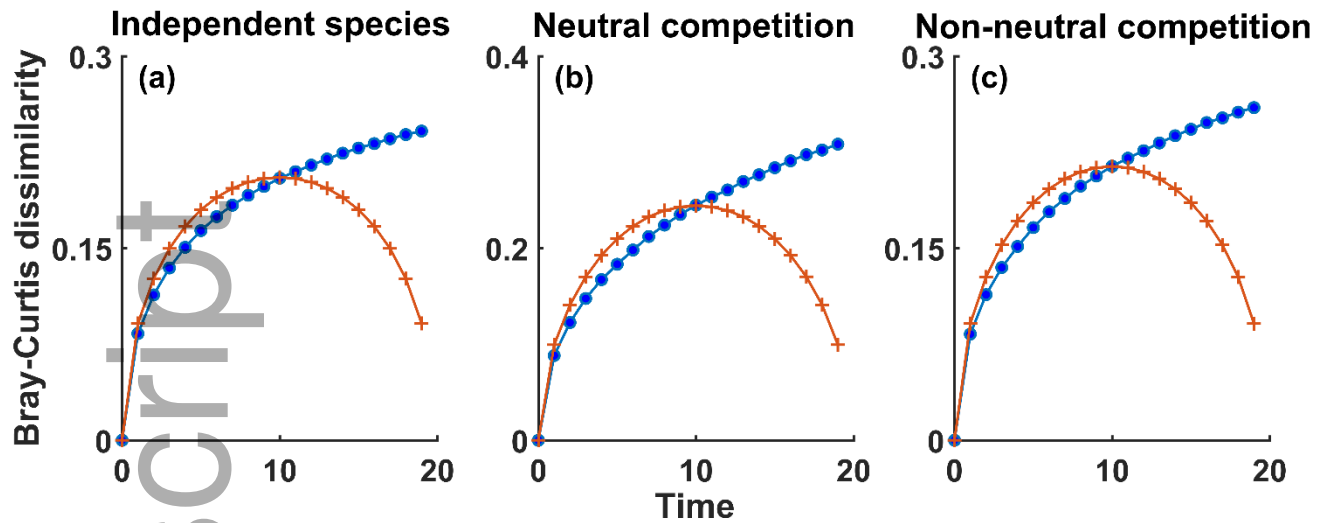


534

535 **Figure 2** - Examples of time series of species richness and abundance under the default  
 536 parameter regime with the three interactions modes – independent species, neutrally competing  
 537 species and non-neutrally competing species. The abundances presented below are of the three  
 538 most common species and the three species around the 75<sup>th</sup> percentile of abundance. Time series  
 539 produced under this (and other) parameter regimes were used for testing trends and excessive  
 540 compositional changes in this work. Since these models are stationary, none of these “trends”  
 541 result from real changes in the communities, but are only a result of the autocorrelation of the  
 542 process. See methods for details about the simulations and their parameter regimes. The species  
 543 pool has 100 species in all cases.

544

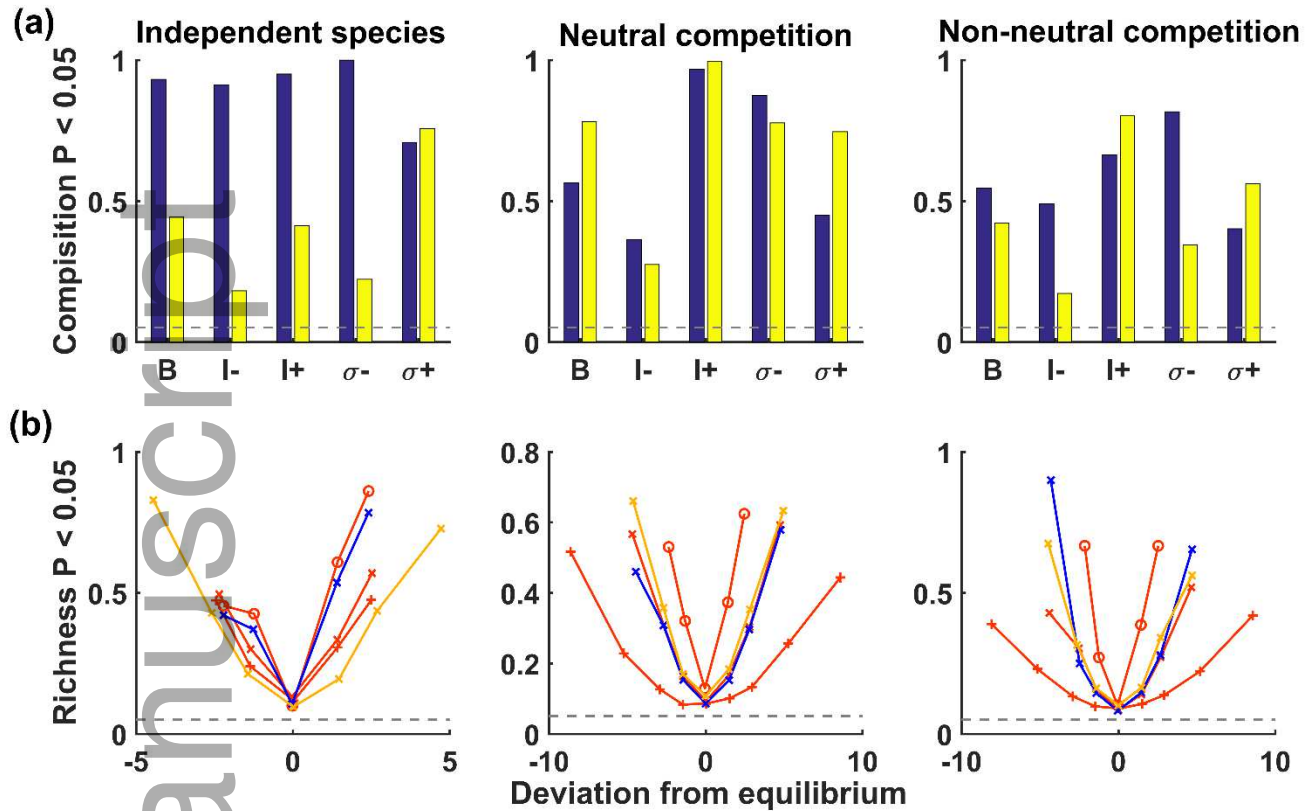
545



546

547 **Figure 3** – Comparison of Bray-Curtis community self-dissimilarity with time between  
 548 “empirical” simulated time series and their resamples, obtained using the cyclic shift algorithm.  
 549 For each scenario (independent species (a), neutral competition (b) and non-neutral competition  
 550 (c)),  $10^4$  synthetic time series were generated and Bray-Curtis compositional dissimilarity in  
 551 every year was compared with the initial year for the empirical communities and resamples. For  
 552 every empirical time series, 500 resamples were calculated and the results are averaged over the  
 553 time series and resamples for every time point. The differences between the empirical and  
 554 resampled average patterns is highly significant for every point but the middle and zero (t-test,  $P$   
 555  $< 10^{-9}$ ). While the “default” parameter regime is presented, other regimes and the Jaccard index  
 556 (Figures S1-S2) show similar results.

557



558

559 **Figure 4** – Proportion of false positive tests (at  $\alpha = 0.05$ ) for excessive compositional  
 560 changes (a) and richness trends (b) for data generated by the multispecies Ricker model.  $10^4$   
 561 synthetic time series were generated for each parameter regime and mode of interspecific  
 562 interactions. For each time series, the slopes versus time of compositional dissimilarity w.r.t the  
 563 first year and of specie richness were calculated. They were then compared with the distributions  
 564 of slopes for 500 resamples (using the cyclic shift algorithm and a two-sided test) of the synthetic  
 565 time series to obtain a P value. The parameter regimes are denoted as “B” or orange X for  
 566 baseline; “I-” or orange O for low immigration, “I+” or orange + for high immigration;  $\sigma$ - or blue  
 567 X for no environmental stochasticity and  $\sigma$ + or yellow X for high environmental stochasticity.  
 568 In (b) communities were assigned to bins based on the deviation of initial richness from  
 569 equilibrium, and the proportion was calculated in each bin. In (a). Jaccard (yellow) and Bray-  
 570 Curtis (blue) dissimilarity were calculated. The dashed grey line marks a proportion of 0.05.

571



572 **Supplementary Materials**

573 **Figure S1** – Comparison of Bray-Curtis community self-dissimilarity with time between  
574 “empirical” simulated time series and their resamples, obtained using the cyclic shift algorithm.

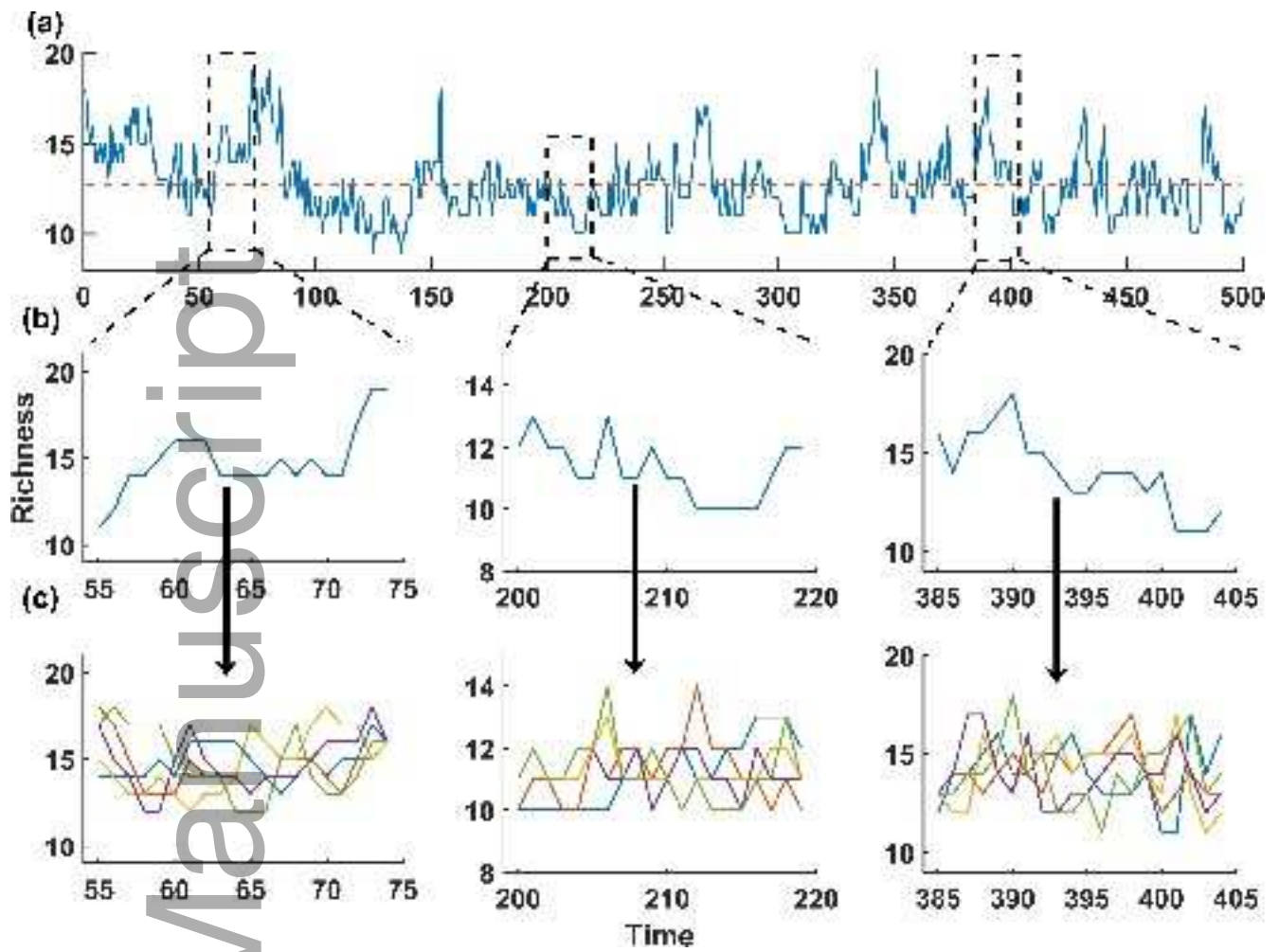
575

576 **Figure S2** – Comparison of Jaccard community self-dissimilarity with time between “empirical”  
577 simulated time series and their resamples, obtained using the cyclic shift algorithm.

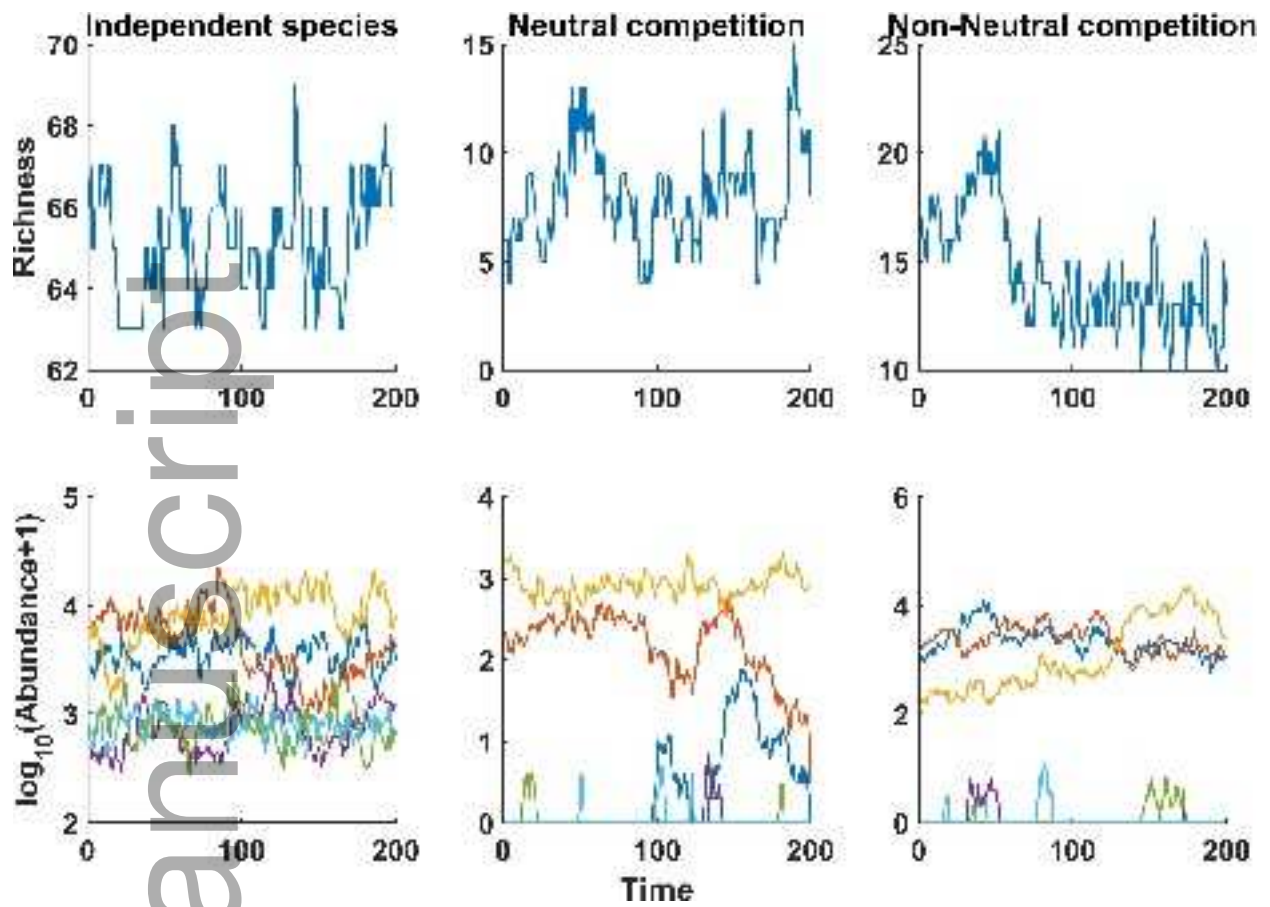
578

579 **SI S2** – code appendix.

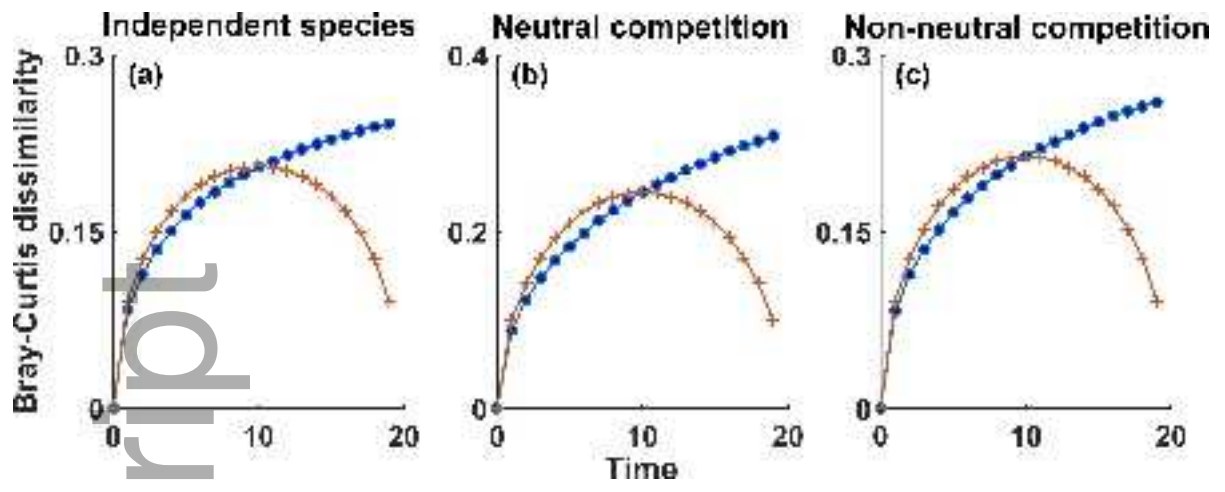
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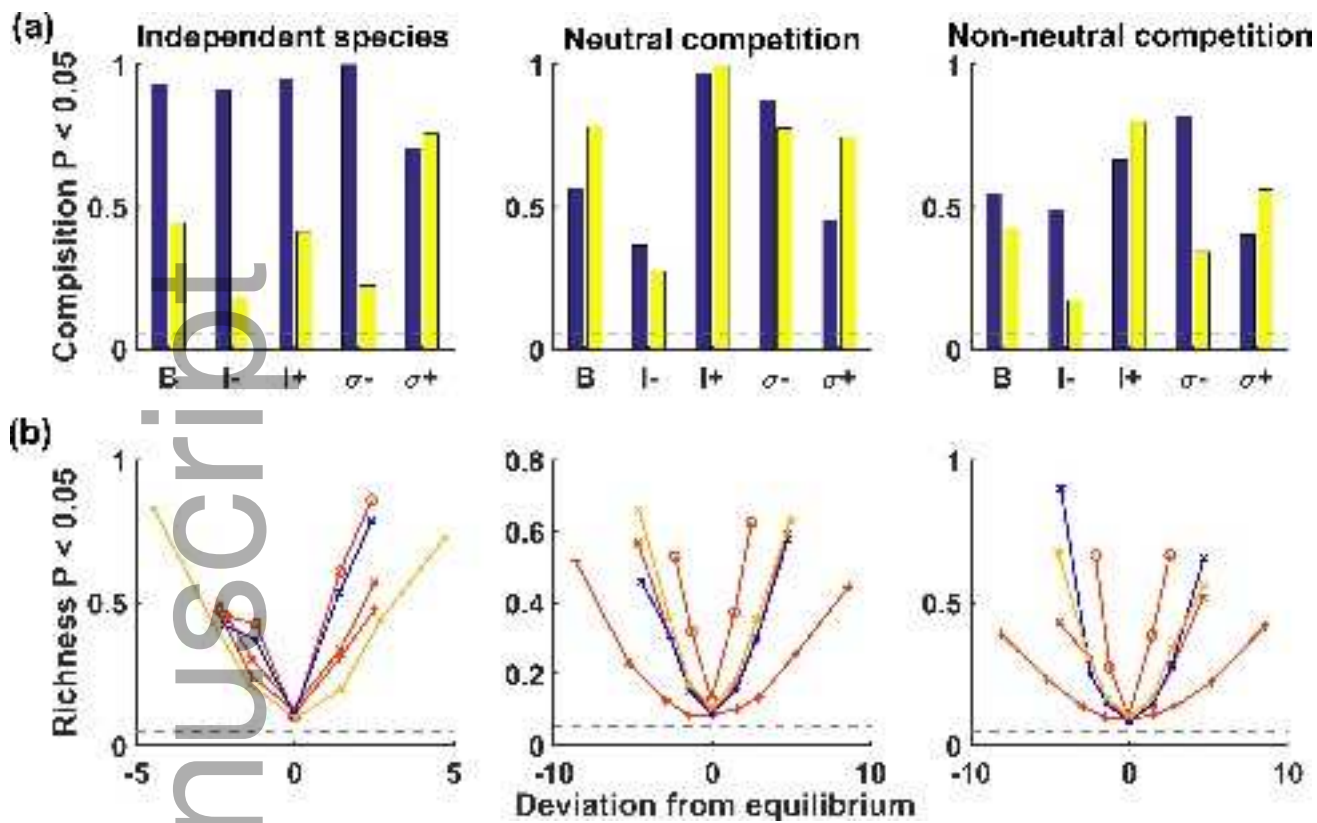


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