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Biodiversity maintenance may be lower under partial niche
differentiation than under neutrality

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Running head: Niche differentiation and persistence

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Abstract

Niche differentiation is normally regarded as a promoter of species coexistence in competitive systems, as it stabilizes species abundances. One might therefore expect lower extinction rates and higher species richness and local persistence times in niche-differentiated communities than in neutral assemblages. Here we compare stochastic niche and neutral dynamics in simulated assemblages, and find that when local dynamics combine with immigration from a regional pool, the effect of niches can be more complex. Trait variation that lessens competition between species will not necessarily give all immigrating species their own niche to occupy. Such partial niche differentiation protects certain species from local extinction, but expedites exclusion of others. Differences in regional abundances and intrinsic growth rates have similar impacts on the distribution of persistence times as niche differentiation and blur the distinction between niche and neutral dynamical patterns, though niche dynamics will influence which species persist longer. Ultimately, unless the number of niches available to species is sufficiently high, niches may actually heighten extinction rates and lower species richness and local persistence times. Our results help make sense of recent observations of community dynamics, and point to the dynamical observations needed to discern the influence of niche differentiation.

Key words: Partial niche differentiation, stochastic niche dynamics, local persistence time, community dynamics, neutral dynamics, competitive coexistence, community assembly, immigration.

19 Introduction

20 Niche differentiation is widely considered a prime force behind species coexistence, and thus
21 instrumental in maintaining biodiversity. Niche differentiation stabilizes communities by guaranteeing
22 positive growth rates of rare species (Chesson, 1991, 2000). Without such stabilization, coexistence
23 is only temporary, and biodiversity can only be maintained if gains from immigration or speciation
24 compensate losses to competitive exclusion or drift as posited in neutral theory (Hubbell, 2001).

25 Views on the implications of niche differentiation for biodiversity maintenance mostly come from
26 deterministic community models with no immigration. However, stochastic formulations, which
27 model the influence of variability in finite populations whose deterministic details are unknown or
28 unrelated to species differences, are more relevant for natural systems. In such settings, coexistence
29 is defined in a probabilistic sense (Schreiber, 2015). Furthermore, many if not most communities in
30 nature are subject to propagule pressure from regional pools. In such open-community scenarios,
31 species may persist for a substantial period of time due to mass effects, and extinction is not an
32 absorbing state since later re-colonization is always possible. One measure of diversity maintenance
33 in this context is species mean persistence time – the average time between introduction through
34 immigration and extirpation through drift or competitive exclusion.

35 Persistence times have been studied as indicators of ecological processes (Leigh et al., 1993;
36 Magurran and Henderson, 2003), and have been explored theoretically in the context of neutral
37 dynamics (Leigh et al., 1993; McGill et al., 2005; Pigolotti et al., 2005; Nee, 2005; Condit et al., 2012;
38 Bertuzzo et al., 2011; Segura et al., 2017). Recent studies found that stabilizing niche differentiation
39 considerably prolongs persistence times (Pigolotti and Cencini, 2013; Carroll and Nisbet, 2015).
40 However, the niche scenarios proposed in these studies tend to be extreme. For example, Pigolotti
41 and Cencini (2013) used a stochastic version of a simplified Lotka-Volterra model where all species
42 interactions are identical except that competition is stronger within than across species (Haegeman
43 and Loreau, 2011). This corresponds to a biological scenario where all species stably coexist and
44 in this sense occupy their own niche. The authors found that niche stabilization increased species
45 persistence times compared with neutral assemblages. Given this extreme degree of stabilization,
46 the higher persistence is not surprising.

47 A niche for every species is unlikely in highly diverse systems such as tropical forests, where it
48 has been argued that the niches-to-species ratio can be low (Hunter and Foster, 1986; Holt, 2006).
49 Even in lower diversity systems, there is no clear evidence that all species can mutually invade
50 from low abundance. Empirical demonstration of frequency dependence is rare (Siepielski and
51 McPeck 2010, but see Adler et al. 2010; Chu and Adler 2015). On the other hand, there is evidence
52 suggesting competition increases with higher phenotypic similarity (Johansson and Keddy, 1991;
53 Jiang et al., 2010; Burns and Strauss, 2011). Models with this type of competitive structure predict
54 limits to similarity between species that can coexist in stable equilibrium; those outside these limits
55 are eventually excluded by stronger competitors (MacArthur and Levins, 1967). However, some
56 species are excluded faster than others, resulting in the spontaneous formation of transient clusters
57 of similar species (Scheffer and van Nes, 2006; Fort et al., 2009). In particular, those with the most
58 unfavorable traits might be excluded faster than under pure drift. Given a continuous supply of
59 immigrants, a neutral scenario may even sustain more species.

60 In addition to niche relations, other types of species differences also affect local dynamics.
61 Environmental filtering may cause non-stabilizing fixed differences in species growth and death rates,
62 which can dramatically change richness, persistence times, and abundance distributions relative
63 to neutrality (Zhou and Zhang, 2008; He et al., 2012). Furthermore, immigration will promote
64 local persistence of regionally common species over regionally rare ones. Although immigration can
65 stabilize communities as it pushes local relative abundances towards regional relative abundances, it
66 is conceptually different from stabilization caused by ecological advantages to rare species, i.e. niches.
67 One wonders whether the effects of niche differences on persistence are similar or fundamentally
68 different from those of species differences unrelated to niches.

69 Here we hypothesize that a local species assemblage where the number of niches available is less
70 than the number of species in the regional pool may have lower diversity and shorter persistence
71 times on average than a completely neutral community of the same size and subject to the same
72 propagule pressure. To test that hypothesis, we perform a simulation-based study of an open local
73 community under stochastic niche dynamics with a adjustable number of niches. We compare
74 species richness, persistence times, and extinction rates against a fully neutral assemblage. We then
75 see how results change when we add differences in regional abundances, immigration, and intrinsic
76 growth rates. Finally, we test how the number of niches affects comparison with neutrality.

77 **Methods**

78 **Simulated dynamics**

79 We use a lottery model to implement stochastic dynamics in a local community subject to immigration
80 from a regional pool. The local community has a fixed number of individuals, and in each time step
81 a single individual dies and is replaced by a new individual. When a death occurs, the probability
82 that it befalls species i is $\sum_j A_{ij} N_i N_j / \sum_{kl} A_{kl} N_k N_l$, where N_i is species i 's abundance and the
83 coefficient $A_{ij} > 0$ reflects the degree of competition between species i and j . The new recruit can
84 be either a local offspring with probability $1 - m$ or an immigrant from the regional pool with
85 probability m . If it is a local offspring, the probability that species i is chosen at this stage is
86 $r_i N_i / \sum_j r_j N_j$, where r_i is the intrinsic growth rate of species i . If the recruit is an immigrant,
87 species i is chosen with probability given by its relative abundance in the regional pool p_i , where
88 $\sum_i p_i = 1$.

89 If we set all $r_i = \text{constant}$ and $A_{ij} = 1$, then per capita birth and death probabilities are
90 the same across species and this model becomes identical to Stephen Hubbell's (2001) neutral
91 community model. Our model is an extension of Hubbell's model where we allow for species
92 differences, which appear as differences in the r_i and A_{ij} . The niche mechanism consists of the
93 map between species traits and the competition coefficients A_{ij} . We note that we are placing
94 density-dependent competitive effects on deaths, but preliminary tests revealed that none of our
95 results change qualitatively by placing them on births instead. We also note that our model is
96 similar to classical Lotka-Volterra dynamics, though in stochastic form. In fact, we numerically
97 verified that it yields the same qualitative behavior as a Gillespie implementation of stochastic
98 Lotka-Volterra dynamics (see Appendix S1).

99 By fixing community size, we can focus on the impact of competition; otherwise, fluctuations in
100 community size would also affect dynamics regardless of the competitive structure. To facilitate
101 comparison we use the same community size in all our scenarios. We set the local community size
102 at 21,000 individuals, which mirrors a typical real-world scenario of trees exceeding 10 cm diameter
103 at breast height in a 50-hectare plot of tropical forest (e.g., Barro Colorado Island, Pasoh Forest
104 Dynamics Plot). We also verified that using a different community size had no qualitative impact
105 on our results. Abundances in the regional pool, which contains 150,000 individuals and 400 species,

106 are either identical or follow a neutral logarithmic (log-series) distribution (Volkov et al., 2003).
107 Additional simulations verified that a larger regional pool had no impact on quantitative results.

108 We start the local community with a random draw of offspring from the regional pool, and then
109 simulate dynamics for 50 million death and replacement events, at which point species abundance
110 distributions appear stationary. We then run for another 50 million death and replacement events
111 while keeping track of all introduction and extirpation events, for a total of 100 million steps,
112 corresponding to roughly 5,000 community turnovers. At the end of a run, we measure species
113 richness, mean extinction rate, and species persistence times. The latter we calculate as the average
114 number of steps that each species remained in the local community between being introduced
115 through immigration and being extirpated due to competitive exclusion or drift. Given the low
116 variation in these indices across replicates of the same scenario (see Results), we decided that 10
117 replicates of each is sufficient.

118 Note that although we are measuring time in terms of events (death immediately followed by
119 replacement), we are not necessarily assuming constant intervals. If time is measured in terms of
120 days or years etc, there will be an exponential distribution of intervals between consecutive events
121 (assuming deaths follow a Poisson process). Approximating the rate of deaths per unit time as fixed,
122 the expected value of the relative persistence times measured in physical time units will be very
123 close to the relative persistence times measured in events.

124 All simulations were coded in the R computer language (version 3.4.1, R Core Team 2017).
125 The code is available at [https://github.com/rafaeldandrea/Persistence-Times-Code/blob/](https://github.com/rafaeldandrea/Persistence-Times-Code/blob/master/PersistenceTimesCode.r)
126 [master/PersistenceTimesCode.r](https://github.com/rafaeldandrea/Persistence-Times-Code/blob/master/PersistenceTimesCode.r).

127 Scenarios

128 We pin competition to phenotypic (trait) similarity by setting $A_{ij} = \exp\left[-\left(\frac{x_i - x_j}{w}\right)^4\right]$, where
129 $x_i = (i - 1)/400$ is the trait value of species i (traits range between 0 and 1). This is a commonly
130 used decreasing function of trait difference (Hernández-García et al., 2009; Pigolotti et al., 2010).
131 Another common choice is Gaussian competition, where the power 4 in the exponential function is
132 replaced with 2, but that has been shown to be mathematically idiosyncratic (Hernández-García
133 et al., 2009), and leads to very slow competitive sorting. The scale constant w determines how
134 quickly competition decreases with trait difference. When $w \approx 0$, each species competes only with

135 itself, corresponding to a case where each species has its own niche (complete niche differentiation).
136 In the opposite extreme $w \rightarrow \infty$, all species compete equally in the same single niche (neutral
137 competition). In between is partial niche differentiation, where there are fewer niches than species:
138 competition is stronger between more similar species, and only those sufficiently niche-differentiated
139 would be able to coexist in the absence of immigration.

140 By analogy with common statistical terminology for null and alternative hypotheses, we will refer
141 to communities lacking niche stabilization as H_0 assemblages, and those with niche stabilization
142 as H_1 assemblages. In terms of our parameters, H_0 assemblages have $w \rightarrow \infty$ and hence $A_{ij} = 1$
143 between all species pairs (neutral competition), whereas in our H_1 assemblages w is finite and A_{ij}
144 vary based on trait differences.

145 Table 1 describes all our scenarios and our corresponding hypotheses as to the impact caused
146 by the factor being varied. Our first scenario, termed the Baseline, isolates the impact of partial
147 niche differentiation by considering H_0 and H_1 assemblages where all species have identical regional
148 abundances and intrinsic growth rates, so that the only differences between species are niche
149 differences. Next we check how niche differences affect persistence when acting in concert with other
150 species differences that do not contribute to stable coexistence. In Variants 1 and 2, some species
151 immigrate more frequently than others because of differences in regional abundances. In Variants 3
152 and 4, some species have higher intrinsic growth rates than others because of physiological constraints
153 or environmental filtering. In Variant 2, we additionally test for the impact of immigration by giving
154 all species ten times the dispersal ability used in the rest of the study ($m = 0.1$ versus $m = 0.01$. As
155 a reference point, immigration rates at Barro Colorado Island are estimated at $m = 0.08$, Chisholm
156 and Lichstein 2009).

157 Finally, we look at the impact of varying the number of niches available to our 400 species. We
158 define the number of niches as the number of species that can coexist without immigration in the
159 deterministic formulation of our model. In all scenarios shown in Figs. 1 and 2 we set $w = 0.063$,
160 which leads to 12 niches and thus about 33 species per niche. By lowering parameter w we raise the
161 number of niches from 12 to 400 (1 species per niche, i.e. full niche differentiation). For this part,
162 we use Variants 1 and 2, where regional abundances are logarithmically distributed as in a neutral
163 metacommunity (Volkov et al., 2003). Results for Variant 1 (where $m = 0.01$) are shown in Fig. 3,
164 and results for Variant 2 (where $m = 0.1$) are shown in the supporting information.

165 Results

166 When regional abundances and intrinsic growth are identical across all species (Baseline scenario),
167 the assemblage with partial niche differentiation (H_1) stands in high contrast with the neutral
168 assemblage (H_0), as shown in Fig. 1. In H_0 , persistence times show no relation to species trait
169 values (Fig. 1A) and do not correlate with species abundances observed at the end of the simulation
170 (correlation index $\rho_{\log(N),\log(T)} = 0.008$). By contrast, in H_1 persistence times and species abundances
171 are highly non-random (Fig. 1B), and correlate strongly with each other ($\rho_{\log(N),\log(T)} = 0.86$, see
172 also Appendix S2: Fig. S1).

173 A distinctive pattern is seen along the trait axis: species lump together, and the lumps or
174 clusters are separated by gaps of low abundance (and corresponding low persistence times). This
175 clustered pattern occurs in all our simulations (see Appendix S2: Fig. S4-S6, S8), and indeed has
176 received attention in the recent literature on niche dynamics (Scheffer and van Nes, 2006; Holt, 2006;
177 Fort et al., 2009, 2010; Pigolotti and Cencini, 2013; D'Andrea and Ostling, 2016). We verified in
178 our simulations that if immigration is turned off, the clusters eventually disappear, and one species
179 remains per each cluster. Each cluster therefore represents a niche, and under immigration each
180 niche is occupied by more than one species. The residents are the species best adapted to their
181 niche, and are the ones that remain in the absence of immigration.

182 There is much higher variation in mean persistence time across species in the partially stabilized
183 assemblage than the neutral counterpart (Fig. 1C; also compare red curves in Figs. 1A and 1B).
184 The histogram of persistence times (Fig. 1C) reveals that (i) a few species in H_1 but none in H_0 are
185 residents, i.e. were present throughout the tracking period of the simulation, never going extinct;
186 (ii) the vast majority of species in H_1 not only are transient but in fact have lower persistence
187 times than in H_0 . Residents benefit from stabilization and can in principle remain indefinitely
188 (barred stochastic fluctuations), thus heavily driving mean persistence times in H_1 . Indeed if
189 residents are discounted, the average persistence time in H_1 drops from higher to lower than the
190 neutral assemblage (Fig. 1D). Importantly, the outsize influence of residents on community-averaged
191 persistence times does not translate to higher diversity or lower extinction. In fact, both species
192 richness and community-averaged extinction rates are lower in the partially stabilized assemblage
193 than under neutrality, whether or not residents are accounted for (Fig. 1D).

194 When some species are more abundant than others in the regional pool causing differences in
195 immigration rates (Variant 1), the persistence time distribution shifts towards the extremes (Fig.
196 2A and 2E): on one hand, transients have shorter persistence times compared to when the pool
197 is homogeneous; on the other hand, the neutral community now also has residents, and in H_1 the
198 number of residents is higher than before. These new residents arise not from stabilization but
199 because of their comparatively high regional pool abundance (Appendix S2: Fig. S2). As a result,
200 H_0 and H_1 now have more similar distribution of persistence times than in the Baseline scenario
201 (compare Fig. 2A, 2E).

202 Keeping the differences in regional abundances and increasing immigration tenfold (Variant
203 2), we see most persistence times increase and many species become residents in both H_0 and H_1
204 assemblages (Figs. 2B, 2F, compare with Figs. 2A, 2E). A few species now have actually lower
205 persistence times due to regional rarity. Overall, regional abundances become stronger determinants
206 of persistence times compared with the lower immigration scenario. Again, H_0 and H_1 communities
207 are more similar to each other than in the Baseline scenario (compare Figs. 2B and 2E). It should
208 be noted that although high immigration may make the persistence time distributions essentially
209 indistinguishable, niche differentiation still influences which species are residents (Appendix S2:
210 Fig. S3). We also note that a comparable increase in immigration when the pool is homogeneous
211 trivially makes all species residents in both the H_0 and H_1 assemblages (results not shown).

212 The introduction of intrinsic growth advantages to species with intermediate trait values (Variant
213 3) dramatically lowers persistence times for most species in H_0 compared to the Baseline, while
214 promoting those few species with the highest intrinsic growth to resident status (compare pale- and
215 dark-colored bars in Fig. 2C). The effects on the H_1 assemblage are more subtle, with persistence
216 times actually increasing for several species (Fig. 2G), and correlating negatively with intrinsic
217 growth ($\rho_{r, \log T} = -0.2$, see also Appendix S2: Fig. S4). However, the qualitative shape of the H_1
218 persistence time distribution is unchanged, indicating that intrinsic growth rates have a small effect
219 on H_1 exclusion dynamics relative to frequency-dependent competition. Again, the H_0 and H_1
220 persistence time distributions become less distinguishable compared with the baseline where all
221 intrinsic growth rates are identical (compare Figs. 2C and 2G).

222 Differences in intrinsic growth rates that are unconnected to the niche-related trait (Variant 4)
223 shorten the persistence times of almost all species in both the H_0 and H_1 assemblages, but once

224 again the effect is much stronger on the assemblage lacking stabilization (Fig. 2D, 2H). As with
225 previous variants, niche and neutral communities are more similar than in the Baseline.

226 In summary, differences in regional abundances and intrinsic growth have a qualitatively similar
227 effect on persistence times as niche differentiation: persistence times of most species is very short,
228 while those of a few species is indefinitely long. As a result, the persistence time distribution is
229 qualitatively similar whether or not niche differentiation is present. On the other hand, relative to
230 the Baseline scenario where all regional abundances and intrinsic growth rates are identical, the effect
231 is much stronger on H_0 communities than H_1 communities (compare the dark- and light-shaded
232 bars in the top and bottom rows of Fig. 2).

233 As we increase the number of niches while keeping regional diversity fixed, all our biodiversity
234 metrics improve from worse to better than in the neutral community (Fig. 3). In particular, as
235 fewer species compete for the same niche tending towards full niche differentiation (one species to
236 one niche, on the left end of the graph), extinction tends to zero and richness escalates. Persistence
237 times increase dramatically. Most of the improvement stems from the larger number of residents;
238 persistence across transients also improves, but more slowly (compare blue and black curves in Fig.
239 3, see also Appendix S2: Fig. S5).

240 We note that the specific degree of stabilization required for higher persistence in the H_1
241 assemblage depends on the particulars of the community, such as immigration rates and niche
242 axis geometry (Appendix S2: Fig. S6, S7), but the qualitative results are the same: biodiversity
243 maintenance can be actually lower in a community with niches compared with a neutral community,
244 unless the number of niches is sufficiently high.

245 Discussion

246 By building on the framework of neutral models (Alonso et al., 2006), our study sheds light on
247 biodiversity maintenance in an open community where species similarity bears competition and
248 the number of species exceeds the number of niches. Partial niche differentiation stabilizes species
249 abundances and may indefinitely prolong local persistence times of certain species, but at the
250 community level it does not guarantee higher richness, longer persistence times, or lower extinction
251 rates. Differences in regional abundances and intrinsic growth rates also affect dynamics, having

252 a bigger impact on the assemblages lacking stabilization entirely. This showcases the robustness
253 of stabilized assemblages against other dynamical forces, in contrast with the susceptibility of
254 neutral dynamics. On the other hand, those species differences have a qualitatively similar impact
255 on persistence times as niche differences: most species go out fast while a few last indefinitely.
256 Moreover, high immigration blurs the dynamical differences between stabilized and non-stabilized
257 communities. We conclude that niche differentiation can raise or lower richness, persistence, and
258 extinction, depending on a series of factors examined in this study, and the effect is qualitatively
259 similar to other types of species differences. It follows that these indices alone cannot distinguish
260 between neutral and partially stabilized dynamics, unless one knows sufficient details about the
261 community of interest to parametrize the niche model.

262 We note that the niche axis in our model is finite, and hence has edge effects. Although some
263 modelers use circular axes to avoid this, we reckoned a finite linear axis is more realistic. In a
264 highly symmetric case like our Baseline scenario where the only differences between species are niche
265 differences, circularity drastically dampens the influence of niches on persistence times (Appendix
266 S2: Fig. S6). This is because the positions of the niches on a finite axis are set, whereas on a circular
267 axis they constantly shift through time, thus mitigating the effects of stabilization. However if other
268 asymmetries occur, such as differences in regional abundances, the effect of circularity disappears
269 (Appendix S2: Fig. S7), making the choice of a finite or circular axis inconsequential. Also, for the
270 reader interested in the common choice of exponent 2 as opposed to 4 in the competition coefficients
271 A_{ij} , we show in the supporting information (Appendix S2: Fig. S8) that the persistence time
272 distribution in that model is much closer to neutrality (even on a finite axis). This is not surprising
273 given the slower and weaker exclusion dynamics.

274 Our niche model shows a distinctive pattern of abundances by traits, mirrored by a similar
275 pattern of persistence times: species are organized in clusters and separated by gaps; those at the
276 center of the clusters are the residents and those at the gaps are the shortest-living transients. Each
277 cluster is a group of species competing for the same niche, and in the absence of immigration only
278 one species remains in each niche. Clusters are a recent extension of classical ideas of limiting
279 similarity (MacArthur and Levins, 1967; Scheffer and van Nes, 2006; Holt, 2006; Pigolotti and
280 Cencini, 2013). Fort et al. (2009) showed mathematically that they arise as a transient state on any
281 deterministic niche model with a circular axis and competition tied to species similarity. Our model

282 is similar but adds demographic stochasticity, immigration, and a finite axis. Clusters have been
283 seen under these circumstances before (Barabás et al., 2013), and we recently proposed that they
284 are a general outcome of niche-axis models (D’Andrea and Ostling, 2016).

285 Note that while not all species have enhanced persistence under partial stabilization, the number
286 of species that do is higher than the number of niches. In other words, it is not the case that only
287 those species with a niche have enhanced persistence relative to neutrality. As we emphasized, the
288 particular number will depend on immigration, regional abundances, environmental filtering, and
289 the map between species traits and degree of competition.

290 In our study we did not account for temporal changes in environmental conditions which may
291 affect competitive interactions and intrinsic growth rates. Environmental stochasticity in neutral
292 models has been recently shown to be an important driver of species abundances (Kalyuzhny et al.,
293 2015; Chisholm et al., 2014), and therefore presumably also of persistence times. It would be an
294 interesting next step to test its effects on stabilized assemblages.

295 Our results are compatible with real-life observations of “core” species that persist for long
296 times and “occasional” populations that regularly undergo local extinction and recolonization events
297 (Magurran and Henderson, 2003). Magurran and Henderson found that occasional species in their
298 study typically had different habitat requirements than core species, which suggest their differences
299 in persistence arise from filtering effects analogous to Variants 3 and 4 in our model (Fig. 2C).
300 However, the division between core and occasional species they find does not line up exactly with
301 habitat requirements. This could occur under either neutral or niche dynamics. Core species may
302 last longer simply on account of their higher regional and local abundance, but our results show
303 how they could also be the beneficiaries of niche stabilization.

304 Upon finding that the estimated levels of immigration on Barro Colorado Island are compatible
305 with neutrality given its observed richness, Condit et al. (2012) wrote that “species interactions,
306 niche partitioning, or density-dependence, while they may be present, do not appear to enhance tree
307 species richness at Barro Colorado.” Our findings confirm that the connection between immigration
308 and resulting richness is not unique to process, implying that Condit et al.’s observations are
309 potentially also compatible with niche differentiation, and indeed that it is possible for niche
310 partitioning to be present while not enhancing richness.

311 In general, insight into whether persistence dynamics are shaped by niches in nature will require
312 more extensive data than collected by Magurran (2003) or Condit et al. (2012). The effect of
313 trait differences on species persistence must be teased apart from the effect of regional and local
314 abundances to achieve such inference.

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410 258.

Tables and Figures

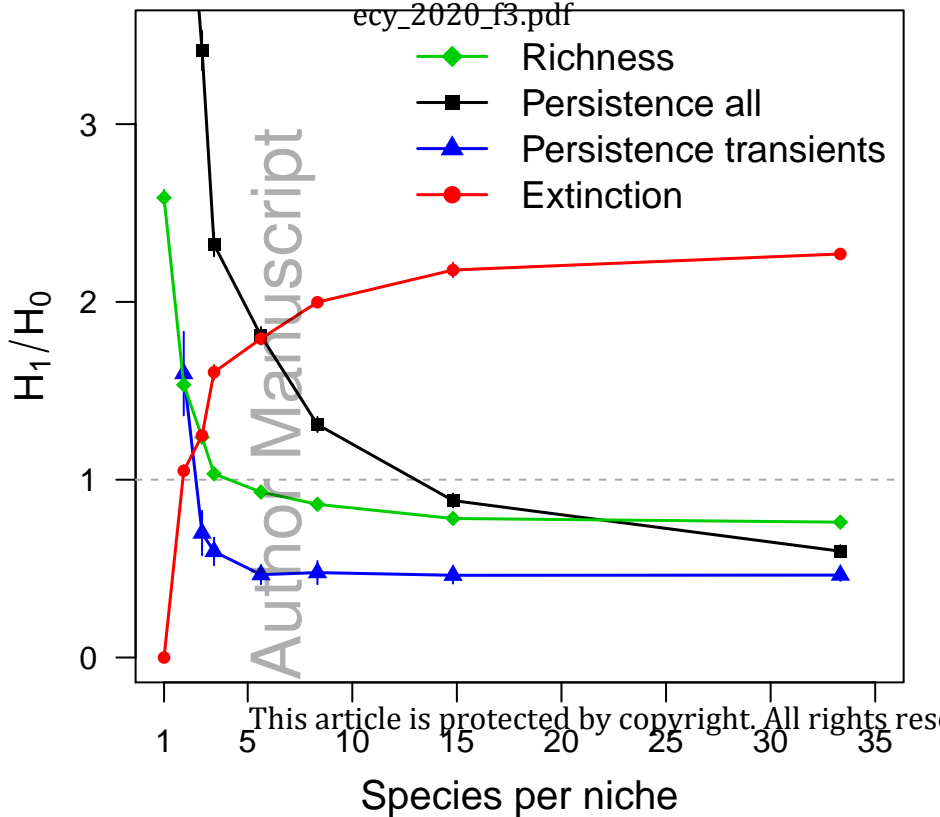
Table 1: Variants 1 through 4 are identical to the baseline scenario except where indicated in the Description and Parameters columns. Settings are applied to both the neutral (H_0) and niche (H_1) simulations where applicable.

Scenario	Description	Parameters	Hypothesis
Baseline	Isolate differences between neutral competition (H_0) and partial niche differentiation (H_1).	$p_i = \text{const.}$ $r_i = \text{const.}$ $m = 0.01$ $w = 0.063$	Some species in H_1 will have enhanced persistence and others lessened persistence relative to H_0 .
Variant 1	Some species are more abundant than others in regional pool \rightarrow Inhomogeneous immigration.	$p_i \sim \text{log-series}$	Even in H_0 , some species will be more prone to extinction than others due to lower rescue effect. Outcomes of H_0 and H_1 will be more similar than in Baseline.
Variant 2	Same as Variant 1 but species have higher dispersal ability \rightarrow Higher immigration.	$p_i \sim \text{log-series}$ $m = 0.1$	Higher immigration increases persistence times and magnifies the effects of regional abundances relative to internal dynamics. Outcomes of H_0 and H_1 even more similar than in Variant 1.
Variant 3	Metabolic costs or other physiological limitations cause lower intrinsic growth of species with extreme trait values.	$r_i = x_i(1 - x_i)$	Species with higher intrinsic growth will have higher persistence and lower extinction rates. Effect is stronger on H_0 assemblage, bringing H_0 outcomes closer to H_1 than in Baseline.
Variant 4	Intrinsic growth rates are determined by factors unrelated to the niche trait, such as environmental filtering for unrelated traits.	$r_i \sim U(0, 1)$	Qualitatively similar impact as Variant 3.

412 **Figure 1. A, B:** Species abundances and persistence times plotted against relative trait values
 413 in an example H_0 assemblage (**A**) and H_1 assemblage (**B**). Stems show $\log N / \log N_{max}$, where N
 414 are species abundances and N_{max} is the highest abundance observed. Red lines show $\log T / \log T_{max}$,
 415 where T are species mean persistence times and $T_{max} \simeq 24,000$ community turnovers is the maximum
 416 possible persistence time, corresponding to our entire tracking period (1 community turnover =
 417 21,000 simulation steps). **C:** Number of species by mean persistence time, $\log T / \log T_{max}$, in
 418 the baseline assemblages with no stabilization (H_0 , blue bars) and partial stabilization (H_1 , red
 419 bars). Shown are averages across ten replicates. Error bars show standard error of the mean. **D:**
 420 Comparison of species richness, community-averaged persistence time, and community-averaged
 421 extinction rates between baseline H_1 and H_0 assemblages. Bars show average ratio H_1/H_0 across
 422 ten replicates, error bars show standard error of the mean.

423 **Figure 2.** Comparison of persistence time distribution, $\log T / \log T_{max}$, between baseline (pale
 424 colors) and variant scenarios (dark colors) as described in Table 1. Top row shows H_0 assemblages,
 425 bottom row shows H_1 assemblages. Results shown are averaged across ten replicates of each scenario,
 426 with error bars showing the standard error of the mean. **A, E:** species have random, logarithmically
 427 distributed regional abundances, independent of trait values; **B, F:** logarithmically distributed
 428 regional abundances and higher immigration rate ($m = 0.1$); **C, G:** intrinsic growth rates r_i peak
 429 at the center of the axis and drop to zero at the edges; **D, H:** species have random, uniformly
 430 distributed r_i values, independent of trait values.

431 **Figure 3.** Comparison of richness, community-averaged persistence times, and community-
 432 averaged extinction rates between neutral assemblages (H_0) and partially differentiated assemblages
 433 (H_1) with increasing number of niches and fixed regional diversity. Data points show the ratio
 434 between the H_1 and H_0 assemblages, error bars show one standard error of the mean, calculated
 435 across 10 replicates. Persistence times are shown averaged across all species in the community
 436 (black) and across transients (blue). As the number of niches increases from 12 to 400, the number
 437 of species per niche decreases from 33 to 1 species per niche. All measured quantities cross the
 438 neutral value (dashed gray line) at different points. In the limit of full niche differentiation (one
 439 species per niche), extinction is zero and local persistence and richness are maximal. Regional
 440 abundances are logarithmically distributed, while all other parameters are set as in the Baseline
 441 scenario (Variant 1, see Table 1. Compare similar plot for Variant 2 in Appendix S2: Fig. S7).



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