

1 **Effects of compositional heterogeneity and**
2 **spatial autocorrelation on richness and diversity**
3 **in simulated landscapes**

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5 **Abstract**

6 Landscape structure plays a key role in mediating a variety of ecological processes affecting bio-
7 diversity patterns, however its precise effects and the mechanisms underpinning them remain
8 unclear. While the effects of landscape structure have been extensively investigated both empiri-
9 cally, and theoretically from a metapopulation perspective, the effects of spatial structure at the
10 landscape scale remain poorly explored from a metacommunity perspective. Here, we attempt
11 to address this gap using a spatially explicit, individual-based metacommunity model to explore
12 the effects of landscape compositional heterogeneity and *per se* spatial configuration on diversity
13 at the landscape and patch level via their influence on long term community assembly processes.
14 Our model simulates communities composed of species of annual, asexual organisms living, re-
15 producing, dispersing, and competing within grid-based, fractal landscapes which vary in their
16 magnitude of spatial environmental heterogeneity and in their degree of spatial environmental
17 autocorrelation. Communities are additionally subject to temporal environmental fluctuation
18 and external immigration, allowing for turnover in community composition. We found that com-
19 positional heterogeneity and spatial autocorrelation had differing effects on richness and diversity
20 and the landscape and patch scales. We also note a slight negative effect of compositional het-
21 erogeneity on median total landscape population size. Landscape level diversity was driven by
22 community dissimilarity at the patch level and increased with greater heterogeneity, while land-
23 scape richness was largely the result of short-term accumulation of immigrants and decreased
24 with greater compositional heterogeneity. Both richness and diversity decreased in variance with

25 greater compositional heterogeneity, indicating a reduction in community turnover over time.
26 Patch-level richness and diversity patterns appeared to be driven by overall landscape richness
27 and local mass effects, resulting in maximum patch level richness and diversity at moderate levels
28 of compositional heterogeneity and high spatial autocorrelation.

29 **Introduction**

30 Land-use change and habitat destruction remain the principle drivers of biodiversity loss today
31 (Newbold et al., 2015; Ellis, 2021; Davison et al., 2021). A major consequence of the two processes
32 is the alteration of the structure of landscapes by changing the types of environments present in
33 the landscape (composition) and by changing the spatial arrangement of those environment types
34 (configuration) (Fahrig, 2003). Landscape structure mediates a large variety of evolutionary and
35 ecological processes such as adaptation and community assembly through its effects on the move-
36 ment and dispersal of organisms (Holt and Barfield, 2011; Tschardt et al., 2012; Forester et al.,
37 2016; Zarnetske et al., 2017; Fahrig, 2020) and thus has important implications for biodiversity
38 conservation. A thorough understanding of the role of landscape structure in mediating these
39 processes is therefore critical to developing effective conservation strategies (Sanderson et al.,
40 2002; Rodewald and Arcese, 2016).

41 Landscape structure has received considerable research attention in recent decades. While
42 greater compositional complexity is expected to result in a larger overall diversity of species
43 (Tews et al., 2004; Stein et al., 2014), the effects of landscape spatial configuration on diversity
44 have been subject to considerable debate (Villard and Metzger, 2014; Hanski, 2015; Fletcher Jr
45 et al., 2018; Fahrig et al., 2019; Semper-Pascual et al., 2021). Configurational effects on diversity
46 have typically been investigated in the context of biodiversity conservation in the face of habitat
47 fragmentation. Habitat fragmentation has traditionally been viewed as negative for biodiversity
48 based on island biogeography and metapopulation theory predictions. Habitat fragmentation is
49 expected to reduce species richness by reducing habitat patch size, and splitting species pop-
50 ulations into smaller, more isolated sub-populations thereby increasing the per patch risk of
51 extinction and reducing the frequency of recolonization (MacArthur and Wilson, 1967; Hanski,
52 1998; Hill and Caswell, 1999). The conclusion that habitat fragmentation is generally negative
53 for biodiversity has been challenged on the grounds that many studies on habitat fragmenta-
54 tion measure effects only at the patch scale and do not effectively discriminated between effects
55 resulting from habitat loss and effects of the spatial arrangement itself (fragmentation *per se*)
56 (McGarigal and Cushman, 2002; Fahrig, 2003; Tschardt et al., 2012; Arroyo-Rodríguez et al.,
57 2017). Indeed, when total habitat area is controlled for, biodiversity responses to fragmentation
58 are often either non-significant or positive (Tschardt et al., 2012; Fahrig, 2017). This apparent

59 lack of a consistent negative effect on species richness has led to the proposal that total habitat
60 amount is the primary determinant of diversity with configuration playing only a minor role
61 (Fahrig, 2013; Watling et al., 2020). This hypothesis has been disputed on the basis of conflicting
62 empirical evidence (Hanski, 2015; Haddad et al., 2017), as well as due to the lack of a mechanistic
63 explanation (Hanski, 2015). Other authors have pointed out that habitat amount and spatial
64 configuration can interact in a variety of complex ways to influence diversity (Boeye et al., 2014;
65 Villard and Metzger, 2014; Rybicki et al., 2020; Püttker et al., 2020).

66 While the effect of landscape structure on biodiversity has been extensively investigated em-
67 pirically, the majority of empirical studies on landscape structure are observational studies which
68 rely fundamentally on correlative approaches and thus can reveal statistical associations, but can-
69 not give direct insight into causal mechanisms underpinning the patterns they observe (Hanski,
70 2015; Ovaskainen et al., 2019). Mechanistic modeling approaches have the advantage of allowing
71 direct control over compositional and configurational structure as well as ecological mechanisms,
72 thus permitting detailed experiments which can provide direct insight into causal mechanisms
73 (Higgins et al., 2012; Hanski, 2015; Cabral et al., 2017). Numerous modeling studies have in-
74 vestigated the impacts of landscape structure from a metapopulation perspective (e.g. Hill and
75 Caswell, 1999). These models often explicitly consider spatial structure, but only consider pop-
76 ulations of a single species. Conclusions regarding community level processes drawn from such
77 studies are thus based on extrapolation from the species to community level. This approach
78 is problematic because different processes acting at different levels of organization can produce
79 counter-intuitive patterns (McGill, 2019). Metacommunity models consider multiple interacting
80 species, but metacommunity modeling simulation studies investigating biodiversity often do not
81 explicitly consider spatial structure or consider it only in very simplified forms with no explic-
82 itly defined spatial geometry (Biswas and Wagner, 2012; Ryberg and Fitzgerald, 2016; Zarnetske
83 et al., 2017; Ai and Ellwood, 2022), while those that do often model landscapes as islands of habi-
84 tat embedded in a homogeneous, typically uninhabitable matrix (e.g. Thompson et al., 2017;
85 Firkowski et al., 2022). Such an assumption is problematic for terrestrial landscapes where stark,
86 abrupt shifts in environmental conditions over space are rare and few areas of the landscape can
87 be said to be truly uninhabitable. Indeed, many species exploit multiple habitat types (Hein
88 et al., 2003; Jules and Shahani, 2003) and different species living within the same habitat may
89 vary considerably in their their tolerance for environmental variation and thus may have different
90 perceptions of what is habitat and non-habitat (Prevedello and Vieira, 2010). It may thus be
91 more appropriate in many cases to model landscapes as habitat mosaics or as fractal environmen-
92 tal gradients (Fischer and B. Lindenmayer, 2006; Franklin and Lindenmayer, 2009; Matthews,
93 2021), but this is not commonly done (but see Münkemüller et al., 2012).

94 Here, we attempt to address this gap using a spatially explicit, individual-based metacom-

95 munity model to systematically explore the effects of landscape structure on patterns of species
96 richness and diversity via their influence on long term community assembly processes. Specifi-
97 cally, we ask how varying the strength of compositional heterogeneity and environmental spatial
98 autocorrelation affects patterns of species richness and diversity at the landscape and patch level.
99 Our model simulates communities composed of species of annual, asexual organisms living, repro-
100 ducing, dispersing, and competing within continuous grid-based fractal landscapes which vary in
101 their magnitude of spatial environmental heterogeneity and in their degree of spatial environmen-
102 tal autocorrelation. Communities are additionally subject to temporal environmental fluctuation
103 and external immigration, allowing for turnover in community composition. Our model produces
104 output data covering "taxonomic" richness and diversity of simulated organisms as well as data
105 on organism niches, fitness, and dispersal behavior. This study, however, will focus specifically
106 results relating to taxonomic richness and diversity.

107 **Model Description**

108 We constructed a spatially explicit, individual-based model, implemented in Julia 1.1.1 (Bezanson
109 et al., 2012), simulating communities of asexual organisms with varying environmental niches and
110 dispersal tendencies in a grid-based landscape of patches with varying environments, based on
111 the model developed by Sieger and Hovestadt (2020). Our model makes several extensions to
112 this framework, including the addition of a second patch environment attribute, as well as the
113 inclusion of two dispersal modes.

114 **Landscape properties**

115 Landscapes consist of spatially autocorrelated toroidal grids of habitat patches generated via and
116 R implementation of the toroidal landscape generation algorithm from (Saupe, 1988). Landscapes
117 dimensions were set at 20 patches by 20 patches for a total of 400 patches per landscape. These
118 dimensions were chosen in order to limit computation time while still being large enough for
119 structure driven patterns to emerge. Landscapes possess two independent spatially variable
120 environmental attributes, one representing patch temperature (T) and a second attribute H
121 representing an additional, unspecified abiotic environmental variable (e.g. a soil property). The
122 degree of spatial autocorrelation of patch environment attributes is determined by the Hurst index
123 parameter during landscape generation. In this study, all landscapes have a Hurst index value of
124 either 0 or 1. In addition to varying spatially, T also fluctuates globally over time, with a mean
125 fluctuation of 0 and a standard deviation of 1. Temporal fluctuations are normally distributed
126 with a standard deviation of 1. Baseline patch attribute values are approximately normally
127 distributed and were standardized to a standard deviation of 1 and a mean of approximately

128 0 by multiplying each the attributes of each patch by 1 over the standard deviation of patch
129 attributes and then calculating the landscape’s mean attributes and subtracting the mean from
130 each patch. The standard deviation can be further modified by gradient strength multiplier G ,
131 which can be used to expand or reduce the range of patch attribute values.

132 **Organism properties**

133 Patches are inhabited by populations of asexual organisms which belong to species which are
134 distinguished from one another by their environmental niches and by their dispersal tendencies.
135 These species behave as a guild of ecologically similar species which compete with each other
136 within a patch. Organism niches are modeled as a Gaussian curve whose center and spread
137 are defined by the niche optimum and tolerance traits. Organisms have optimum and tolerance
138 traits for both patch environment attributes. Organisms also possess two traits which define their
139 dispersal behavior, an emigration probability trait defining the chance of an organism emigrating
140 from its natal patch, and a trait defining the organism’s probability of dispersing via random
141 global dispersal versus nearest neighbor dispersal. Organism traits are summarized in table 1.
142 Organism traits are initialized by randomly by drawing from a distribution. Niche optimum
143 traits are drawn from a normal distribution with a μ of 0 and σ equal to G . Tolerance traits are
144 drawn from a log normal distribution with a μ and σ of 0 and 1 respectively. Dispersal traits are
145 drawn from a uniform distribution with a minimum of 0 and a maximum of 1.

146 **Organism life-cycle**

147 Organisms have annual life cycles with complete replacement of the population at the end of a
148 generation. Life cycles consist of discrete reproduction, competition, and dispersal phases (Figure
149 2). During the reproductive phase, organisms reproduce asexually to produce offspring with
150 identical traits to their parents. The number of offspring is drawn from a Poisson distribution,
151 with the expected reproductive output determined by an organism’s fitness within its patch
152 environment within a given time step as given by equation 1. Here, E_{fert} is the expected number
153 of offspring, R_0 is an organism’s intrinsic maximum expected offspring (kept at a constant value
154 of 15), T_{patch} and H_{patch} are the temperature and habitat values for a given patch. Reproductive
155 output is additionally limited by a trade-off between niche breadth and maximum expected
156 offspring, the strength of which is determined by the trade-off parameter a . (Chaianunporn and
157 Hovestadt, 2012; Sieger et al., 2019); lower values produce stronger trade-offs. As the effect
158 of varying a is functionally the same as the effect of varying the strength of G , a is kept at
159 a constant value of 3 in this study. After reproduction, offspring undergo a maturation phase
160 in which they compete on an equal basis with other offspring within the same patch. Survival
161 of the competition phase is density dependent and regulated via the Beverton-Holt equations

162 (Equations 2. and 3.; Beverton & Holt 1957), where S_A is the expected surviving offspring, L_0 is
 163 the total offspring, and K is the carrying capacity of a patch if all organisms in the patch have an
 164 E_{fert} equal to R_0 and thus perfect fitness. Note that because patch carrying capacity is affected
 165 by E_{fert} , maladaptation may reduce the realized carrying capacity of a patch. The value of K
 166 is set at 150 individuals, which allows for relatively stable patch populations while maintaining
 167 low computation time. The number of surviving offspring are determined by drawing a random
 168 number from a binomial distribution with a mean of S_A . Surviving offspring are then able to
 169 disperse to a new patch and start the cycle anew.

$$E_{fert} = R_0 \cdot e^{\frac{-(T_{patch}-T_{opt})}{2T_{sd}^2}} \cdot e^{\frac{-(H_{patch}-H_{opt})}{2H_{sd}^2}} \cdot e^{\frac{-T_{sd}}{2\alpha^2}} \cdot e^{\frac{-H_{sd}}{2\alpha^2}} \quad (1)$$

$$S_A = \frac{1}{1 + a \cdot L_0} \quad (2)$$

$$a = \frac{R_0 - 1}{K \cdot R_0} \quad (3)$$

170 Dispersal

171 Mature organisms can disperse to other patches in the landscape by two different methods, nearest
 172 neighbor dispersal or random global dispersal. In nearest neighbor dispersal, the organism moves
 173 to an adjacent patch with the coordinates $x + p$ and $y + q$, where p and q are integers between
 174 -1 and 1. If the destination patch's coordinates are outside the bounds of the landscape, the
 175 dispersing organism is instead moved to the opposite side of the landscape. In random global
 176 dispersal, the organism is moved to a random patch in the landscape. Whether or not an organism
 177 disperses and its mode of dispersal are determined by drawing a random number from a uniform
 178 distribution and checking whether it is less than or equal to P_{disp} . If the organism disperses,
 179 another random number is drawn from a uniform distribution and compared with P_{global} to
 180 determine whether the organism uses nearest neighbor or random global dispersal.

181 Immigration from external sources

182 New organism species can immigrate into the landscape from the outside. The number of new
 183 immigrants is randomly drawn from a Poisson distribution with an expected value of E_{immi} . In
 184 our simulations, E_{immi} is set at a constant expected value of 2.5 immigrants per patch. This
 185 amounts on average to approximately 0.0011% of the expected local offspring production for a
 186 patch with a perfectly adapted population at carrying capacity. Immigrants are generated with
 187 randomized traits within a patch and added to the new generation along with existing offspring.
 188 Since immigrants arrive in the landscape from places which may have considerably different

189 environmental conditions, immigrant niche optima are drawn from broader distributions than
190 those used for initialization. Distribution parameters for immigrant traits are summarized in
191 table 2.

192 Initialization and experiment design

193 Landscapes are initialized from text file inputs containing the T and H values for each patch.
194 Landscapes are uninhabited at initialization and can be colonized by immigrant species over the
195 course of the simulation. We ran simulations over two sets of 30 landscapes, one set generated
196 with a Hurst index of 1 and the other generated with a Hurst index of 0. These simulations
197 were repeated for eight different values of G ($G \in 0, 0.05, 0.1, 0.3, 0.7, 1, 1.3, 1.7$), resulting in a
198 total of 16 scenarios with 30 replicates each. Simulations were run for 10,000 time steps. Model
199 parameters are summarized in table 3. Data on landscape total population size, richness, and
200 Shannon-Wiener diversity were recorded for every time step of the simulation for a combined
201 total of 300,000 observations for each combination of Hurst index and G . Data on the individual
202 organisms, the patches they inhabit, and their species were recorded at the end of the final time
203 step of the simulation. Patch level statistics calculated from data on individuals for population
204 size, richness, and Shannon-Wiener diversity for a combined total of 12,000 observations for
205 each combination of Hurst index and G . Replicates were numbered 1 through 30. The replicate
206 numbers were used as random number generator seeds to ensure replicability.

207 Analysis

208 Data visualization was performed in R 3.6.3 (R Core Team, 2020) using the ggplot2 package
209 (Wickham, 2016). We did not perform any statistical significance tests as such tests are not
210 useful or meaningful in the context of mechanistic modeling due to the extreme sensitivity of
211 such tests to small differences when used with a very large numbers of observations (White et al.,
212 2014). Instead, results were assessed visually via plots. We assessed landscape-level patterns
213 via the distribution of landscape richness and Shannon-Weiner diversity between the 5000th and
214 10,000th time steps, and patch-level patterns via the distribution of patch richness and Shannon-
215 Weiner diversity at the end of the simulation.

216 Results

217 Landscape total population rapidly increases within the first 50 time steps, settling into a stable
218 median slightly below the landscape carrying capacity of 60000 individuals (150 individuals per
219 patch) around which it fluctuated. Median total population declined slightly with increasing G
220 at both the landscape and patch levels (Figure 3). Richness and diversity at both the landscape

221 and patch level responded to both compositional heterogeneity and spatial autocorrelation, with
222 differing responses occurring at the landscape at patch levels (Figure 4). Responses to composi-
223 tional heterogeneity were non-linear in all cases with notable shifts typically starting at $G=0.1$.
224 At the landscape level, median richness decreased with increasing G starting at $G=0.1$, declin-
225 ing relatively steeply at first with diminishing declines beyond $G=0.7$. From $G=0.7$ onwards, a
226 slight difference emerges between Hurst index scenarios with Hurst index=0 scenarios showing
227 showing higher landscape richness. Landscape diversity showed an opposing pattern, increas-
228 ing in median value with greater G , rapidly at first with increases diminishing beyond $G=0.7$.
229 The precise relationship between landscape diversity and G was affected by spatial autocorre-
230 lation. Below $G=0.1$, landscape diversity was higher in Hurst index=1 scenarios, while above
231 this threshold, landscape diversity was higher in Hurst index=0 scenarios. Patch richness and
232 diversity were unimodal in relation to G , peaking at $G=0.3$ and gradually declining thereafter.
233 This pattern was notably pronounced for patch diversity, while for patch richness the response to
234 G was more muted. Median patch diversity was consistently higher in Hurst index=1 scenarios,
235 while a similar though less consistent pattern occurred with patch richness.

236 Discussion

237 Our simulation results showed that landscape structure had differing effects at the landscape and
238 patch levels resulting from different processes acting at different scales. Total population size
239 was slightly negatively affected by compositional heterogeneity. This was expected due to the
240 greater chance for niche mismatches in dispersing organisms in high heterogeneity, resulting in
241 more inconsistent individual fitness and a reduction in realized patch carrying capacities. Land-
242 scape level diversity in this model resulted from community dissimilarity at the patch-level due
243 to greater environmental heterogeneity and more fragmented spatial configuration. This finding
244 aligns with the predictions of the dominance of β -diversity hypothesis (Tscharntke et al., 2012)
245 and with empirical studies finding heterogeneity driven β -diversity to be an important driver of
246 landscape-scale diversity (Quinn and Harrison, 1988; Tscharntke et al., 2002; Clough et al., 2007;
247 Kessler et al., 2009; Wintle et al., 2019). The increase in diversity occurred despite a pattern
248 of decreasing landscape-level richness in relation to environmental heterogeneity. Likewise, we
249 found different patterns for landscape-level and patch-level richness and diversity, similar to pre-
250 vious empirical research documenting contrasting biodiversity patterns at different scales (Chase
251 and Leibold, 2002; Hendrickx et al., 2007; Flohre et al., 2011; Tello et al., 2015; Gao et al., 2021).
252 Richness and diversity patterns at the patch level appear to be primarily related to overall land-
253 scape richness (Tscharntke et al., 2012) and the strength of mass effects resulting from spillover
254 from neighboring patches (Leibold et al., 2004). Our model demonstrates that these patterns

255 and processes can result from the combined effects of spatial autocorrelation and increasing sub-
256 division of the landscape among different environments on rates of successful colonization and
257 extinction. These findings have potentially important implications for biodiversity conservation
258 as they suggest that there may be a trade-off in optimizing the design of biodiversity reserves for
259 diversity at the patch versus landscape level.

260 Increasing the compositional heterogeneity of a landscape increases the number of distinct
261 environmental conditions in the landscape. The increasing range of environments in the land-
262 scape increases the number of environment types available for organisms to exploit while also
263 imposing increasing fitness costs for generalist organisms and increasing the risks of dispersal
264 (Hastings 1983). Increasing compositional heterogeneity thus results in increasingly distinct lo-
265 cal communities and increasingly local competition. This effect can be further compounded by
266 highly fragmented spatial configurations, which may restrict organisms from colonizing all of
267 their available habitat (Bascompte and Solé, 1996; Hill and Caswell, 1999; McNerny et al., 2007)
268 and prevent competitors from interacting with each other (Boeye et al. (2014)), thus slowing
269 or preventing competitive exclusion. Taken together, these effects may account for the higher
270 diversity and the tendency toward slightly higher richness in landscapes with low spatial autocor-
271 relation, as well as the lower patch-level diversity and the tendency toward lower patch richness
272 in highly heterogeneous landscapes. Conversely, extremely homogeneous landscapes have only
273 a narrow range of exploitable habitats and impose little cost to dispersal, resulting in intense,
274 landscape-wide competition and producing homogeneous landscape communities dominated by a
275 small number of highly competitive organisms. Meanwhile, moderate compositional heterogeneity
276 allows for the formation of distinct local communities dominated by locally adapted organisms,
277 but also permits enough dispersal for the emergence of source-sink dynamics leading to mass
278 effects Leibold et al., 2004, which would explain why patch level richness and diversity peak at
279 moderate levels of heterogeneity.

280 The increasing subdivision of the landscape among different environment types also appears to
281 affect establishment and survival of immigrant populations. In homogeneous landscapes, a certain
282 portion of immigrants will be highly likely to establish populations due to the large number of
283 suitable patches in the landscape. However, most immigrant populations will remain small due
284 to intense, global competition with abundant, competitively dominant organisms. The small size
285 of immigrant populations and the lack of bet-hedging opportunities in homogeneous landscapes
286 renders these populations vulnerable to stochastic or disturbance-induced extinction (Lande,
287 1993; Hanski, 1998), which may explain why variance in landscape richness and diversity is
288 greater in more homogeneous landscapes. Homogeneous landscapes can accumulate large numbers
289 of species in the short term, but can also lose them very suddenly due to extreme environmental
290 fluctuations. In highly heterogeneous landscapes, immigrants are unlikely to land in a suitable

291 patch, but those that do face only limited, local competition and are thus able to achieve larger
292 population sizes on average than immigrants in homogeneous landscapes. This results in a
293 landscape community which is less rich overall, but also less globally dominated by a small
294 number of highly abundant species. Due to their larger population sizes and the bet-hedging
295 opportunities afforded by a spatially heterogeneous environment, these populations are likely to
296 survive extreme environmental fluctuations (Sieger and Hovestadt, 2020), resulting in a more
297 stable landscape community composition in the longer term.

298 As with all models, our model makes a number of simplifying assumptions. Organisms in
299 this model possess annual life cycles with no overlap between generations. The inclusion of
300 longer lived, iteroparous organisms would alter model dynamics due to the additional bet-hedging
301 options such organisms have against temporal environmental variation as reproduction can be
302 spread out over time, or timed to maximize their offspring's chances of survival (Danforth, 1999;
303 Hopper, 1999; Gremer and Venable, 2014), resulting in a lower extinction rate and slower turnover
304 in community composition. In a model with competing annual and perennial organisms, this
305 should result in a pattern of succession ending with long lived organisms dominating the land-
306 scape. On the other hand, the slower population turnover in long-lived organisms may slow the
307 process of adaptation to changing conditions and result in extinction debts (Hylander and Ehrlén,
308 2013). Similarly, dormancy can serve to increase population persistence by serving as a sort of
309 "dispersal through time" (Buoro and Carlson, 2014), allowing organisms to spread out risk tem-
310 porally or avoid unfavorable conditions, which could increase landscape level diversity. Model
311 results may also be affected by the dispersal strategies employed by organisms. Organisms in this
312 model are limited to two modes of dispersal, both of which are undirected and independent of
313 population density or other local conditions. Undirected, state- and fitness-independent dispersal
314 carries significant risk that a dispersing organism will end up in an unsuitable habitat or disperse
315 at an inopportune time. As such, fitness, and therefore population persistence, will be highly
316 sensitive to spatial context. Informed and directed dispersal has the potential to greatly reduce
317 the risks of dispersal (Lakovic et al., 2015), enabling more frequent dispersal in otherwise high
318 risk spatial contexts (Sieger and Hovestadt, 2021). Directed long distance dispersal could improve
319 population persistence in the landscape by facilitating colonization of otherwise isolated patches,
320 but could also reduce β -diversity by allowing competitively dominant species to spread to suitable
321 habitat more easily in more fragmented landscapes (Grainger and Gilbert, 2016; Catano et al.,
322 2017). Biotic interactions such as mutualisms, facilitation, and trophic interactions also have the
323 potential to shape biodiversity patterns in a variety of complex ways (Wardle, 2006; McIntire
324 and Fajardo, 2014; Mod et al., 2016; Sandor et al., 2022), but only competition is considered in
325 this study.

326 Conclusions

327 Our study demonstrates the important role played by both compositional and configurational
328 landscape structure in shaping community assembly processes, something which has previously
329 received little attention in metacommunity simulation studies. Our model reproduced several
330 patterns documented by previous empirical studies or predicted by theoretical research, all arising
331 as a result of the effects of landscape structure on colonization, dispersal, and extinction rates. We
332 found that different processes can dominate at different scales, leading to different relationships
333 between richness, diversity, and landscape structure at the landscape and patch level. Our
334 findings thus carry potentially significant implications for the design of biodiversity reserves
335 as they suggest conservation trade-offs between different spatial structures at different spatial
336 scales. Given the ongoing biodiversity crisis, there is an urgent need for additional research on
337 the mechanisms underpinning spatial biodiversity patterns. Future studies should consider the
338 roles of additional processes such as trophic interactions and mutualisms, as well as potential
339 interactions with climate change.

340 References

- 341 Ai, D. and Ellwood, M. F. (2022). A spatially implicit model fails to predict the structure of
342 spatially explicit metacommunities under high dispersal. *Ecological Modelling*, 474:110151.
- 343 Arroyo-Rodríguez, V., Galán-Acedo, C., and Fahrig, L. (2017). Habitat fragmentation. *The*
344 *International Encyclopedia of Primatology*, 2:51.
- 345 Bascompte, J. and Solé, R. V. (1996). Habitat fragmentation and extinction thresholds in spa-
346 tially explicit models. *Journal of Animal ecology*, pages 465–473.
- 347 Bezanson, J., Karpinski, S., Shah, V. B., and Edelman, A. (2012). Julia: A fast dynamic language
348 for technical computing. *arXiv preprint arXiv:1209.5145*.
- 349 Biswas, S. R. and Wagner, H. H. (2012). Landscape contrast: a solution to hidden assumptions
350 in the metacommunity concept? *Landscape Ecology*, 27:621–631.
- 351 Boeye, J., Kubisch, A., and Bonte, D. (2014). Habitat structure mediates spatial segregation and
352 therefore coexistence. *Landscape Ecology*, 29:593–604.
- 353 Buoro, M. and Carlson, S. M. (2014). Life-history syndromes: Integrating dispersal through
354 space and time. *Ecology Letters*, 17(6):756–767.
- 355 Cabral, J. S., Valente, L., and Hartig, F. (2017). Mechanistic simulation models in macroecology
356 and biogeography: state-of-art and prospects. *Ecography*, 40(2):267–280.

- 357 Catano, C. P., Dickson, T. L., and Myers, J. A. (2017). Dispersal and neutral sampling mediate
358 contingent effects of disturbance on plant beta-diversity: a meta-analysis. *Ecology Letters*,
359 20(3):347–356.
- 360 Chaianunporn, T. and Hovestadt, T. (2012). Evolution of dispersal in metacommunities of
361 interacting species. *Journal of Evolutionary Biology*, 25(12):2511–2525.
- 362 Chase, J. M. and Leibold, M. A. (2002). Spatial scale dictates the productivity–biodiversity
363 relationship. *Nature*, 416(6879):427–430.
- 364 Clough, Y., Holzschuh, A., Gabriel, D., Purtauf, T., Kleijn, D., Kruess, A., Steffan-Dewenter, I.,
365 and Tschamntke, T. (2007). Alpha and beta diversity of arthropods and plants in organically
366 and conventionally managed wheat fields. *Journal of Applied Ecology*, 44(4):804–812.
- 367 Danforth, B. N. (1999). Emergence dynamics and bet hedging in a desert bee, *perdita portalis*.
368 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266(1432):1985–1994.
- 369 Davison, C. W., Rahbek, C., and Morueta-Holme, N. (2021). Land-use change and biodiversity:
370 Challenges for assembling evidence on the greatest threat to nature. *Global Change Biology*,
371 27(21):5414–5429.
- 372 Ellis, E. C. (2021). Land use and ecological change: A 12,000-year history. *Annual Review of*
373 *Environment and Resources*, 46:1–33.
- 374 Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual review of ecology,*
375 *evolution, and systematics*, 34(1):487–515.
- 376 Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis.
377 *Journal of Biogeography*, 40(9):1649–1663.
- 378 Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual review of ecology,*
379 *evolution, and systematics*, 48:1–23.
- 380 Fahrig, L. (2020). Why do several small patches hold more species than few large patches? *Global*
381 *Ecology and Biogeography*, 29(4):615–628.
- 382 Fahrig, L., Arroyo-Rodríguez, V., Bennett, J. R., Boucher-Lalonde, V., Cazetta, E., Currie, D. J.,
383 Eigenbrod, F., Ford, A. T., Harrison, S. P., and Jaeger, J. A. (2019). Is habitat fragmentation
384 bad for biodiversity? *Biological Conservation*, 230:179–186.
- 385 Firkowski, C. R., Thompson, P. L., Gonzalez, A., Cadotte, M. W., and Fortin, M.-J. (2022).
386 Multi-trophic metacommunity interactions mediate asynchrony and stability in fluctuating
387 environments. *Ecological Monographs*, 92(1):e01484.

- 388 Fischer, J. and B. Lindenmayer, D. (2006). Beyond fragmentation: the continuum model for
389 fauna research and conservation in human-modified landscapes. *Oikos*, 112(2):473–480.
- 390 Fletcher Jr, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt,
391 R. D., Gonzalez, A., Pardini, R., and Damschen, E. I. (2018). Is habitat fragmentation good
392 for biodiversity? *Biological conservation*, 226.
- 393 Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P.,
394 Clement, L. W., Dennis, C., Eggers, S., et al. (2011). Agricultural intensification and biodi-
395 versity partitioning in european landscapes comparing plants, carabids, and birds. *Ecological*
396 *Applications*, 21(5):1772–1781.
- 397 Forester, B. R., Jones, M. R., Joost, S., Landguth, E. L., and Lasky, J. R. (2016). Detecting
398 spatial genetic signatures of local adaptation in heterogeneous landscapes. *Molecular ecology*,
399 25(1):104–120.
- 400 Franklin, J. F. and Lindenmayer, D. B. (2009). Importance of matrix habitats in maintaining
401 biological diversity. *Proceedings of the National Academy of Sciences*, 106(2):349–350.
- 402 Gao, M., Guo, Y., Liu, J., Liu, J., Adl, S., Wu, D., and Lu, T. (2021). Contrasting beta diversity
403 of spiders, carabids, and ants at local and regional scales in a black soil region, northeast china.
404 *Soil Ecology Letters*, 3:103–114.
- 405 Grainger, T. N. and Gilbert, B. (2016). Dispersal and diversity in experimental metacommunities:
406 linking theory and practice. *Oikos*, 125(9):1213–1223.
- 407 Gremer, J. R. and Venable, D. L. (2014). Bet hedging in desert winter annual plants: optimal
408 germination strategies in a variable environment. *Ecology letters*, 17(3):380–387.
- 409 Haddad, N. M., Gonzalez, A., Brudvig, L. A., Burt, M. A., Levey, D. J., and Damschen, E. I.
410 (2017). Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography*,
411 40(1):48–55.
- 412 Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706):41–49.
- 413 Hanski, I. (2015). Habitat fragmentation and species richness. *Journal of Biogeography*,
414 42(5):989–993.
- 415 Hein, S., Gombert, J., Hovestadt, T., and Poethke, H. (2003). Movement patterns of the bush
416 cricket *Platycleis albopunctata* in different types of habitat: matrix is not always matrix.
417 *Ecological Entomology*, 28(4):432–438.

- 418 Hendrickx, F., MAELFAIT, J.-P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron,
419 S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., et al. (2007). How landscape struc-
420 ture, land-use intensity and habitat diversity affect components of total arthropod diversity in
421 agricultural landscapes. *Journal of Applied Ecology*, 44(2):340–351.
- 422 Higgins, S. I., O’Hara, R. B., and Römermann, C. (2012). A niche for biology in species distri-
423 bution models. *Journal of Biogeography*, 39(12):2091–2095.
- 424 Hill, M. and Caswell, H. (1999). Habitat fragmentation and extinction thresholds on fractal
425 landscapes. *Ecology Letters*, 2(2):121–127.
- 426 Holt, R. D. and Barfield, M. (2011). Theoretical perspectives on the statics and dynamics of
427 species’ borders in patchy environments. *The American Naturalist*, 178(S1):S6–S25.
- 428 Hopper, K. R. (1999). Risk-spreading and bet-hedging in insect population biology. *Annual*
429 *review of entomology*, 44(1):535–560.
- 430 Hylander, K. and Ehrlén, J. (2013). The mechanisms causing extinction debts. *Trends in ecology*
431 *& evolution*, 28(6):341–346.
- 432 Jules, E. S. and Shahani, P. (2003). A broader ecological context to habitat fragmentation: why
433 matrix habitat is more important than we thought. *Journal of Vegetation Science*, 14(3):459–
434 464.
- 435 Kessler, M., Abrahamczyk, S., Bos, M., Buchori, D., Putra, D. D., Gradstein, S. R., Höhn, P.,
436 Kluge, J., Orend, F., Pitopang, R., et al. (2009). Alpha and beta diversity of plants and
437 animals along a tropical land-use gradient. *Ecological Applications*, 19(8):2142–2156.
- 438 Lakovic, M., Poethke, H.-J., and Hovestadt, T. (2015). Dispersal timing: emigration of insects
439 living in patchy environments. *PLoS One*, 10(7):e0128672.
- 440 Lande, R. (1993). Risks of population extinction from demographic and environmental stochas-
441 ticity and random catastrophes. *The American Naturalist*, 142(6):911–927.
- 442 Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F.,
443 Holt, R. D., Shurin, J. B., Law, R., and Tilman, D. (2004). The metacommunity concept: a
444 framework for multi-scale community ecology. *Ecology letters*, 7(7):601–613.
- 445 MacArthur, R. H. and Wilson, E. O. (1967). The Theory of Island Biogeography. MacArthur
446 RH, editor. *Monographs in Population Biology*. Princeton University Press, 10.
- 447 Matthews, T. J. (2021). On the biogeography of habitat islands: the importance of matrix effects,
448 noncore species, and source-sink dynamics. *The Quarterly review of biology*, 96(2):73–104.

- 449 McGarigal, K. and Cushman, S. A. (2002). Comparative evaluation of experimental approaches
450 to the study of habitat fragmentation effects. *Ecological applications*, 12(2):335–345.
- 451 McGill, B. J. (2019). The what, how and why of doing macroecology. *Global Ecology and*
452 *Biogeography*, 28(1):6–17.
- 453 McNerney, G., Travis, J., and Dytham, C. (2007). Range shifting on a fragmented landscape.
454 *Ecological Informatics*, 2(1):1–8.
- 455 McIntire, E. J. and Fajardo, A. (2014). Facilitation as a ubiquitous driver of biodiversity. *New*
456 *phytologist*, 201(2):403–416.
- 457 Mod, H. K., Heikkinen, R. K., le Roux, P. C., Wisz, M. S., and Luoto, M. (2016). Impact of biotic
458 interactions on biodiversity varies across a landscape. *Journal of Biogeography*, 43(12):2412–
459 2423.
- 460 Münkemüller, T., De Bello, F., Meynard, C., Gravel, D., Lavergne, S., Mouillot, D., Mouquet,
461 N., and Thuiller, W. (2012). From diversity indices to community assembly processes: a test
462 with simulated data. *Ecography*, 35(5):468–480.
- 463 Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Boerger, L.,
464 Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono,
465 S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., Ingram, D. J.,
466 Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D. L. P., Martin, C. D.,
467 Meiri, S., Novosolov, M., Pan, Y., Phillips, H. R. P., Purves, D. W., Robinson, A., Simpson,
468 J., Tuck, S. L., Weiher, E., White, H. J., Ewers, R. M., Mace, G. M., Scharlemann, J. P. W.,
469 and Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*,
470 520(7545):45+.
- 471 Ovaskainen, O., Rybicki, J., and Abrego, N. (2019). What can observational data reveal about
472 metacommunity processes? *Ecography*, 42(11):1877–1886.
- 473 Prevedello, J. A. and Vieira, M. V. (2010). Does the type of matrix matter? A quantitative
474 review of the evidence. *Biodiversity and Conservation*, 19:1205–1223.
- 475 Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto,
476 H., Pardini, R., Vieira, M. V., Banks-Leite, C., and Fonseca, C. R. (2020). Indirect effects
477 of habitat loss via habitat fragmentation: A cross-taxa analysis of forest-dependent species.
478 *Biological Conservation*, 241:108368.
- 479 Quinn, J. F. and Harrison, S. P. (1988). Effects of habitat fragmentation and isolation on species
480 richness: evidence from biogeographic patterns. *Oecologia*, 75:132–140.

- 481 R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation
482 for Statistical Computing, Vienna, Austria.
- 483 Rodewald, A. D. and Arcese, P. (2016). Direct and indirect interactions between landscape
484 structure and invasive or overabundant species. *Current Landscape Ecology Reports*, 1:30–39.
- 485 Ryberg, W. A. and Fitzgerald, L. A. (2016). Landscape composition, not connectivity, determines
486 metacommunity structure across multiple scales. *Ecography*, 39(10):932–941.
- 487 Rybicki, J., Abrego, N., and Ovaskainen, O. (2020). Habitat fragmentation and species diversity
488 in competitive communities. *Ecology Letters*, 23(3):506–517.
- 489 Sanderson, E. W., Redford, K. H., Vedder, A., Coppolillo, P. B., and Ward, S. E. (2002). A con-
490 ceptual model for conservation planning based on landscape species requirements. *Landscape
491 and urban planning*, 58(1):41–56.
- 492 Sandor, M. E., Elphick, C. S., and Tingley, M. W. (2022). Extinction of biotic interactions
493 due to habitat loss could accelerate the current biodiversity crisis. *Ecological Applications*,
494 32(6):e2608.
- 495 Saupe, D. (1988). Algorithms for random fractals. In Peitgen, H.-O. and Saupe, D., editors, *The
496 Science of Fractal Images*, pages 71–136. Springer New York, New York, NY.
- 497 Semper-Pascual, A., Burton, C., Baumann, M., Decarre, J., Gavier-Pizarro, G., Gómez-Valencia,
498 B., Macchi, L., Mastrangelo, M. E., Pötzschner, F., and Zelaya, P. V. (2021). How do habitat
499 amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use
500 change? *Proceedings of the Royal Society B*, 288(1942):20202466.
- 501 Sieger, C. S., Cobben, M. M., and Hovestadt, T. (2019). Environmental change and variability
502 influence niche evolution of isolated natural populations. *Regional Environmental Change*,
503 19:1999–2011.
- 504 Sieger, C. S. and Hovestadt, T. (2020). The degree of spatial variation relative to temporal
505 variation influences evolution of dispersal. *Oikos*, 129(11):1611–1622.
- 506 Sieger, C. S. and Hovestadt, T. (2021). The effect of landscape structure on the evolution of two
507 alternative dispersal strategies. *Ecological Processes*, 10:1–13.
- 508 Stein, A., Gerstner, K., and Kreft, H. (2014). Environmental heterogeneity as a universal driver
509 of species richness across taxa, biomes and spatial scales. *Ecology letters*, 17(7):866–880.
- 510 Tello, J. S., Myers, J. A., Macía, M. J., Fuentes, A. F., Cayola, L., Arellano, G., Loza, M. I.,
511 Torrez, V., Cornejo, M., Miranda, T. B., et al. (2015). Elevational gradients in β -diversity

512 reflect variation in the strength of local community assembly mechanisms across spatial scales.
513 *PLoS One*, 10(3):e0121458.

514 Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., and Jeltsch,
515 F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance
516 of keystone structures. *Journal of biogeography*, 31(1):79–92.

517 Thompson, P. L., Rayfield, B., and Gonzalez, A. (2017). Loss of habitat and connectivity erodes
518 species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*,
519 40(1):98–108.

520 Tschardtke, T., Steffan-Dewenter, I., Kruess, A., and Thies, C. (2002). Contribution of small
521 habitat fragments to conservation of insect communities of grassland–cropland landscapes.
522 *Ecological Applications*, 12(2). ISBN: 1939-5582.

523 Tschardtke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson,
524 J., Clough, Y., Crist, T. O., Dormann, C. F., et al. (2012). Landscape moderation of
525 biodiversity patterns and processes-eight hypotheses. *Biological reviews*, 87(3):661–685.

526 Villard, M.-A. and Metzger, J. P. (2014). Beyond the fragmentation debate: a conceptual model
527 to predict when habitat configuration really matters. *Journal of Applied Ecology*, 51(2):309–
528 318.

529 Wardle, D. A. (2006). The influence of biotic interactions on soil biodiversity. *Ecology letters*,
530 9(7):870–886.

531 Watling, J. I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L. M.,
532 Fang, R., Hamel-Leigue, A. C., Lachat, T., and Leal, I. R. (2020). Support for the habitat
533 amount hypothesis from a global synthesis of species density studies. *Ecology letters*, 23(4):674–
534 681.

535 White, J. W., Rassweiler, A., Samhoury, J. F., Stier, A. C., and White, C. (2014). Ecologists
536 should not use statistical significance tests to interpret simulation model results. *Oikos*,
537 123(4):385–388.

538 Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York.

539 Wintle, B. A., Kujala, H., Whitehead, A., Cameron, A., Veloz, S., Kukkala, A., Moilanen, A.,
540 Gordon, A., Lentini, P. E., and Cadenhead, N. C. (2019). Global synthesis of conservation
541 studies reveals the importance of small habitat patches for biodiversity. *Proceedings of the
542 National Academy of Sciences*, 116(3):909–914.

543 Zarnetske, P. L., Baiser, B., Strecker, A., Record, S., Belmaker, J., and Tuanmu, M.-N. (2017).
544 The interplay between landscape structure and biotic interactions. *Current Landscape Ecology*
545 *Reports*, 2:12–29.

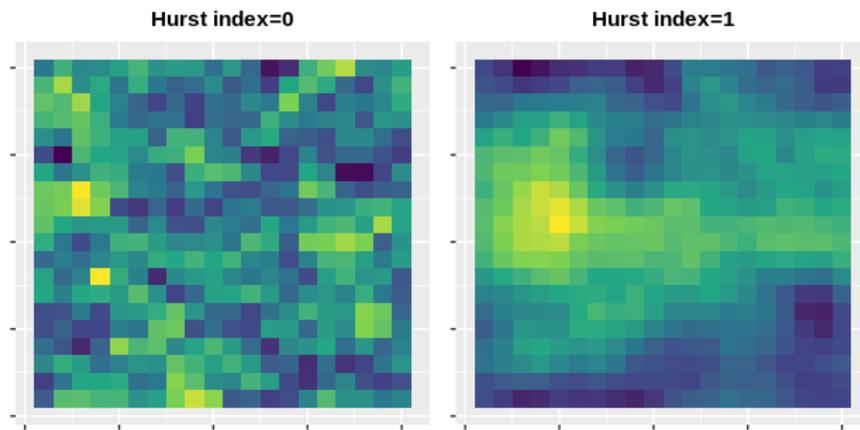


Figure 1. Example landscapes with low (Hurst index=0) and high (Hurst index=1) spatial autocorrelation. Colors represent patch attribute values.

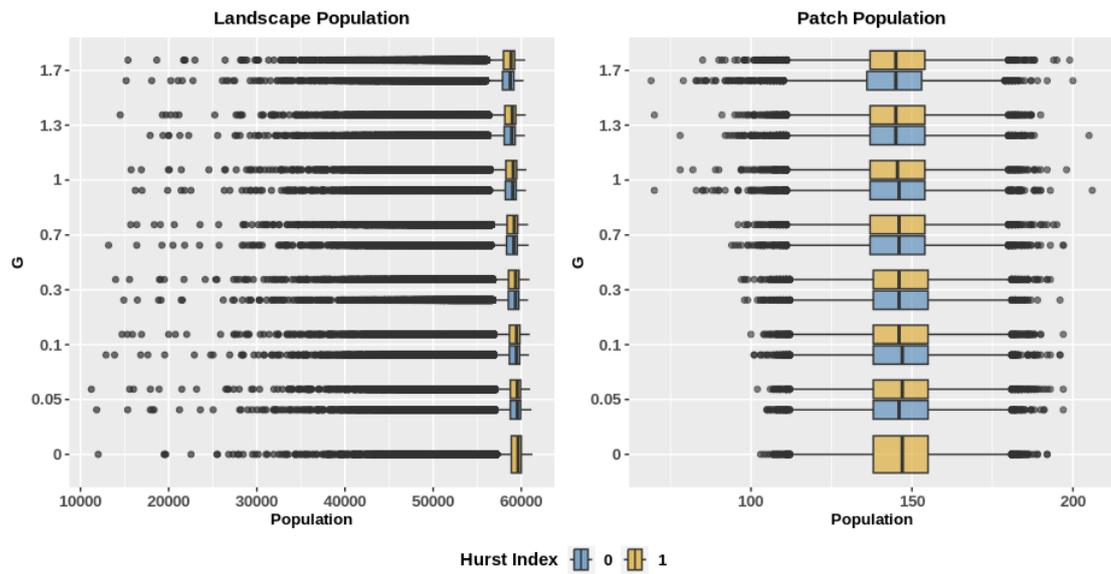


Figure 2. Box plots of landscape and patch level total population by G and Hurst index scenario. Landscape population distributions are shown for time steps 5000 to 10000. Patch distributions are shown for time step 10000.

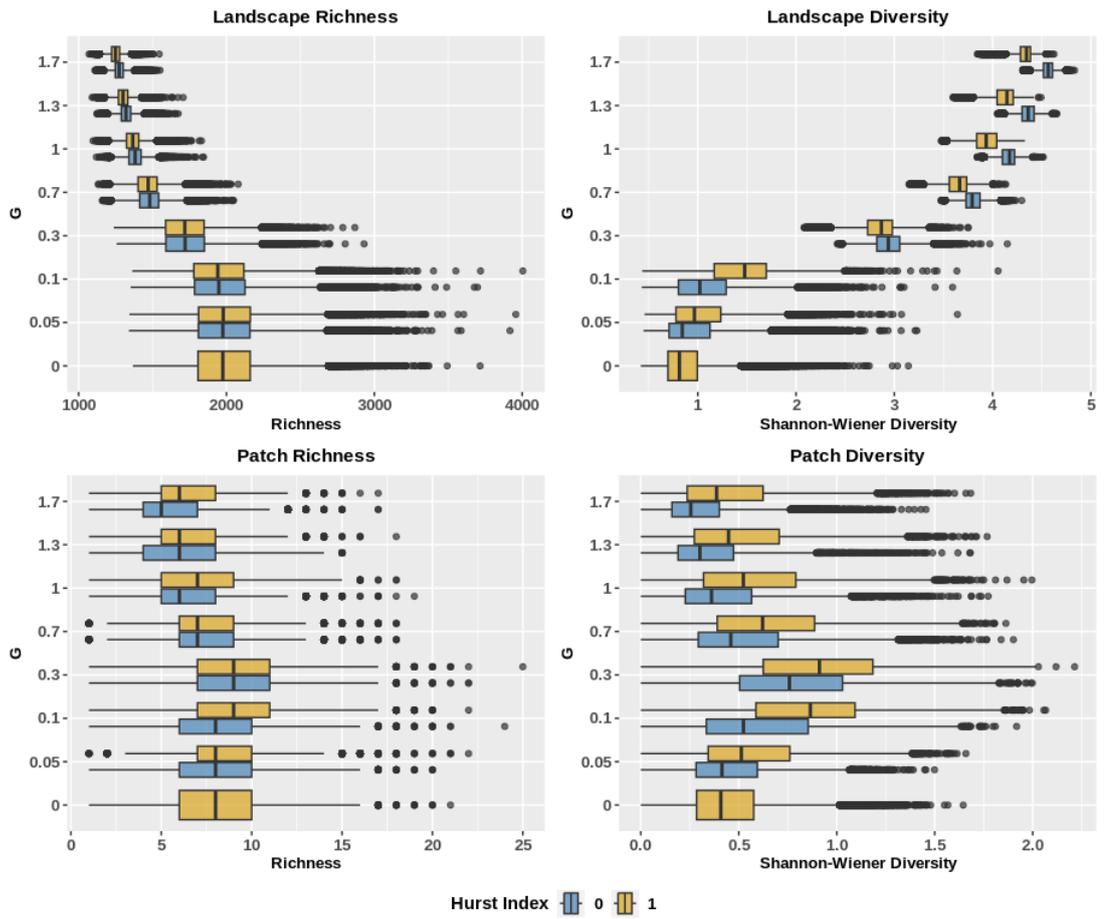


Figure 3. Box plots of richness and Shannon diversity by G and Hurst index scenario. Landscape level richness and diversity distributions are shown for time steps 5000 to 10000. Patch distributions are shown for time step 10000.

Table 1. Organism Traits & Initialization Distribution Parameters.

Trait	Symbol	Distribution	Parameters
Temperature Optimum	T_{opt}	Normal	$\mu = 0, \sigma = G$
Temperature Tolerance	T_{tol}	Log-Normal	$\mu = 0, \sigma = 1$
Habitat Optimum	H_{opt}	Normal	$\mu = 0, \sigma = G$
Habitat Tolerance	H_{tol}	Log-normal	$\mu = 0, \sigma = 1$
Dispersal Chance	P_{disp}	Uniform	0,1
Dispersal Mode Preference	P_{global}	Uniform	0,1

Table 2. Immigrant trait distributions and parameters.

Trait	Distribution	Parameters
T_{opt}	Uniform	$\mu = T_{trend}, \sigma = 1.5 * G$
T_{tol}	Log-Normal	$\mu = 0, \sigma = 1$
H_{opt}	Uniform	$\mu = 0, \sigma = 1.5 * G$
H_{tol}	Log-Normal	$\mu = 0, \sigma = 1$
P_{disp}	Uniform	0,1
P_{global}	Uniform	0,1

Table 3. Summary of model parameters.

Parameter	Symbol	Value
Landscape dimensions		20*20 patches
Total simulation time-steps	t_{max}	10,000
Niche breadth trade-off	a	3
Patch Expected immigrants	E_{immi}	2.5
Gradient strength multiplier	G	$\in 0, 0.05, 0.1, 0.3, 0.7, 1, 1.3, 1.7$
Landscape Hurst Index	$Hurst$	$\in 0, 1$