

Effects of compositional heterogeneity and spatial autocorrelation on richness and diversity in simulated landscapes

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Abstract

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

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

Introduction

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

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

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

Model Description

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

Landscape properties

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

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

Organism properties

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

Organism life-cycle

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

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

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

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

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

Dispersal

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

Immigration from external sources

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

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

Initialization and experiment design

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

Analysis

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

Results

Landscape total population rapidly increases within the first 50 time steps, settling into a stable median slightly below the landscape carrying capacity of 60000 individuals (150 individuals per patch) around which it fluctuated. Median total population declined slightly with increasing G 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.

Conclusions

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

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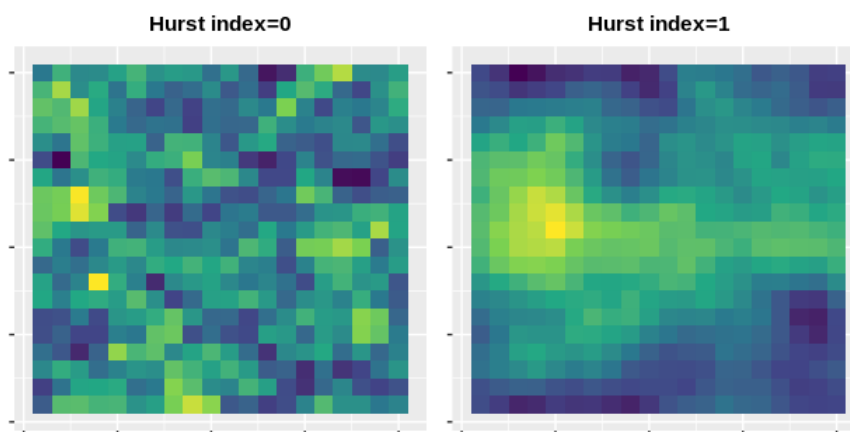


Figure 1. Example landscapes with low (Hurst index=0) and high (Hurst index=1) spatial autocorrelation. Colors represent patch attribute values.

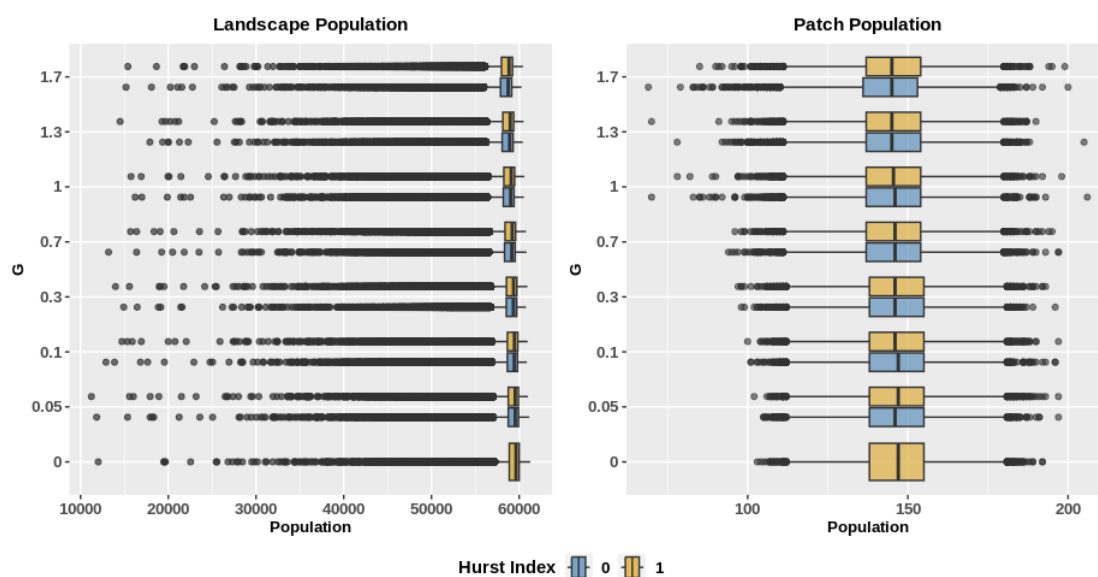


Figure 2. Box plots of landscape and patch level total population by G and Hurst index scenario. Landscape population distributions are shown for time steps 5000 to 10000. Patch distributions are shown for time step 10000.

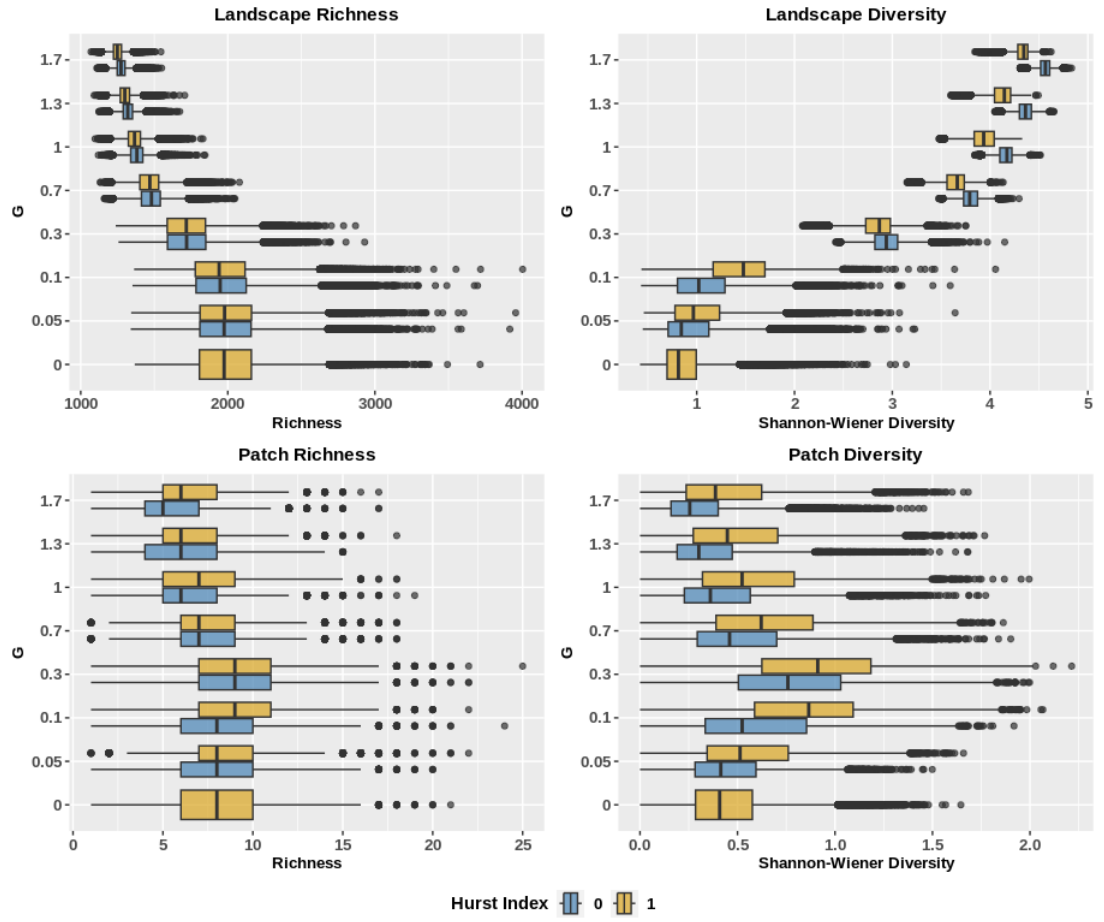


Figure 3. Box plots of richness and Shannon diversity by G and Hurst index scenario. Landscape level richness and diversity distributions are shown for time steps 5000 to 10000. Patch distributions are shown for time step 10000.

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 | $Hurst$ | $\in 0, 1$ |