Effects of landscape compositional heterogeneity and spatial autocorrelation on environmental niche and dispersal in simulated organisms

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Abstract

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Abstract

Local adaptation, environmental tolerance, and dispersal mutually influence the evolution of one another and each are in turn influenced by landscape spatial structure. While each of the three have been investigated frequently in isolation in relation to spatial structure, the three have rarely been considered together. In this study, we explored how the magnitude of landscape environmental heterogeneity (compositional heterogeneity), and environmental spatial autocorrelation jointly affect the evolution of environmental niche optima, tolerance, dispersal frequency, and dispersal distance using a spatially explicit individual based model simulating organisms living, reproducing, and dispersing within grid-based fractal landscapes. Compositional heterogeneity tended to have the strongest influence over patterns while spatial autocorrelation typically played a mediating role. We found that niche adaptation and dispersal patterns were driven by a balance between pressure to avoid risk imposed by spatial heterogeneity and pressure to hedge against risk imposed by temporal environmental fluctuations. Dispersal frequency and dispersal distance were affected differently by spatial structure, underscoring the importance of considering the two independently.

Introduction

Organisms exist within environments which vary over both time and space. Organisms can cope with spatial variation in their environments by adapting their niche optima to local conditions. Given adequate genetic variation in the population, such adaptation can occur quickly. However, successful adaptation requires organisms to cope with short term temporal variation in the environment (Hoffmann and Sgrò, 2011). Organisms can deal with temporally variable environments by adapting their tolerances to local temporal variance. Alternatively, organisms can avoid periods of unfavorable conditions or hedge reproductive bets via dispersal (Venable and Brown, 1988; Kisdi, 2002), reducing the need to tolerate temporal variance in the environment (Bonte et al., 2012). However, because dispersal requires organisms to move through space and settle in new habitats, organisms relying on dispersal to avoid temporal environmental variance must be sufficiently capable of tolerating the spatial heterogeneity they encounter in their environments (Futuyma and Moreno, 1988; Bonte et al., 2012). Tolerance to this spatial variation may not necessarily be conferred by tolerance to temporal variation as the environmental factors that vary over space may be different from those that vary over time. Since tolerances are critical to the ability of organisms both to stay in place and disperse, both strategies are subject to constraints (Bonte et al., 2012; Hillaert et al., 2015) imposed by trade-offs between tolerance to environmental variation and performance under optimal conditions Morin and Chuine (2006); Ravigné et al. (2009); Herren and Baym (2022), or trade-offs between tolerances to variation in different environmental factors. Moreover, the evolution of local adaptation and environmental tolerances are themselves affected by and organism's dispersal behavior through its effects on immigration and gene flow (Kirkpatrick and Barton, 1997; Ronce and Kirkpatrick, 2001; Lenormand, 2002; Billiard and Lenormand, 2005; Bridle et al., 2010, 2019). Dispersal and movement behavior in turn is informed by the risks imposed by spatial environmental heterogeneity and the selection it imposes, meaning that the evolution of local adaptation and environmental tolerances are dependent on spatial context (Bonte et al., 2006; Richardson et al., 2014; Forester et al., 2016), including the magnitude of compositional environmental heterogeneity and its spatial arrangement (Fahrig, 2017). This dependence on on spatial context has important implications for conservation, particularly in the face of climate change, as certain spatial structures may help or hinder local adaptation (Claudino and Campos, 2014), range shifts (Burton et al., 2010; Synes et al., 2015; Årevall et al., 2018), and recolonization of habitat after disturbance (Leimar and Norberg, 1997), making a thorough understanding of the effects of spatial structure on adaptation and dispersal key to creating effective conservation strategies (Holt and Barfield, 2011; Årevall et al., 2018).

Studies investigating dispersal and adaptation commonly adopt a mechanistic modeling approach due to the large temporal and spatial scales such processes can occur over, the difficulty of observing them in nature, and the difficulty of experimentally manipulating conditions in the field (Hanski, 2015; Ovaskainen et al., 2019). A mechanistic modeling approach has the advantage of allowing detailed experimental control over conditions while also enabling direct insight into causal mechanisms underpinning patterns by explicitly ecological and evolutionary processes (Cabral et al., 2017; Hanski, 2015; Higgins et al., 2012). While numerous modeling studies have explored aspects of local adaptation (García-Dorado, 1987; Bridle et al., 2010; Claudino and Campos, 2014; Kisdi et al., 2020), tolerance and niche breadth (Hillaert et al., 2015; Sieger et al., 2019; Kisdi et al., 2020), and dispersal (Hamilton and May, 1977; Gros et al., 2006; Duputié and Massol, 2013; Hillaert et al., 2015), few studies consider all three simultaneously. In their review of individual-based models examining eco-evolutionary dynamics, Romero-Mujalli et al. (2019) found no studies which simultaneously modeled the evolution of local adaptation, dispersal, and phenotypic plasticity. Moreover, the authors also noted that studies focused on local adaptation were often not spatially explicit (e.g. (Kisdi et al., 2020)). Modeling studies on local adaptation which do consider spatial environmental variation tend to do so only in very simplified manners, often assuming simple linear gradients e.g. (Hillaert et al., 2015; Leidinger et al., 2021). Meanwhile, studies modeling dispersal often explicitly consider spatial structure, but typically assume a binary habitat-non-habitat dichotomy e.g. (Gros et al., 2006; Claudino and Campos, 2014). Such assumptions are problematic, particularly for terrestrial environments, as environmental shifts in space are often gradual and many species exploit multiple habitat types (Hein et al., 2003; Jules and Shahani, 2003), meaning it may be more appropriate in many cases to model landscapes as fractal environmental gradients or habitat mosaics (Fischer and B. Lindenmayer, 2006; Franklin and Lindenmayer, 2009). Sieger and Hovestadt (2020) used continuous fractal landscapes to explore the effect of the ratio of temporal to spatial heterogeneity on the evolution of dispersal frequency using an individual-based model which notably modeled niche optimum, tolerance, and dispersal together as evolving traits. While the authors considered the magnitude of variation in patch environments (compositional heterogeneity), they did not explore the effects of spatial configuration despite its importance as a component of environmental spatial structure Fahrig (2017). Moreover, the authors assumed only random global dispersal, and did not consider how environmental heterogeneity could affect other components of dispersal strategy such as dispersal distance, which may be affected by spatial heterogeneity independently of dispersal frequency (Gros et al., 2006; Bonte et al., 2010). In this study, we use an extended version of the model of Tardanico and Hovestadt (2023), developed as an extension of the model of (Sieger and Hovestadt, 2020), in order to systematically explore the effects of landscape structure on adaptation and dispersal strategy of annual asexual organisms with varying environmental niches and dispersal probabilities living, reproducing, and competing in continuous fractal landscapes. We extended the model by considering both temporally static and temporally variable patch environment attributes as well as by permitting dispersing organisms to choose between random global or nearest neighbor dispersal strategies, thus incorporating dispersal distance explicitly into the model. We specifically ask how the magnitude of spatial environmental variation, or compositional heterogeneity, and spatial environmental autocorrelation jointly affect the evolution of environmental niche optima, tolerances to environmental variation, dispersal frequency, and preference for shorter or longer distance dispersal, including the evolution of syndromes in these traits. In addition to data on organism traits such as niche optima, tolerances, and dispersal behavior, our model also records information on organism lineages and thus may be used to explore diversity patterns, which we previously explored in (Tardanico and Hovestadt, 2023). This study, however, will restrict itself to dealing with patterns of adaptation in organism traits.

Methods

We used the model which we developed for our previous study (Tardanico and Hovestadt, 2023). As we made no modifications to the simulation model from our previous study, the description of the model and its mechanics have been recycled from Tardanico and Hovestadt (2023).

Landscape properties

Landscapes consist of grids of habitat patches. Patches possess two attributes one representing patch temperature (T) and second attribute (H) representing an additional, unspecified environmental variable (e.g. a soil property). Spatial distributions for the two patch attributes were generated via an R implementation of the spatially autocorrelated landscape generation algorithm from Saupe (1988). This algorithm is capable of generating fractal landscapes with varying degrees of spatial autocorrelation between grid cell values depending on the value of the Hurst index parameter. Landscapes generated with this algorithm are toroid and opposite edges connect seamlessly to each other, thereby preventing edge effects from occurring at landscape edges. In this study, all landscapes were generated with a Hurst index of either 0 or 1. A Hurst index of 1 produces completely spatially autocorrelated landscapes where patches always have similar environments to their immediate neighbors, while a Hurst index of 0 produces a largely random spatial distribution of patch environments. Spatial distributions for the two patch attributes are generated independently, meaning that T and H attributes do not necessarily correlate with each other spatially. However, T and H spatial distributions for the same landscape were generated with matching generation parameters, including the Hurst index. Thus a landscape with a highly autocorrelated spatial distribution for the T attribute will always have an equally spatially autocorrelated H attribute distribution. Values for patch environmental attributes were drawn from a normal distribution and standardized to a mean of 0 and a standard deviation of 1, such that the average frequency of different patch environment values was constant regardless of spatial configuration. Landscape dimensions were set at 20 by 20 patches for a total of 400 patches in a landscape. These dimensions were chosen in order to limit computation time while still being large enough for structure driven patterns to emerge. Landscape compositional heterogeneity, the magnitude of spatial variation in the T and H attributes was controlled by the simulation parameter G. By multiplying patch attribute values by G, the range of values could be expanded or reduced. In addition to varying spatially, the T attribute fluctuates over time such that the T attribute for patches varies from one time step to the next. Fluctuations in T are global and affect all patches in a landscape equally. Fluctuations in T are normally distributed with a mean of 0 and a standard deviation of 1 and modify patch T attributes by adding the value of the fluctuation to the patch's T attribute.

Organism properties

Patches are inhabited by populations of asexual organisms belonging to lineages which behave as a guild of ecologically similar species who compete with each other within a patch. In addition to possessing a "taxonomic" identity, lineages possess varying environmental niches and dispersal tendencies, which serve to differentiate lineages functionally from one another. Organism niches are modeled as Gaussian curves whose center and spread are defined by a niche optimum and tolerance trait respectively. Organisms possess separate optimum and tolerance traits for T and H. T niche optimum and tolerance are represented by the T_{opt} and T_{tol} traits respectively, while H optimum and tolerance represented by the $_{opt}$ and H_{tol} traits. Organisms also possess two dispersal traits, P_{disp}, which defines the probability of an organism dispersing from its natal patch, and P_{global} which defines an organism's preference for one of two possible dispersal modes. Dispersal is explained further in the section below. Organism traits are summarized in table 1. Trait values are generated when a lineage first appears in a landscape by drawing random values from statistical distributions. Niche optima 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 traits are summarized in table 1.

Dispersal

Organisms can disperse from their natal patches to other patches. Individual organisms may disperse once during their life cycle. Whether or not an organism disperses from its natal patch is determined by drawing a random number from a uniform distribution and comparing the value with an organism's P_{disp} trait. If the random number is less than or equal to the organism's P_{disp}

Table 1. Organism Traits & Initialization Distribution Parameters. Modified from Tardanico and Hovestadt (2023).

Trait	**Symbol**
Temperature Optimum	T_{opt}
Temperature Tolerance	T_{tol}
Habitat Optimum	H_{opt}
Habitat Tolerance	H_{tol}
Dispersal Chance	P_{disp}
Dispersal Mode Preference	P_{global}

trait value, the organism will disperse. Dispersing organisms must then choose a dispersal mode. Two different modes of dispersal are possible within this model, serving as short and long distance modes. We chose to explicitly incorporate dispersal distance as a separate trait due to previous research indicating that landscape spatial structure affects dispersal distance differently from dispersal frequency (Gros et al., 2006). Organisms can disperse via nearest neighbor dispersal or random global dispersal. We chose these two dispersal methods because they are computationally lightweight, simple to implement, and already in widespread use in modeling studies (**???**Kisdi et al., 2020). The dispersal mode is selected by drawing a random number from a uniform distribution between 0 and 1 and comparing its value with an organism's P_{global} trait. If the number's value is less than or equal to the organism's P_{global} trait, the organism disperses via random global dispersal. If not, the organism disperses via nearest neighbor dispersal. In nearest neighbor dispersal, an organism moves to a random patch with the coordinates $x + p$ and $y + q$, where x and y are the coordinates for the natal patch and p and q are integers between -1 and 1. If the target patch's coordinates are outside the bounds of the landscape, the organism is instead moved to the opposite side of the landscape. In random global dispersal, a random patch within the landscape is selected as the target patch. In both dispersal modes, the target patch must have different coordinates from the natal patch and will be re-selected if the target coordinates leave a dispersing organism in its natal patch.

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. 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 tolerance and maximum expected offspring, meaning that organisms with broader tolerances produce fewer offspring on average. This trade-off serves to prevent organisms from having infinitely large tolerances. The strength of this trade-off 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.

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

$$S_A = \frac{1}{1 + a \cdot L_0} \tag{2}$$

$$a = \frac{R_0 - 1}{K \cdot R_0} \tag{3}$$

Immigration from external sources

New organisms 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. Statistical distribution parameters for immigrant traits are summarized in table 2.

Table 2. Immigrant trait distributions and parameters. From Tardanico and Hovestadt (2023).

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

0.1 Experiment design

Landscapes were initialized from text files containing spatial distributions for the two patch attributes. Landscapes were initially empty with no pre-existing populations and were then allowed to be colonized by immigrant organisms over the course of the simulation. As with before, simulations were run for a total of 10,000 time steps. Simulations were run once for each landscape in a set for a total of 30 unique replicates. Fluctuations for each time step were generated at initialization. To ensure replicability, each replicate in a scenario was run with a unique, preset random number generator seed. We ran 7 different G scenarios ($G \in 0.05, 0.1, 0.3, 0.7, 1, 1.3, 1.7$) and 2 Hurst index scenarios (0 and 1) for a total of 14 different scenarios. The simulation program recorded means and variances for trait values and fitness at each time step for entire landscapes, as well as a census of each individual organism in a landscape at the 10,000th timestep, including its lineage identity, trait values, and the patch it inhabited. The program then used the census data to calculate mean trait values and fitness for each patch in the landscape. We calculated two fitness metrics in this study, an organism's expected number of offspring, and the expected proportion of the maximum possible offspring. Model parameters used in this study are summarized in table 3.

Table 3. Summary of model parameters used in the experiment.

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	$\in 0.05, 0.1, 0.3, 0.7, 1, 1.3, 1.7$
Landscape Hurst Index	$Hurst$	$\in 0, 1$

0.2 Data analysis

We analyzed simulation output data in R (R Core Team, 2020). Analysis was conducted for individual organisms at time step 10,000 belonging to lineages with total landscape populations larger than 50 individuals. We did this in order to restrict the analysis to lineages with established populations and eliminate transient lineages with extreme or highly mismatched traits which were likely to die out soon after appearing in the landscape. Due to the large size of the data set, we opted to sample 10,000 individuals from each scenario. In some cases, environmental fluctuations caused population crashes at the final time step, meaning there were not enough individuals to obtain a full sample of 10,00 individuals. This resulted in a data set with a total of 139,477 observations. We assessed the data visually using ggplot2 R package (Wickham, 2016) and evaluated R^2 correlations between the six organism traits using the ggally package (Schloerke et al., 2024). We did not make use of statistical significance tests due to their lack of meaning within a mechanistic modeling context and their unreliability due to extreme sensitivity when sample sizes are extremely large (White et al., 2014).

Results

0.3 Organism Traits

Organism traits responded diversely to G and the Hurst index (Fig. 1). Since these patterns were largely identical at the landscape level and when aggregated at the patch level, this subsection will focus on landscape level patterns. Niche optima traits T_{opt} and H_{opt} matched the frequency distributions for their respective patch attributes, with median values close to 0 and variances which increased with increasing G. Median T tolerance (T_{tol}) showed little variation with G, but did increase in variance. T_{tol} was unaffected by the Hurst index. H tolerance (H_{tol}) increased in both median and variance with greater G. This increase was monotonic under a Hurst index of 1, while under a Hurst index of 0 the increase was non-monotonic between G=0.05 and G=0.3. Dispersal probability (P_{disp}) responded non-monotonically to increasing G, shifting from high median values and relatively large variances to very low median values with small variances across a transition zone occurring between G=0.05 and G=0.3. This transition zone range was affected by the Hurst index, with the transition starting earlier and declining somewhat more mildly under a Hurst index of 1. From G=0.3 onwards, P_{disp} increased slightly with greater G. Within this range, P_{disp} was slightly higher under a Hurst index of 1. Global dispersal probability (P_{global}) was highly variable in nearly all scenarios and responded non-monotonically to increasing G, initially decreasing around G=0.1 and then rebounding thereafter. This pattern was notably stronger under a Hurst index of 1. Median P_{global} was consistently higher under a Hurst index of 0.

0.4 Relationships between Organism Traits

Compositional heterogeneity and spatial autocorrelation affected the correlational relationships between organism traits (Figure 2). Compositional heterogeneity had the strongest effect on correlations between traits; spatial autocorrelation tended to mediate the strength of those correlations. In scenarios with a Hurst index of 1, trait correlations tended to be slightly stronger,

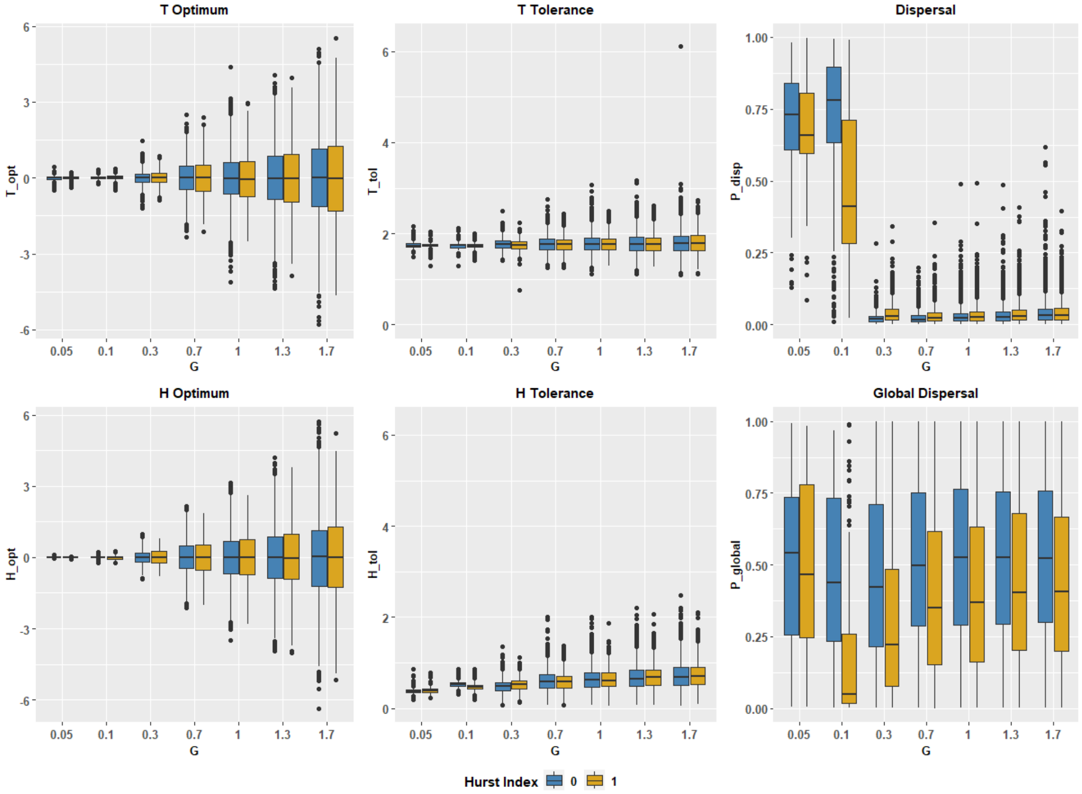

Figure 1. Box plot of distributions for organism trait values by G and Hurst index scenario at time step 10,000.

although this effect was not universal.

Trait correlations shifted between three distinct patterns as G increased. The first pattern occurred at G=0.05 and was characterized by strong but dramatically inconsistent relationships between traits. At G=0.1, this pattern gave way to a pattern characterized by negative correlations between absolute value niche optima (T_{opt} and H_{opt}), P_{disp} and positive correlations between P_{disp}, P_{global}, and H_{tol}. A negative correlation between P_{global} and absolute value niche optima traits occurred under a Hurst index of 1 under this pattern, but not under a Hurst index of 0. Further increases in G resulted in a shift to a third pattern characterized by positive associations between absolute value niche optima, P_{disp}, and H_{tol}, and negative associations between P_{disp} and P_{global}, and between P_{global} and absolute value H_{opt}. Additionally, under a Hurst index of 1 there was a slight but consistent negative relationship between P_{global} and H_{tol} while the relationship between P_{disp} and P_{global} was slightly stronger. Associations were typically stronger with absolute value H_{opt} than T_{opt}.

T_{tol} exhibited weak and inconsistent correlations with other traits across all scenarios, with a slightly higher tendency towards weak positive correlations with absolute value niche optima traits in Hurst index=0 scenarios at or above G=0.3. Correlations with T_{tol} tended to be strongest overall below G=0.3; in G=0.1 and G=0.05 scenarios, T_{tol} had a consistent negative correlation with P_{disp}.

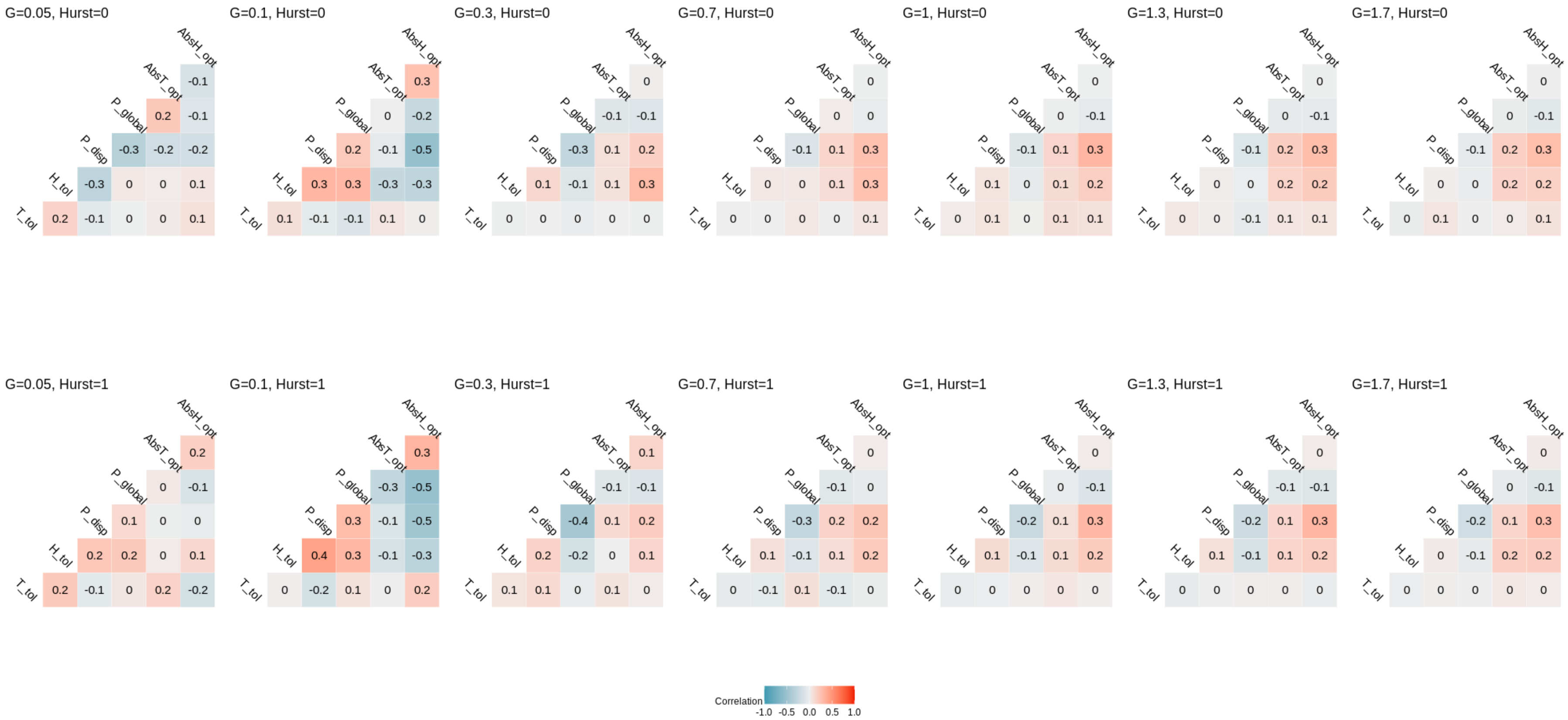

Figure 2. R^2 correlations between trait values by G and Hurst index scenario for individual organisms. Niche optima are absolute value transformed.

0.5 Adaptation and Fitness

Organisms were overall well adapted to their local patch conditions, with niche optima closely correlating with patch environment attributes. This correlation was strongest for H_{opt}, with T_{opt} tending to be more variable in relation to patch T (Figure 3). Species inhabiting more extreme patches had a tendency toward greater mismatches between niche optima and patch attributes; this pattern was stronger for the T attribute than the H attribute.

Accordingly, fitness was relatively high, with the vast majority of organisms having at over 80% of their maximum fertility without accounting for reduced fertility due to the tolerance trade-off. Factoring in the tolerance trade-off, most individuals had expected at least 75% of their maximum fertility (Figure 3). Fertility declined slightly and increased in variance with increasing G.

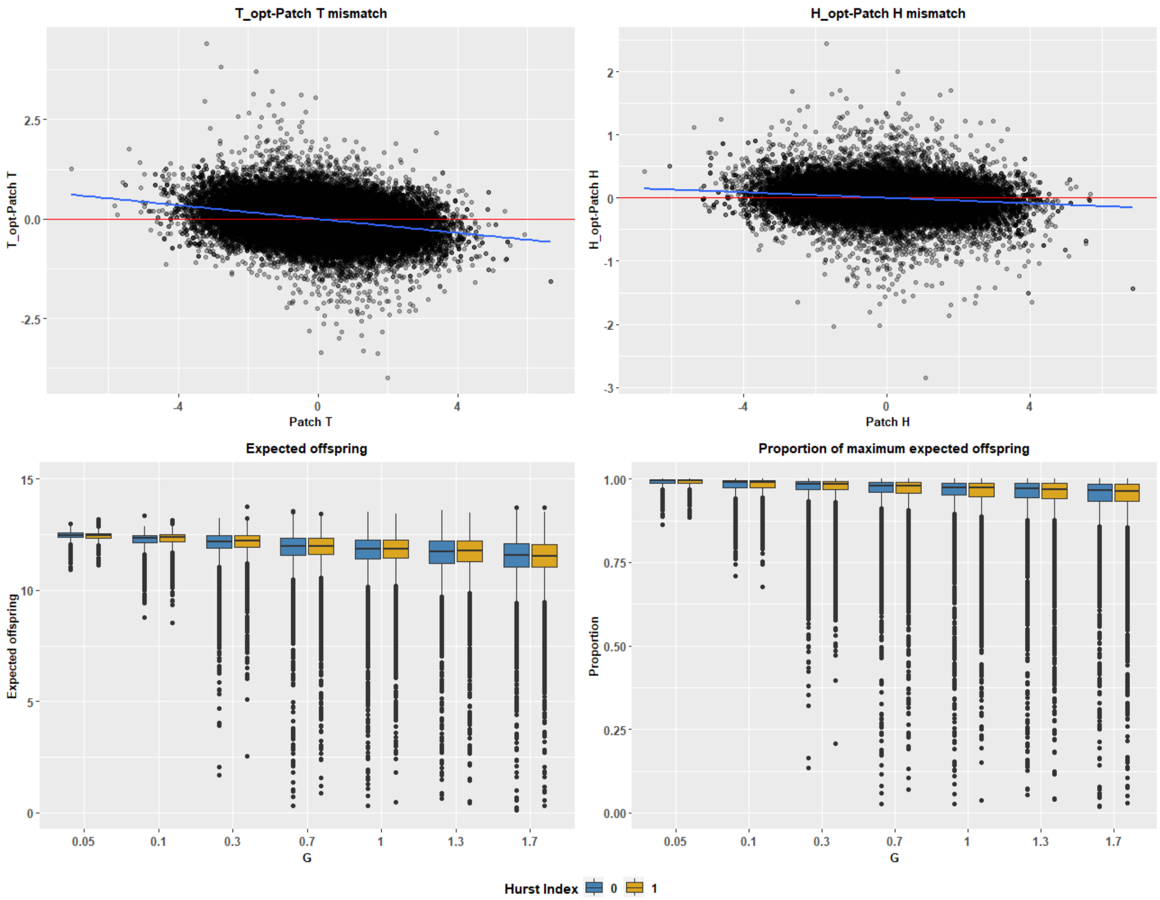

Figure 3. Individual local adaptation and fitness as measured by fertility. Top: Difference between individual niche optima and respective patch attributes vs. patch attribute. Bottom: Box plots of distributions at time step 10,000 by scenario of individual expected offspring and the proportion of maximum expected offspring, the expected number of offspring under optimal conditions.

Discussion

Landscape spatial structure affected niche traits and local adaptation, dispersal traits, and correlational relationships between traits. Patterns were most strongly influenced by compositional heterogeneity (G), with spatial autocorrelation (Hurst index) mostly playing a mediating role. Dispersal traits were an exception to this and were notably affected by both compositional heterogeneity and spatial autocorrelation. Niche optima distributions reflected the distributions of patch environment attributes in the landscapes and organisms were typically well adapted to their local patches, in line with theoretical studies findings that greater spatial heterogeneity selects for local adaptation due to the risk imposed by the landscape of immigrating into an unsuitable habitat (Hastings, 1983; Futuyma and Moreno, 1988). Tolerance traits behaved differently for the two environmental attributes. T tolerance was notably higher than habitat tolerance and was weakly affected by landscape structure, resembling the results of Sieger and Hovestadt (2020), and lacked any consistent relationships with other traits under most scenarios. H tolerance, on the other hand, showed a clear relationship with landscape structure at both the patch and landscape level. The difference in behavior of the two tolerance traits indicates that tolerance is determined primarily by the degree to which environmental variation can be avoided. In this model, and for many climate related environmental variables, temporal fluctuations are both unpredictable and can occur synchronously over a large area and thus affect organisms independently of spatial context or dispersal capabilities. Such environmental variation selects for broad niches that permit consistent fitness over a large range of conditions (Lynch and Gabriel, 1987; Futuyma and Moreno, 1988; Devictor et al., 2008; Lin and Wiens, 2017), potentially overriding effects of smaller scale spatial variation. Purely spatial environmental variation, on the other hand, can be avoided substantially by restricting movement and dispersal, allowing organisms to retain more specialized niches.

Dispersal trait responses to compositional heterogeneity and spatial autocorrelation were nonlinear in nature and were largely consistent with established literature regarding relationships between dispersal frequency, dispersal distance, and spatial heterogeneity (Burgess et al., 2016). Dispersal shifted from a pattern of high dispersal probabilities at low levels of compositional heterogeneity to very low dispersal probabilities once heterogeneity increased beyond a threshold range, with slight increases in dispersal occurring at very high levels of compositional heterogeneity. Global dispersal probability shifted from a maximum at very low compositional heterogeneity to a minimum around the threshold range at which dispersal probability shifted and rebounded thereafter. Frequent dispersal is expected under very low spatial heterogeneity because there is little spatial variation in fitness and thus little risk to dispersal, while kin competition imposes a positive selection on dispersal (Hamilton and May, 1977; Nakajima and Kurihara, 1994; Gandon, 1999). Moreover, kin competition selects for longer dispersal distances as this allows organisms to minimize the chance of encountering kin in a destination patch (Hovestadt et al., 2001; Rousset and Gandon, 2002), resulting in a preference for random global dispersal under very low heterogeneity. Increasing compositional heterogeneity beyond a certain threshold resulted in a decline in dispersal chance across a transition zone as compositional heterogeneity began to exceed the limits of tolerances and impose increasingly significant fitness costs to dispersal (Hastings, 1983; Holt, 1985). This threshold itself was dependent on spatial autocorrelation and selection on dispersal traits within the transition zone was strongly divergent between autocorrelation scenarios. In the G=0.1 scenarios, high autocorrelation produced an extremely broad range of dispersal probabilities and the lowest global dispersal probabilities of any scenario, while dispersal trait distributions under low autocorrelation were similar to other low heterogeneity scenarios. The discrepancy between the two autocorrelation scenarios when G=0.1 is the result of several factors. Under low autocorrelation, unpredictable spatial variation selects for higher H tolerance, reducing risks associated with dispersal and making organisms less sensitive to spatial variance in the environment. In contrast, the predictability of spatial variation in highly autocorrelated landscapes results in lower H tolerance and thus greater sensitivity to spatial context. As a consequence, dispersal in the high autocorrelation G=0.1 scenarios is subject to a range of different selective pressures depending on an organism's environmental niche. Organisms adapted to common habitats, or those with broad tolerances face relatively low dispersal risks as suitable habitat is plentiful, while organisms with more narrow niches, or those adapted to rarer or more extreme environments face high risks when dispersing resulting in selective pressure toward lower dispersal probabilities. The predictability of spatial variation in high autocorrelation scenarios also strongly favors nearest neighbor dispersal over random global dispersal if dispersal is undirected, as it will almost always result in an organism landing in a suitable patch under moderate compositional heterogeneity, while random global dispersal carries significant risk of emigration into an unsuitable patch (Bonte et al., 2010). In the absence of spatial autocorrelation, there is no meaningful advantage to either dispersal method, causing global dispersal to behave as a largely neutral trait. At G=0.3 and above, spatial heterogeneity strongly selects for low dispersal probabilities; dispersal probabilities in these scenarios were similar to those observed by Sieger and Hovestadt (2020). Increases in dispersal and global dispersal probabilities with further increases in G above 0.3 indicate increasing selection for bet-hedging against temporal heterogeneity due to decreasing habitat area. Dispersal was slightly but consistently higher in highly autocorrelated scenarios at and above G=0.3 while global dispersal probability was consistently lower. These findings are consistent with the results of (Hovestadt et al., 2001), which also found that higher spatial autocorrelation favored increased local dispersal propensity and distance and disfavored global dispersal.

Patterns of correlation between traits responded in a non-linear fashion, with abrupt shifts in patterns at two thresholds of compositional heterogeneity, one above G=0.1 and another threshold below G=0.1. Above G=0.1, patterns were highly similar between scenarios, with absolute value niche optima showing consistent positive relationships with tolerances and dispersal chance, and a consistent negative relationship between dispersal chance and global dispersal that diminishes with greater heterogeneity. Meanwhile, patterns at G=0.1 were characterized by positive associations between dispersal chance, global dispersal, and H tolerance, and negative associations between H tolerance and dispersal traits, and absolute value niche optima. These results mirror those of Sieger and Hovestadt (2020), which found a shift in the location of the most frequent dispersers from the most common habitats to rare patches with more extreme environments as spatial heterogeneity increased, driven by greater selection for bet-hedging strategies in organisms living in extreme patches. Similarly, trait correlation patterns in our model above G=0.1 are consistent with increasingly strong selection for bet-hedging strategies as niche optima move further away from average landscape conditions. This is further supported by a pattern of lower fitness in organisms adapted to more extreme conditions and the tendency for such organisms to be adapted to slightly more average conditions than those they experienced in their habitat patches. These patterns appear to be consequences of the smaller habitat area available to organisms with more extreme niche optima. The small habitat area reduces the population sizes that can be supported and renders such organisms particularly vulnerable to temporal environmental fluctuations (Lande, 1993; Hanski, 1998; Hill and Caswell, 1999), increasing the importance of risk spreading strategies for population persistence. The need for insurance against temporal fluctuations may partly explain the slight tendency of "regression toward the mean" (Sieger and Hovestadt, 2020) for niche optima in extreme patches as this apparent maladaptation may potentially expand the number of patches an organism can survive in at any given time. Below G=0.1, trait correlations became highly idiosyncratic and inconsistent. This is likely due to a combination of very low variance in niche traits, weak selection within the range of values they occupy, very weak selection on dispersal traits, and highly uneven landscape communities dominated by a small number of lineages, leading to correlational patterns which are highly influenced by stochasticity and priority effects.

This model makes a number of simplifying assumptions for ease of implementation, computation, and analysis which, if altered, could affect selection on traits and resulting trait patterns. Our model assumes that organisms are asexual with an annual life cycle with no overlapping generations and does not consider other life histories or reproductive strategies. Longer lifespans allow for multiple bouts of reproduction which can serve to hedge reproductive bets in the face of temporal by spreading reproduction out over time (Danforth, 1999; Hopper, 1999; Gremer and Venable, 2014). Inclusion of competing annual semelparous organisms and perennial iteroparous organisms would likely produce a pattern of succession over the course of the simulation with annual organisms dominating in the early stages and being gradually replaced by perennial organisms as the simulation progresses. Longer lifespans may also have the effect of reducing population turnover resulting in slower shifts in community level trait patterns. Inclusion of overlapping generations, meanwhile, has the potential to alter selection on dispersal traits as a result of the effect of age structure on kinship competition (Ronce et al., 2000). Including dormancy would provide organisms, including organisms with annual, semelparous life cycles, with an alternative means of hedging against reproductive risk by serving as a kind of dispersal through time (Buoro and Carlson, 2014). As dormancy and dispersal serve similar bet hedging functions, the addition of dormancy as a possible strategy would likely reduce dispersal frequency. Organisms in our model are limited to two dispersal modes, and dispersal is assumed to be both undirected and unaffected by an organism's local environment or fitness. Undirected, uninformed dispersal can incur a notable fitness cost due to the risk that an organism will emigrate to an unsuitable patch or at an inopportune time (Hastings, 1983; Bonte et al., 2010), necessitating greater tolerance which comes at the cost of maximum expected reproductive output in this model. Informed and directed dispersal can greatly reduce dispersal risk related fitness costs, particularly for long distance dispersal and under strong or unpredictable spatial environmental variation (Lakovic et al., 2015; Sieger and Hovestadt, 2021). Reducing these fitness costs would likely permit more frequent dispersal and a higher reproductive output due to reduced selection for high tolerance. Finally, interactions with other organisms could affect selective pressures on traits in a variety of complex ways (Chaianunporn and Hovestadt, 2012, 2019), but this model only considers competition.

Conclusions

Our study systematically explored the role of compositional heterogeneity and spatial autocorrelation in shaping both adaptation to environmental conditions and dispersal behavior in a temporally variable environment, something which to our knowledge has not been systematically explored by previous studies. Our model reproduced a number of patterns observed in previous theoretical studies stemming from varying degrees of selective pressure imposed by the spatial and temporal environments. We found that niche adaptation and dispersal patterns were primarily driven by a balance between pressure to avoid risk imposed by spatial heterogeneity and pressure to hedge against risk imposed by large scale temporal environmental fluctuations. Compositional heterogeneity tended to have the strongest influence over patterns while spatial autocorrelation typically played a mediating role. We found that dispersal frequency and dispersal distance were affected differently by spatial structure, underscoring the need to consider the two independently.

Future studies should explore alternative life-history and dispersal scenarios, as well as exploring how a shifting environment interacts with landscape spatial structure to influence patterns of adaptation and dispersal behavior.

Conflicts of interest

The authors declare no conflicts of interest.

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Author contributions

J.T. and T.H. jointly conceptualized the model. J.T. implemented the model. J.T. and T.H. analyzed the data. J.T. wrote the manuscript and created the figures and supplementary material. T.H. reviewed and provided feedback on multiple drafts of the manuscript.

Data Availability

Simulation output data used in this manuscript as well as configuration files and shell scripts used to run the simulations and the R scripts used for analysis are archived on the Dryad Digital Repository: `doi:10.5061/dryad.mgqnk997t` (Reviewer link: `https://datadryad.org/stash/share/ZqHBR2sSrV_LUXcpjI9IPOHRne_ajU9xX7ONWK6hrt4`). Code for the simulation program used to generate the data is available from GitHub: `https://github.com/jtardanico/TardanicoHovestadt2023_Landscapes`.

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