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Spatial storage effect facilitates evolutionary rescue in rapidly changing environments

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Abstract

The storage effect is a plausible natural mechanism that generates balanced genetic polymorphism in temporally varying environments. Balanced polymorphism may facilitate evolutionary rescue, promoting the persistence of populations otherwise destined for extinction. However, it is unknown whether the storage effect can be established in small populations whose size is allowed to vary, and if so, whether it will lead to evolutionary rescue. In this study, we investigate whether the spatial storage effect emerges and facilitates evolutionary rescue across small populations of variable sizes that inhabit heterogeneous, temporally varying environments and exchange migrants. We use an eco-evolutionary model to examine the phenomenon under a wide set of conditions, including the magnitudes and periods of temporal variation, habitat harshness, migration rates, the degrees of spatial heterogeneity, and increasing fitness oscillations over time, all within the framework of the logistic population growth model. We find that the storage effect emerges and that it increases the persistence of populations in harsh, temporally varying habitats beyond levels expected in the absence of the mechanism. This mechanism demonstrates how rapid evolution broadens the known conditions for population persistence in the face of rapid and continuous environmental changes.

Keywords: spatial storage effect, eco-evolutionary dynamics, evolutionary rescue, temporally varying environments, rapid evolution, balanced polymorphism

Introduction

Many populations experience temporally varying selection resulting from seasonal, periodic, or random environmental fluctuations (de Villemereuil et al., 2020; Kroeker et al., 2019; Reed & Hobbs, 2004; Wittmann et al., 2017). With global climate change (Ordanovich et al., 2023; Planton et al., 2008), anthropogenetic habitat alterations (Martínez-Abraín & Jiménez, 2015; Schwitzer et al., 2011; Thompson et al., 2018), and invasions into novel habitats (Lee & Bell, 1999), the scale of these temporal dynamics is changing. Global climate change, in particular, is expected to increase the magnitude of environmental variation via extreme temperature (Sheridan & Lee, 2018) and precipitation events (Kunkel et al., 2003; Rudgers et al., 2023). These changes may become a major driving force of evolution on contemporary timescales (Grant et al., 2017). In response, populations can become extinct, expand their range, or adapt to rapidly changing conditions (Pease et al., 1989; Bowler & Benton, 2005; Duputié et al., 2012; Hetem et al., 2014; Holt et al., 2005; Holt et al., 2022). The latter represents a particular mode of evolution, referred to as rapid evolution (Hairston et al., 2005; Messer et al., 2016; Promy et al., 2023; Stern & Lee, 2020), where populations undergo rapid shifts in allele frequencies on contemporary timescales (Bergland et al., 2014; Stern et al., 2022). However, whether balanced, rapidly shifting allele frequencies can arise and promote population persistence in small populations facing temporally varying environments and stochastic fluctuations in size remains unclear—this is the central question of this study.

The conditions that drive rapid evolution in temporally varying environments differ notably from those under traditionally considered gradual evolution (Messer et al., 2016). Rapid evolution occurs on ecological time scales (Thompson, 1998) and requires notable genetic variation (Bell, 2013; Promy et al., 2023). First, rapid evolution occurring on ecological time scales implies that ecological and evolutionary processes jointly shape population dynamics (Yamamichi et al., 2023). Interactions between ecological and evolutionary processes are known to produce specific patterns of genetic change in populations (Kim, 2023; Kim & Gulisija, 2010; Yoshida et al., 2007). Nonetheless, how such interactions contribute to rapid evolution in temporally varying environments is underexplored. In particular, the studies that examine eco-evolutionary dynamics tend to focus on directional selection (Yamamichi et al., 2023) or deterministic dynamics (Kim, 2023). Second, rapid evolution may be contingent on the levels of genetic variation (Bell, 2013; Promy et al., 2023) since it is more likely to occur if adaptive alleles are already present in a population (Barrett & Schulter, 2008; Guzella et al., 2018). Such variation may be supplied by a high rate of benefi-

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cial de novo mutation (Gillespie, 1984), which is unlikely in small populations facing the risk of extinction (Barrett & Schulter, 2008; Matuszewski et al., 2015; Messer & Petrov, 2013). Therefore, rapid adaptation in small populations might depend on elevated levels of genetic diversity that have been maintained over time by balancing selection, known as balanced polymorphism (Hedrick, 1974, 1976, 1986, 2006; Kimura & Crow, 1964). However, it is unclear how the eco-evolutionary dynamics affects the maintenance of genetic polymorphism in temporally varying environments.

Classical population genetics theory suggests that the maintenance of genetic variation is restricted to heterozygote advantage across environments (Dempster, 1955; Gillespie, 1973; Wallace, 1968) and is unlikely in finite populations (Hedrick, 1976). Recent models incorporating forms of the storage effect, originally explored in the context of species coexistence (Chesson &, Warner,1981), emerged as plausible mechanisms of balancing selection in temporally varying environments (Gulisija & Kim, 2015; Gulisija & Plotkin, 2017; Gulisija et al., 2016; Park & Kim, 2019; Svardal et al., 2011, 2015; Yamamichi & Hoso, 2016). The storage effect arises in temporally varying habitats under strong density regulation (competition), when a portion of a population is (partially) protected from selection. Such heterogeneous, varying selection enables less abundant genotypes to capitalize on favorable conditions while being protected from unfavorable conditions in a portion of a population that experiences milder negative selection. In a sense, a protected subpopulation "stores" diversity until conditions change. For example, storage of genetic polymorphism in populations can occur due to partial protection from selection in different life stages (e.g., seed banks, long-lived adults, diapause, etc.) (Bertram & Masel, 2019; Ellner & Hairston, 1994), under phenotypic plasticity (Gulisija et al., 2016), under maternal effects (Yamamichi & Hoso, 2016), or across habitats with a spatially heterogeneous magnitude of variation (Gulisija & Kim, 2015). The latter is referred to as the spatial storage effect and is a mechanism that easily establishes under a wide range of naturally plausible scenarios, including variation of the levels of selection, the rate of migration across a structured population, and the degree of spatial heterogeneity in selection (Gulisija & Kim, 2015). Moreover, this mechanism has been explored under eco-evolutionary dynamics and has been found to arise when population carrying capacity fluctuates (Kim, 2023), when modeled under deterministic dynamics. However, none of the studies on the storage effect incorporated stochastic changes in population sizes nor allowed for possible extinction. Thus, it remains unclear if the storage effect generates notable genetic diversity under population eco-evolutionary dynamics and, if so, how it impacts population persistence amid stochastic perturbations to population size.

Genetic diversity may prevent population extinction (Bradshaw, 1991; Messer & Petrov, 2013; Thompson, 1998). That is, threatened populations can be "rescued" from extinction by adaptation: a phenomenon known as "evolutionary rescue" (Bell & Gonzalez, 2009, 2011; Carlson et al., 2014; Gonzalez et al., 2013; Martin et al., 2013; Orr & Unckless, 2014; Wilson et al., 2017). The presence of adaptive alleles (i.e., genetic variation) is a limiting factor for evolutionary rescue (Marrec & Bitbol, 2020; Schiffers et al., 2013). Rapidly changing conditions may require rapid evolutionary rescue from balanced polymorphism in small populations, given the limited influx of adaptive mutants from de novo mutations. In this scenario, a form of the storage effect, such as the spatial storage effect, could maintain sufficient balanced polymorphism needed for rapid evolution as environments shift. Therefore, it is imperative to investigate whether the spatial storage effect can arise in small populations under eco-evolutionary population dynamics, maintain genetic diversity over time, and lead to evolutionary rescue under continuously changing conditions.

An important consideration when investigating evolutionary rescue under the spatial storage effect is population persistence in the absence of evolution. Under the conditions favoring the spatial storage effect, where populations in distinct temporally varying regimes exchange migrants, migration may support population persistence without evolution by supplying individuals through a source-sink dynamic (Gaggiotti, 1996; Pulliam, 1988). A source-sink dynamic occurs when a population inhabiting favorable conditions (source) supplies migrants to a population in a poor-quality habitat (sink) (Amarasekare, 2004; Dias, 1996; Pulliam, 1988), thus maintaining population size (Adler, 1993). As long as the migration rates remain moderate, migration promotes persistence by maintaining connectivity between spatially heterogeneous populations, thus protecting fragmented populations (Ronce & Kirkpatrick, 2001). The main question that arises is whether the spatial storage effect can increase the rates of population persistence to a higher level than migration alone, thus representing a case of evolutionary rescue.

This study explores whether the storage effect emerges and promotes evolutionary rescue in small populations in rapidly changing environments. We develop a population model of the spatial storage effect (Gulisija & Kim, 2015), arising across two populations experiencing different magnitudes of varying selection and environmental harshness. These populations exchange migrants and undergo size changes according to the logistic growth model. We employ Monte Carlo simulations across a wide range of parameters, including a range of migration rates, the rate of environmental oscillations, the magnitude of varying selection, and the magnitude of mean environmental harshness, generating scenarios that match contemporary ecological processes, including population extinction. We demonstrate that the storage effect establishes and facilitates evolutionary rescue in small populations with stochastic changes in size, generating persistence that exceeds that under source-sink dynamics in rapidly changing environments.

Model and methods

Eco-evolutionary model

We model eco-evolutionary dynamics at a single locus across two populations that occupy distinct habitats and exchange a limited number of migrants, thus generating conditions that favor the spatial storage effect. The populations originate from a larger stable ancestral population that is under drift (or reduced magnitude of varying selection)-mutation balance for the two alleles, ancestral and derived, a and d. At the onset of temporally varying selection, the initial allele frequencies of the derived and ancestral alleles within new

Table 1. Symbols and parameters used in the study.

Syntax	Description
$N_{i,t}$	Size of population *i* at a time *t*
K_i	Carrying capacity of population *i*
$G_{i,t}$	Growth in number of individuals in population *i* at time *t*
h (model/drift)	Expected heterozygosity across populations under the heterogenous temporally varying selection relative to neutral expectation
$p_{i,t}$	Frequency of ancestral allele in population *i* at time *t*
$q_{i,t}$	Frequency of derived allele in population *i* at time *t*
P	Number of generations in a cycle of varying selection (phase)
$s_{\max}$	Maximum numerator fitness deviation due to varying selection
m_i	Emigration rate from population *i*
δ_i	Intrinsic growth rate in population *i*
S_i	Mean environmental effect in population *i*
β	Relative increase in the magnitude of fitness oscillations over time

populations are sampled from the equilibrium distribution of allele frequencies from the ancestral population (Figure S1). Then, one population experiences temporally varying selection (population V, with size $N_{V,\ t}$ at a time *t*), while the other (population R, with size $N_{R,\ t}$ at a time *t*) serves as a refuge that is under drift or a reduced magnitude of temporally varying selection, continuing under the ancestral conditions. To facilitate the presentation of the eco-evolutionary model below, we show the symbols used in the study in Table 1, where *i* indicates population V or R. Figure S2 presents a schematic representation of the model and its hypothesized dynamics.

We simulate eco-evolutionary dynamics across two populations forward in time (Kim & Wiehe, 2008). During each discrete generation, the populations are subjected to forces of stochastic mutation under a recurrent mutation rate μ, stochastic migration, temporally varying selection, and stochastic reproduction in the framework of the logistic population growth model. Migration is reciprocal, such that the proportion of individuals, given by the migration rate (m_i), is randomly selected to emigrate from a population. The number of migrants from a population ($M_{i,t}$) is $m_i N_{i,t}$ and may be notably smaller than the V, due to unfavorable conditions.

Temporal environmental variation, implemented as a genotype-based relative fitness deviation at time *t* (s_t), in combination with the overall environmental harshness (S_i = mean environmental effect in population *i*) and population growth rate ($G_{i,t}$), impacts the number of individuals of each genotype in each generation such that:

$$N'_{id,t} = \left(1 - S_i + C_{i,d} s_t\right) \times G_{i,t} \times N_{id,t}\ , \tag{1}$$

and

$$N'_{ia,t} = \left(1 - S_i - C_{i,a} s_t\right) \times G_{i,t} \times N_{ia,t}, \tag{2}$$

where $N_{id,t}$ represents the number of individuals carrying the derived allele and $N_{ia,t}$ represents the number of individuals carrying the ancestral allele in the population *i* at the time *t* prior to density-regulated selection, where *i* = V or R. S_i is a general habitat effect that both alleles experience equally and thus does not induce selective dynamics. $S_V > 0$ represents a harsh new habitat for the V population, while the R population resides in a non-harsh habitat with $S_R = 0$, consistent with source-sink dynamics (Pulliam, 1988).

The selection (non-neutral evolution) is imposed by s_t and is such that alleles have opposite effects, so that when an allele is advantageous, the other one is deleterious and vice versa, oscillating in effects as the environment changes. Over the cycle of fitness oscillations, both alleles experience the same magnitude and periods of fitness advantages and disadvantages, resulting in alleles being quasi-neutral (Hartl & Cook, 1973). In V population, $C_{V,a} = 1$ always—the ancestral allele experiences the full magnitude of fitness oscillations. When $C_{V,a} \neq C_{V,d}$ the two alleles experience different magnitudes of fitness oscillations, which provides an overall advantage to the allele with lower magnitude of fitness oscillations (Felsenstein, 1976), thus introducing a directional effect, in addition to the temporally varying selection. R population always experiences a lower magnitude of temporal oscillations ($0 \leq C_{R,.} < C_{V,.}$) and acts as the refuge needed to establish the spatial storage effect. Then, $C_{R,a}$ is the portion of relative fitness oscillations in R compared to the ancestral allele in V population, and captures the degree of spatial heterogeneity in temporally varying selection.

The variation in fitness emulates seasonal oscillations such as those due to changes in temperature, precipitation, or resource availability. The s_t is generated using the sine function with maximum deviation $s_{\max}$, such that $s_t$provides either a selective advantage or disadvantage at time *t* for the derived allele

$$s_t = s_{\max} \sin\left(2\pi \times \frac{t + r}{P}\right). \tag{3}$$

Here, *t* represents a generation within an oscillation cycle of *P* generations, while *r* is randomly selected between 0 and *P* and determines the starting point within the sine function for the simulation. This ensures that the derived allele is randomly advantageous or deleterious at the onset of each simulation run. If $s_{\max} = 0$, alleles evolve under neutrality.

The population size changes based on a logistic growth equation with

$$G_{i,t} = 1 + \delta_i \times \left(1 - \frac{N_{i,t}}{K_i}\right). \tag{4}$$

The number of individuals for the two alleles in each population in the next generation is sampled from the Poisson distribution with mean $N_{ia,t}{'}$ and $N_{id,t}{'}$ during the stochastic reproduction step.

Increasing the magnitude of varying selection over time

To simulate the increasing magnitude of fitness oscillations over time, we modify the numerator fitness deviation such that

$$s'_t = s_t \left(1 + \beta \frac{t}{t_{\max}}\right), \tag{5}$$

where β is the total relative increase in the magnitude of fitness oscillations over time.

Measuring genetic diversity and persistence

The expected heterozygosity in a population (i) at time t is

$$h_{i,t} = 2\ p_{i,t}q_{i,t}, \tag{6}$$

where $p_{i,t}$ is the frequency of the ancestral allele, a, and $q_{i,t}$ is the frequency of the derived allele, d, in a population i at time t. The weighted heterozygosity at time t across V and R is, thus,

$$h_t = \frac{2 \times\ p_{V,t}q_{V,t} \times\ N_{V,t}}{N_{V,t} +\ N_{R,t}} + \frac{2 \times p_{R,t}q_{R,t}\ \times\ N_{R,t}}{N_{V,t} +\ N_{R,t}}, \tag{7}$$

We report expected heterozygosity under the spatially heterogeneous temporally varying selection (model) relative to neutral expectation under the same mutation and migration rates,

$$h\ \left(\frac{\text{model}}{\text{drift}}\right) = \frac{\frac{\Sigma_n \frac{\Sigma_t h_{\text{model},\ t}}{T_{\text{model}}}}{n}}{\frac{\Sigma_n \frac{\Sigma_t h_{\text{drift},\ t}}{T_{\text{drift}}}}{n}}, \tag{8}$$

where n is the number of replicate simulations and $T.$ represents expected survival time under heterogeneous varying selection or drift. As both heterozygosity in residents and immigrants play a role in rapid adaptation in V, we measure heterozygosity at the level of the meta-system. The weighted heterozygosity assures that we estimate a probability of randomly choosing two different alleles within a population and not across populations, which is inflated by genetic differentiation (see Gulisija & Kim, 2015).

Measuring extinction

Each simulation run continues until the maximum allotted time ($100K_i$ generations) or until V becomes extinct. Extinction is defined by the subpopulation size falling below the critical value of 100 individuals (Gomulkiewicz & Holt, 1995). The maximum simulation time is an arbitrary period where persistence serves as a proxy for differential extinction rates under different parameters across time. That is, some populations will stably persist indefinitely (dash-dot line in Figure S3), while others will eventually become extinct. However, the rate of their extinction may differ across settings. With a long simulation time, we ensure that the difference in persistence reflects the difference in the rate of extinction under different parameters (colored lines, Figure S3).

Controls

We generated three controls. (1) Drift, where the force driving allele frequency changes within populations is stochasticity due to finite population size, with $s_{\max} = 0$. This control allows us to assess the presence and strength of the spatial storage effect. We define the relative heterozygosity h (model/drift) > 1.05, as an indicator that the storage effect has been established. (2) Monomorphic populations, which evolve in the absence of evolution (no mutation), where the frequency of the ancestral allele is always 1.0 in both populations. This control measures levels of survival under source-sink dynamics ($C_{\mathrm{R},.} = 0$, $C_{\mathrm{V},.} = 1$), here under reciprocal migration, in the absence of genetic diversity. (3) Uniform selection ($C_{\mathrm{R},.} = C_{\mathrm{V},.} = 1$), where forces driving population dynamics are temporally varying selection, genetic diversity, and migration, without spatial heterogeneity in the magnitude of selection. This control allows us to assess the levels of survival under the influx of mutants in the absence of conditions for the storage effect. While we retain $S_{\mathrm{V}} > 0$ and $S_{\mathrm{R}} = 0$, potentially allowing for source-sink dynamics, here both populations experience adverse conditions due to varying environments, as opposed to control (2).

Implementation and parameter settings

For each parameter combination, we conducted 4,000 replicate frequency-based forward-in-time simulation runs. We assume a constant carrying capacity of $K_i = 4{,}000$ individuals in each population, a maximum simulation time of $100K_i$ (400,000 generations), and a starting population size of 2,000 individuals in each population (V and R). We examine evolution under a wide range of magnitudes of varying selection, $s_{\max} = 0.0$ (drift), 0.1, 0.15, 0.2, 0.25, 0.3, or 0.35 in combination with a period of the oscillating cycle, $p = 12$, 24, or 48, and migration rates m_i, where at carrying capacity the number of reciprocal migrants is equal to $m_iK_i \in [1,100]$, in increments of 1. For the simulations where the magnitude of fitness oscillations increases over time, $s_{\max}$ effectively increases from 0.2 to 0.3 throughout the simulation, i.e., $\beta = 0.1$. The mean environmental effect in the harsh habitat was $S_{\mathrm{V}} = 0.3$, 0.35, 0.4, or 0.45, with $S_{\mathrm{R}} = 0.0$, and the proportion of fitness oscillations in R, $C_{\mathrm{R},.} = 0$, 0.167, 0.33, 0.5, 0.667, or $1 \times C_{\mathrm{V},.}$ (uniform control). Recurrent mutation occurs at a rate of $\mu K_i = 0.05$ per generation. In both populations, $\delta_i = 0.5$ within the logistic growth model.

Results

We find that the spatial storage effect arises in small populations of variable size experiencing heterogeneous temporal variation across a range of simulated parameters (Figure S4). In turn, the spatial storage effect increases persistence and average survival time by lowering the minimum number of migrants required to sustain a population compared to source-sink dynamics (Control 2; migration alone) (Figures 1 and 2, Figure S5). On the other hand, we observe no persistence under uniform temporally varying selection (Control 3). Despite $S_{\mathrm{V}} > 0$ and $S_{\mathrm{R}} = 0$, the source-sink dynamics did not arise when both populations experienced adverse conditions due to varying selection. Furthermore, this suggests that the influx of mutations alone is insufficient to maintain populations under varying selection when its magnitude does not vary across space.

The benefits of the storage effect are maintained when there is an increase in the magnitude of fitness oscillations over time (Figure 3) or through the introduction of milder temporally varying selection in the refuge, which reduces the level of spatial heterogeneity across the populations (Figure S6). Furthermore, the effect arises under changes in carrying capacity, and under asymmetric migration and selection (Figures S7–S9). We give details in the subsections below and then offer insight into how balanced polymorphism can buffer the effects of demographic stochasticity and enhance persistence in small, size-varying populations.

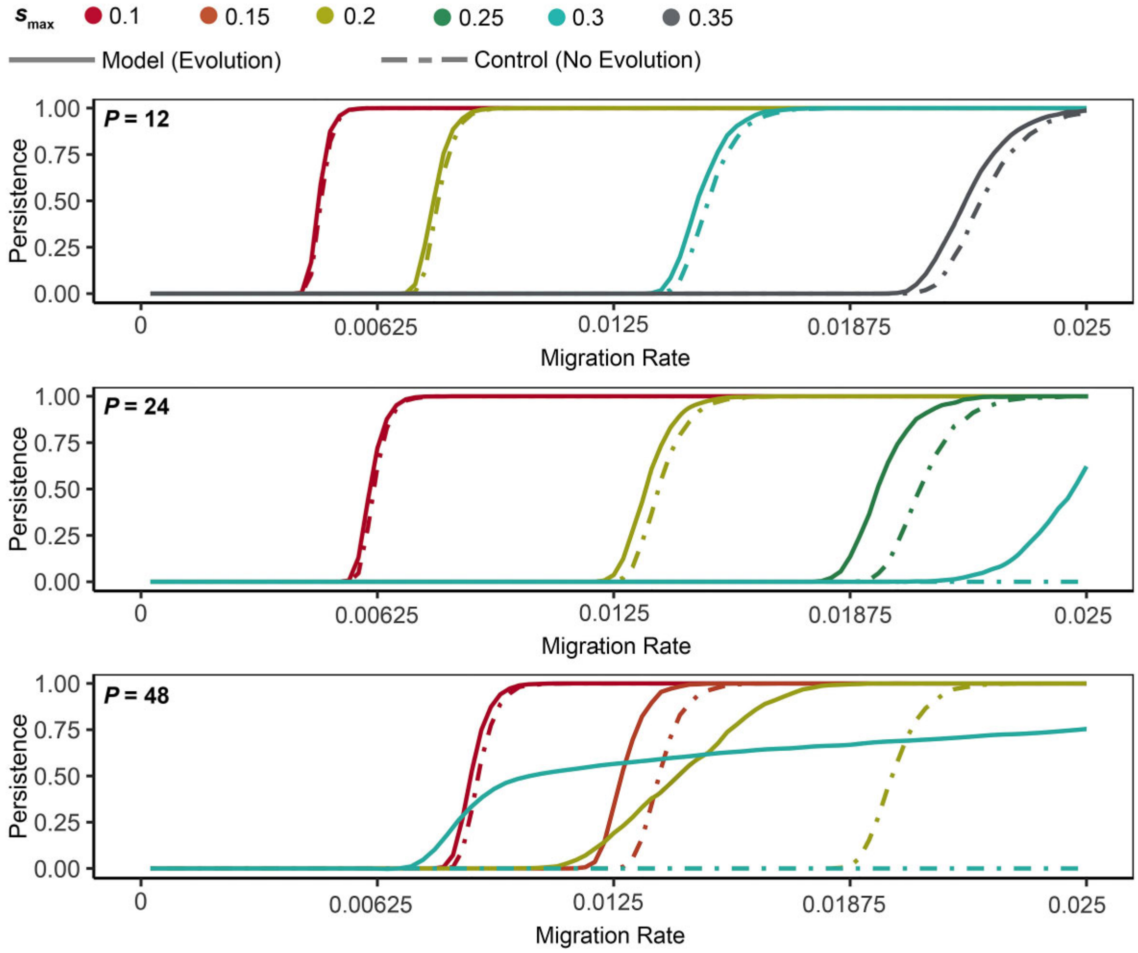

Figure 1. Population persistence for at least 100K_i generations in a harsh habitat that is under temporally varying selection under the heterogeneous temporally varying selection (evolution, model, solid lines) and source-sink dynamics (no evolution, control, dashed lines). Simulations assumed $p = 12$ (top), $p = 24$ (middle), and $p = 48$ (bottom), with $s_{max} = 0.1$ (red), 0.15 (orange), 0.2 (light green), 0.25 (green), 0.3 (turquoise), and 0.35 (grey). The x-axis shows m_i, such that at the carrying capacity, the number of reciprocal migrants $m_iK_i \in [1,100]$. The environmental mean effect, $S_V = 0.35$, while the recurrent mutation rate, $\mu = 0.0000125$ (model). Simulations were conducted over 4,000 replicate runs with a starting size of 2,000 individuals, a carrying capacity (K_i) of 4,000, and $C_{R,.} = 0$ and $C_{V,.} = 1$. These results demonstrate that the storage effect led to the increased population persistence by reducing the minimum number of migrants required for the same level of persistence as the control. The curves were smoothed using a loess function.

The spatial storage effect generates balanced polymorphism that leads to increased persistence of small populations in temporally varying environments

Population genetics theory suggests that the spatial storage effect in finite constant-size populations increases with population size and the magnitude of varying selection but decreases with the rate of environmental change (Gulisija & Kim, 2015). Here, we modeled rapidly changing conditions that emulate seasonal changes in environments, where a small population experiences a season for six, twelve, or twenty-four discrete generations ($p = 12$, 24, or 48), but under stochastically varying population sizes. In addition, we focused on populations with a limited influx of migrants, where migration is not likely to ensure persistence. We find that the spatial storage effect arises under reduced density dependence in small populations, and follows patterns reported by population genetics theory (Gulisija & Kim, 2015). In particular, previous research suggests that in rapidly shifting environments, such as $p = 12$, the spatial storage effect would be more effective in populations approaching panmixia. Indeed, we find that under $p = 12$ and low migration rates, balanced polymorphism is absent (Figure S4). However, as p increases, so do the levels of balanced polymorphism, as suggested by previous findings (Gulisija & Kim, 2015), leading to the emergence of the spatial storage effect across a broad set of parameters (Figure S4), despite relatively small and stochastically changing population sizes (Figure 4).

Over the range of parameters, we observe a reduction in the minimum number of migrants needed for a population to persist at the same rate under the spatial storage effect compared to source-sink dynamics (Figure 1, Figure S5). While persistence is observed under the source-sink dynamics, genetic diversity uniformly increases persistence compared to this control, more so when the spatial storage effect is observed. That is, with rapid environmental change ($p = 12$), the modest increase in persistence relative to the monomorphic control is primarily driven by the continual influx of new mutants when the storage effect is absent (Figure 1). However, as p increases, balanced polymorphism arises even under low migration rates (see Gulisija &

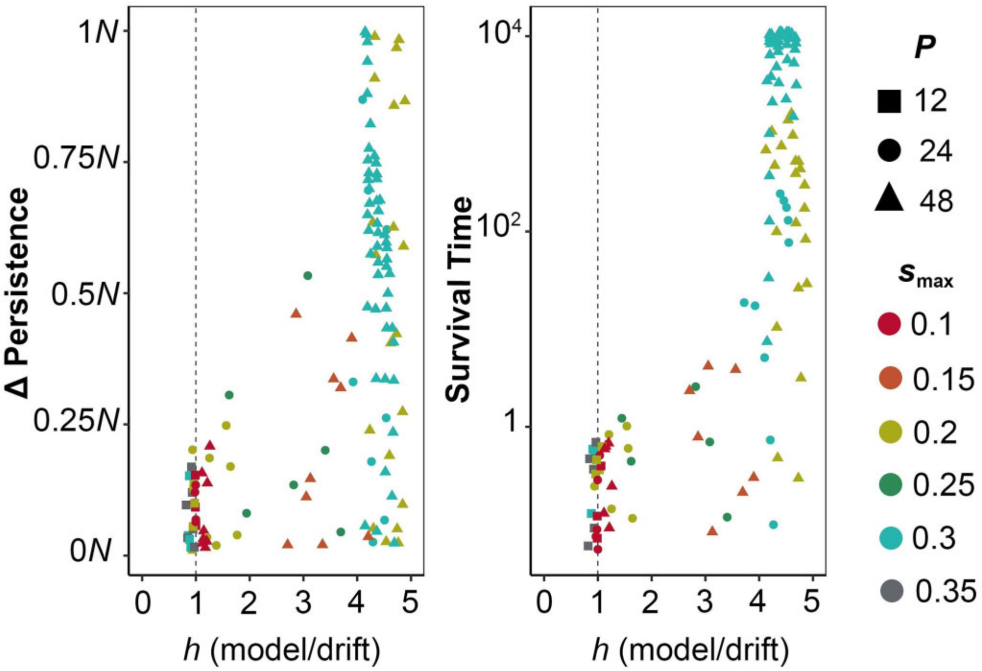

Figure 2. Impact of the level of genetic polymorphism on the differential persistence and the time at which a population became extinct (survival time) compared to monomorphic controls. Survival time was quantified as its relative increase in polymorphic populations compared with monomorphic controls [(test-control)/control]. Note a nonlinear scale display on the y-axis. Simulations assumed a variety of S_V (S_V = 0.3, 0.35, 0.4, 0.45) and s_{max} (s_{max} = 0.1, 0.15, 0.2, 0.25, 0.3, and 0.35) with $C_{R,.} = 0$ and $C_{V,.} = 1$, and $p = 12$, $p = 24$, and $p = 48$, and were conducted over 4,000 replicate runs in temporally varying environments with a starting size of 2,000 individuals, carrying capacity (K_i) of 4,000, and recurrent mutation rate $\mu = 0.0000125$. We included test populations with at least 5% higher persistence compared to the control populations to avoid a cluster of points around zero in cases where migration alone results in full persistence. A level of persistence and an average survival time appear to increase with levels of genetic polymorphism, with values to the right of the vertical dashed line falling under the spatial storage effect.

Kim, 2015). Here, population persistence notably improves across a range of parameters, including the rate of environmental change (number of generations that experience environmental oscillations, p = 24 or 48), the magnitude of varying selection (s_{max}), the migration rate (m_i), and a range of harshness in habitats (S_V) (Figure 1 and Figure S5). The effect is larger with higher levels of balanced polymorphism (Figure 2, refer to Figure 1 and Figure S4). For example, with p = 24 when the number of migrants approaches a rate equivalent to 100 migrants, and with p = 48 with a migration rate equivalent to about 50 or more migrants, under the carrying capacity, we observe notable increases in population persistence corresponding to a notable increase in the level of diversity (Figure S4). Under these conditions, we observe that all populations (Figure 1, light green line) or a considerable proportion of populations (Figure 1, turquoise line) persist until the maximum simulation time for p = 48, while all populations under source-sink dynamics (no evolution) become extinct at the same settings, including the same migration rate.

Differences in persistence between polymorphic and monomorphic populations increase markedly with greater diversity under the spatial storage effect (Figure 2, left panel), highlighting balanced polymorphism as the key to notably elevated persistence. Additionally, under the spatial storage effect, survival time increases with heterozygosity, highlighting its crucial role in delaying extinction (Figure 2, right panel). That is, even when populations did not reach the maximum simulation time, they still survived for longer than those under the source-sink dynamics alone, more so if balanced polymorphism was present. This is an important effect since a longer survival time could provide more opportunities for the environmental conditions to change or for the population to expand its range into a more favorable habitat, thus ultimately avoiding extinction.

Robustness of the persistence-promoting effect to environmental and demographic settings

Next, we modeled the incremental increase in the magnitude of environmental oscillations (s_{max} = 0.2 → 0.3) over the course of simulations as arises under global climate change (Rudgers et al., 2018) (Figure 3). Here, the increase in the magnitude of varying selection produces patterns of persistence at intermediate levels compared to the constant magnitude at starting and ending levels for the test and control populations, as well as corresponding intermediate levels of heterozygosity (Figure 3, right panels). Hence, in the cases where the spatial storage effect leads to a sizable increase in persistence at constant s_{max}, it also leads to a proportional increase in persistence under increasing selection magnitude. These results indicate that populations will be more likely to persist for a longer time when the magnitude of environmental oscillations increases gradually than during the sudden onset of strong environmental oscillations, such as migration to a new variable habitat or during an extreme climate event.

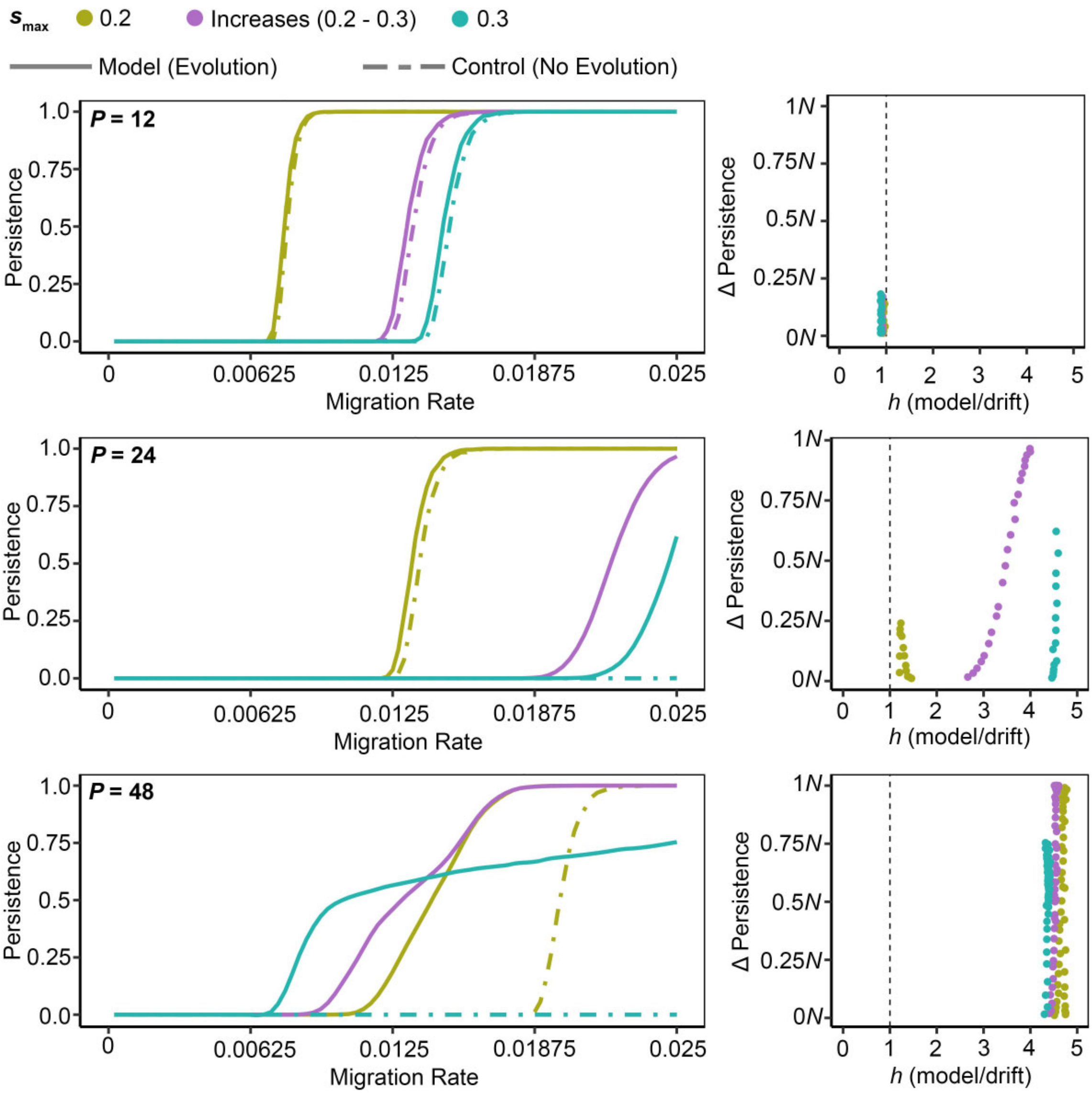

Figure 3. The population persistence in a habitat that is under temporally varying selection for at least $100K_i$ (400,000) generations when the magnitude of varying selection increases. Simulations assumed $p = 12$ (top), $p = 24$ (middle), $p = 48$ (bottom), each with $s_{max} = 0.2$ (light green), increasing from 0.2 to 0.3 (purple), or 0.3 (turquoise), with $S_V = 0.35$ and $C_{R,.} = 0$ and $C_{V,.} = 1$. The left panels show the persistence for test populations under the recurrent mutation with $\mu = 0.0000125$ (solid line) or under the monomorphic control (source-sink dynamics, dashed line), with the x-axis showing m_i, such that $m_iK_i \in [1,100]$. The right panels show the level of persistence given the heterozygosity level. Simulations were conducted over 4,000 replicate runs with a starting size of 2,000 individuals and a carrying capacity (K_i) of 4,000 in each subpopulation. Note that the populations that experienced a gradual change in selection ($s_{max} = 0.2$ to 0.3) had higher rates of persistence compared to the populations that were immediately placed under a high level of selection ($s_{max} = 0.3$). The curves were smoothed using a loess function.

Next, we decrease the level of spatial heterogeneity by introducing temporally varying selection to the R population, with the magnitude of $C_{R,.}s_{max}$ and $C_R < 1$. Despite the reduction in spatial heterogeneity, an increase in population persistence is still evident, but to a lesser degree than when there is no temporal variation in R. The relative increase in persistence gradually diminishes as $C_{R,.}$ increases from 0 (control) to 0.1667 and 0.33 (Figure S6). Notably, this pattern disappears when $C_{R,.} \geq 0.5$, as both the test populations (diversity and migration) and the control populations (migration alone) fail to persist, except for a small number of survivors with $C_{R,.} = 0.5$, $P = 48$, and $M_i > 93$. In general, decreasing the degree of heterogeneity between populations creates overall harsher conditions, and the opportunities for population persistence rapidly shrink (the minimum number of required migrants increases) for both test and control settings.

We also demonstrate the generalizability of our results across different carrying capacities. Deterministically, when population size falls below carrying capacity, the number of offspring produced increases [Eq. (4)]. Larger carrying capacity then provides greater buffering against population declines, thereby reducing the minimum number of migrants needed for population persistence, than the lower ones. However, this reduction occurs proportionally in both the model and control populations (Figure S7), so the overall pattern of increased persistence due to the storage effect remains consistent across changes in K_i.

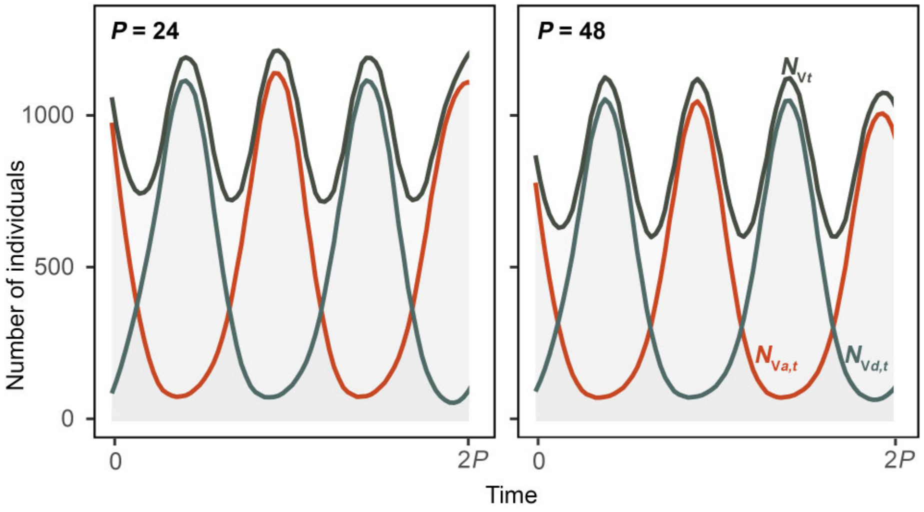

Figure 4. The expected number of individuals that carry the ancestral ($N_{Va,t}$) or derived ($N_{Vd,t}$) allele over 2p generations in stably oscillating V populations of total size $N_{V,t}$, where the storage effect was established ($h = 3.40$, and 3.90 for $p = 24$ and 48) under $P \times s_{\max} \times m_i$ of 24 ×0.25 × 0.02125 and 48 ×0.15 × 0.01375, under the heterogenous temporally varying selection. Simulations were conducted over 4,000 replicate runs with a starting size of 2,000 individuals and a carrying capacity (K_i) of 4,000. The number of individuals was measured after 399,000 generations of density-regulated varying selection in 3,834 and 3,816 persisting populations for $p = 24$ and 48. The curves were smoothed using a loess function.

Robustness of the persistence-promoting effect to asymmetry in migration and selection

Next, using a sample of trajectories where the storage effect either fails to emerge or does emerge ($p \times s_{\max} = 12 \times 0.35$, 24×0.25, and 48×0.15), we examine how increased persistence responds to asymmetries in migration rates between populations (Figure S8) and differences in selection magnitude between alleles (Figure S9).

In our model, although migration rates are symmetric between the two populations, the number of migrants is not, as it depends on the population size, $m_i N_{i,t}$, which is expected to be smaller in V (since $S > 0$, $N_{V,t} < N_{R,t}$). In V, the number of emigrants is expected to be smaller than the number of immigrants, even with an equal migration rate. We tested how introducing asymmetric migration rates, either increasing or decreasing this asymmetry between emigration and immigration, further affects the presence of the storage effect and resulting population persistence (Figure S8). In monomorphic populations, a reduction in emigration rates marginally increases persistence, likely because fewer individuals leave the perturbed population, thereby allowing for more effective source–sink dynamics. Under the introduction of mutation, when no storage effect was observed ($p = 12$), this effect was only slightly enhanced with reduced emigration rates. When emigration rates were increased, neither the control nor the model populations persisted, likely due to the rapid depletion of individuals from V. However, under the storage effect ($p = 24$ and 48), varying migration rates had a dramatic influence on persistence: lower migration rates increased persistence more than observed in the absence of the storage effect, while higher emigration elevated the levels of balanced polymorphism (not shown) and strongly enhanced persistence, even when no populations persisted in the absence of diversity, such as under $m_V/m_R = 1.25$ with $p = 24$ or 1.5 with $p = 48$. These results are in accordance with previous constant-sized population results, indicating the storage effect increases at nontrivial migration rates (Gulisija & Kim, 2015).

Our main results assume symmetric selection magnitudes between the two alleles ($s_{\max}$), as our primary aim was to examine population persistence under varying selection without introducing directional bias. In nature, however, alleles are not necessarily quasi-neutral (Hartl & Cook, 1973), and directional selection can arise when one allele has a lower or higher magnitude of fitness oscillations (Felsenstein, 1976). Although the storage effect is somewhat robust to small differences in mean fitness, it breaks down when selection strongly favors one allele in constant-sized populations (Gulisija & Kim, 2015). Here, we tested how differences in selection magnitude between ancestral and derived alleles influence the persistence-promoting effect of the storage effect in populations of variable size. Reducing the selection magnitude on the derived allele increases persistence, likely due to an overall reduction in the harshness of the environment. In contrast, increasing the variability in fitness of the derived allele can reduce persistence when the storage effect is absent ($p = 12$) (Figure S9, top panel). However, when the storage effect is present, it remains robust to increases in selection magnitude on the derived allele and continues to enhance persistence relative to the control (Figure S9, middle and bottom panels).

Overall, the emergence of the storage effect appears to be most strongly influenced by the degree of spatial heterogeneity in selection and by the migration rate. The general trend of increased persistence under the storage effect is robust to parameter perturbations and asymmetries, suggesting that, broadly, the storage effect can enhance population survival beyond what is expected in its absence and reduce the number of migrants required for the same level of persistence.

On how balanced polymorphism promotes population persistence

Here, we provide an intuition on how balanced polymorphism promotes the persistence of small populations in temporally varying environments.

Consider the change in the size of the subpopulations of carriers for each genotype, *d* and *a*, in V population under the eco-evolutionary population dynamics given in (1) and (2), i.e., $N_{\mathrm{V}d,t}{}' = (1.0 - S_{\mathrm{V}} + s_t) \times G_{\mathrm{V},t} \times N_{\mathrm{V}d,t}$, and $N_{\mathrm{V}a,t}{}' = (1.0 - S_{\mathrm{V}} - s_t) \times G_{\mathrm{V},t} \times N_{\mathrm{V}a,t}$. Here, s_t is a selection parameter, a genotype-based relative fitness deviation at time *t* due to varying selection. The ecological parameters are the environmental harshness S_{V} and density-dependent population growth rate $G_{\mathrm{V},t}$. The expected change in population size due to the selection on carriers of *d* allele is then

$$\Delta N_{\mathrm{V}d,t} \propto s_t \times G_{\mathrm{V},t} \times N_{\mathrm{V}d,t}\,,$$

while due to the change in the number of *a* carriers

$$\Delta N_{\mathrm{V}a,t} \propto -(s_t \times G_{\mathrm{V},t} \times N_{\mathrm{V}a,t}),$$

where $N_{\mathrm{V}d,t} = N_{\mathrm{V},t} \times q_{\mathrm{V},t}$ and $N_{ia,t} = N_{\mathrm{V},t} \times p_{\mathrm{V},t} = N_{\mathrm{V},t}\,(1 - q_{\mathrm{V},t})$, with $p_{\mathrm{V},t}$ being the frequency of the ancestral allele, *a*, and $q_{\mathrm{V},t}$ being the frequency of the derived allele, *d*, where $N_{\mathrm{V}d,t} = N_{\mathrm{V},t} \times q_{\mathrm{V},t}$ and $N_{ia,t} = N_{\mathrm{V},t} \times p_{\mathrm{V},t} = N_{\mathrm{V},t}\,(1 - q_{\mathrm{V},t})$. Then, the expected change in population size, $\Delta N_{\mathrm{V},t}$, due to varying selection is a sum of changes in the number of individuals due to selection on *d* and due to selection on *a*:

$$\Delta N_{\mathrm{V},t} \propto [s_t \times G_{\mathrm{V},t} \times N_{\mathrm{V},t} \times q_{\mathrm{V},t} - (s_t \times G_{\mathrm{V},t} \times N_{\mathrm{V},t}(1 - q_{\mathrm{V},t}))].$$

The smallest expected absolute change in population size due to selection, with expression above being zero, occurs when $q_{\mathrm{V},t} = 1 - q_{\mathrm{V},t}$, i.e., $p_{\mathrm{V},t} = q_{\mathrm{V},t} = 0.5$–under maximum polymorphism, since here, selection is symmetric and its effects on the two alleles cancel out. On the other hand, the largest expected absolute change in population size due to selection $|\Delta N_{\mathrm{V},t}| \propto s_t \times G_{\mathrm{V},t} \times N_{\mathrm{V},t}$ occurs when $q_{\mathrm{V},t} = 1$ or 0, i.e., in a monomorphic population. The degree of variation in population size is a decreasing function of genetic variance (heterozygosity), $2p_{\mathrm{V},t}q_{\mathrm{V},t}$.

For a small population, over a cycle of environmental variation, less perturbation to population size is expected to occur in a polymorphic population compared to a monomorphic population with the same parameters, which results in a smaller risk of reaching the absorbing state of extinction. The balanced polymorphism due to the spatial storage effect will therefore allow small populations to stably persist when they would perish otherwise.

Here, evolution occurs as a change in the number of individuals of two genotypes. While one subpopulation rapidly declines, the other counterbalances this effect by a rapid increase, thereby stabilizing the overall population size and enabling smaller populations to persist at a higher rate than would be possible in the absence of balanced polymorphism.

For illustration, we present total population size, $N_{\mathrm{V},t}$, with genotype subpopulation sizes, $N_{\mathrm{V}a,t}$ and $N_{\mathrm{V}d,t}$ under our eco-evolutionary model, which allows stochastic size fluctuations, and where the storage effect was detected (Figure 4). While each genotype subpopulation oscillates notably and intermittently drops to near extinction, their mirrored oscillations balance each other, resulting in milder total population fluctuations (Figure 4, top lines). This stability maintains total population sizes, which oscillate around 1,000 individuals, demonstrating the mechanism behind the increased persistence described above.

Notably, the figure above shows that population sizes at equilibrium still vary temporally. These size oscillations can have important implications for selective dynamics, as they may increase or decrease competition between genotypes, allowing the realized mode of selection to fall between two theoretical extremes. At one end is soft selection (Wallace, 1975), where local density dependence maintains constant population sizes, leading to intense competition in which a genotype's success depends on its fitness, i.e., fecundity and survival, relative to other genotypes. Importantly, soft selection is thought to be more permissive of genetic polymorphism (Chen & Kassen, 2020; Christiansen, 1975; Dempster, 1955). At the other end is hard selection (Wallace, 1975), where offspring numbers depend solely on each genotype's fecundity and survival rather than the presence of other genotypes, and thus, both genotype frequencies and total population size may vary. Here, selection acts in a density-independent manner and tends to homogenize genetic variation. Our model assumptions fall between the two extremes: density dependence is maintained through a tendency toward carrying capacity, but its strength varies with current population size [Eq. (4)]. This results in a less rigid system than the strict soft selection typically assumed in traditional population genetics theory. Although the theoretical foundations of the storage effect typically assume strong competition under constant population sizes (see Chesson & Warner, 1981), we show that the effect remains robust even when these assumptions are relaxed and population sizes fluctuate. In fact, as shown in Figure 4, the average population size is lower and more variable under the longer environmental period, yet genetic polymorphism is higher. Furthermore, when we introduce directional selection favoring or disfavoring the derived allele—thereby introducing asymmetric variation in the number of offspring between alleles—the storage effect still promotes persistence (Figure S9). The polymorphism-promoting effect holds across different carrying capacities as well (Figure S7). These findings suggest that the storage effect can operate robustly under mixed regimes of hard and soft selection, as might realistically arise in nature.

Discussion

In this study, we investigated whether the spatial storage effect can arise in finite populations inhabiting spatially heterogeneous variable habitats under relaxed density dependence and whether it can promote their persistence. Indeed, the spatial storage effect arises and promotes population persistence beyond levels expected in the absence of balanced polymorphism, thus leading to evolutionary rescue in rapidly changing environments. Here, the rapid population decline due to selection against seasonally detrimental genotypes is offset by a rapid increase due to selection favoring seasonally beneficial genotypes across environments. We demonstrate that this effect arises not only in small populations with stochastically fluctuating sizes but also across a range of parameter perturbations, including asymmetries in emigration and immigration rates, as well as in fitness oscillations between alleles.

Temporally varying selection is likely to arise in populations where parents and offspring experience different environmental conditions, driven by changes in factors such as temperature, precipitation, or salinity (e.g., Bickley & Anderson, 2025; Rudgers et al., 2023). Since habitats may be spatially heterogeneous, the strength of selection may also vary across space. For instance, brackish coastal waters are known to exhibit salinity fluctuations (Bickley & Anderson, 2025) that are notably greater than those in adjacent freshwater or open marine environments. In arid regions, plants often inhabit patches exposed to extreme and highly variable precipitation patterns over time (Rudgers et al., 2023). However, if organisms disperse to nearby agricultural areas or riparian zones such as river bosques, these severe drought conditions may be absent. Such environmental contrasts create ideal conditions for the spatial storage effect.

The theory of the storage effect has a long tradition in community ecology, with recent extensions into population genetics. The concept of the storage effect in the context of species coexistence was pioneered by Peter Chesson (Chesson, 1982, 1994, 2000; Chesson & Warner, 1981). The theory proposes that environmental variability can promote coexistence in competitive systems under heterogeneous, varying selection by enabling less abundant species to capitalize on favorable conditions while being partially buffered from detrimental conditions as environments change. Recently, the storage effect has been adapted to population genetics, emerging as a key mechanism that explains the existence of temporally varying balanced polymorphism. For example, heterogeneous varying selection may arise across life stages with reduced effect in overlapping generations (Ellner & Hairston, 1994; Turelli et al., 2001), in the presence of phenotypic plasticity (Gulisija et al., 2016), under maternal effects (Yamamichi & Hoso, 2016), or when the magnitude of varying selection differs across spatial gradients (Gulisija & Kim, 2015). Gulisija & Kim (2015) found that the spatial storage effect promotes long-lived balanced polymorphism across a wide range of naturally plausible parameters in competitive systems modeled within the Wright-Fisher population framework (Gulisija & Kim, 2015). More recently, Yuseob Kim (2023) extended this work to incorporate eco-evolutionary dynamics, proposing that correlated oscillations in both carrying capacity and allelic fitness may produce outcomes that differ from traditional population genetics predictions. While this work was groundbreaking in incorporating the spatial storage effect into an eco-evolutionary framework, it did not examine stochastic perturbations to population size or explore the possibility of population extinction.

Our study incorporates demographic stochasticity, relaxing density dependence while allowing for extinction. This framework enables an evaluation of the role of the spatial storage effect in population persistence—an aspect that had not been previously examined, despite the recognition that balanced polymorphism is critical for adaptation to changing conditions (Barrett & Schluter, 2008). We find that the storage effect not only promotes population persistence under eco-evolutionary dynamics but also exhibits the same key population genetics properties observed in constant-size Wright-Fisher models, under constant carrying capacity. This suggests that since the balancing genetic effects of the spatial storage effect are preserved between the constant-sized populations (Gulisija & Kim, 2015) and the eco-evolutionary dynamics examined here, the persistence-promoting effect may extend to other scenarios where other forms of the storage effect generate balanced polymorphisms, which were previously explored only in the framework of population genetics theory (Gulisija & Kim, 2015; Gulisija & Plotkin, 2017; Gulisija et al., 2016; Park & Kim, 2019; Svardal et al., 2011, 2015; Yamamichi & Hoso, 2016).

Extending population genetics models to incorporate a combination of soft and hard selection is essential for a realistic understanding of how environmental change impacts biodiversity. Two main processes that operate in populations are population size fluctuations and evolutionary change, yet they tend to be separated in theoretical studies (Yamamichi et al., 2023). Without examining the two processes jointly, we cannot consider how genetic adaptation rescues populations otherwise destined to perish (Bell & Gonzalez, 2009; Gomulkiewicz & Holt, 1995; Gonzalez et al., 2013). The theory of evolutionary rescue provides a framework that incorporates demographical and evolutionary dynamics in populations whose sizes vary (Alexander et al.,., 2014; Lindsey et al., 2013; Orr & Unckles, 2008, 2014; Uecker & Hermisson, 2016; Uecker et al., 2014; Wilson et al., 2017). In particular, Uecker et al. (2014) introduced habitat structure within a source–sink framework and examined the effects of migration and genetic variation on evolutionary rescue, reporting significant impacts of both. However, the study focused on directional selection and did not include varying fitnesses or balanced polymorphism.

Despite evolutionary rescue's relevance to populations facing rapidly changing environments, few studies have explored evolutionary rescue under temporally varying selection (e.g., Carja & Plotkin, 2019). However, this connection needs to be explored since conditions that change quickly may necessitate rapid adaptation from balanced genetic polymorphism. To predict the fate of future populations that are at risk for extinction due to increasingly extreme shifts driven by climate change (Fischer et al., 2013; Rahmstorf & Coumou, 2011; Rudgers et al., 2018; Sheridan & Lee, 2018), a synthesis of models of balancing selection and those of population size dynamics in rapidly changing environments is essential. Here, we propose a model that utilizes stochastically varying population sizes and incorporates the spatially heterogeneous temporally varying selection to examine conditions for rescue from balanced polymorphism in the face of rapid environmental change.

A caveat of this study is that we only examine one form of the storage effect, the spatial storage effect. The spatial storage effect relies on strong spatial heterogeneity across an environment and reciprocal migration. As a proof-of-concept, we examined a scenario involving populations that exchange migrants proportionally to their sizes, which are allowed to stochastically vary. This form of the storage effect requires reciprocal migration, more so when environments oscillate rapidly (Gulisija & Kim, 2015), which may have resulted in the absence of balanced polymorphism with short cycles, $p = 12$. How the other common forms of the storage effect, which do not rely on migration, impact eco-evolutionary dynamics in rapidly changing conditions is not clear. For example, the genomic storage effect arises under phenotypic plasticity (Gulisija et al., 2016) and does not depend on migration but on genetic recombination. Broader forms of the storage effect need to be addressed in future studies in order to ascertain if the mechanisms offer more widely applicable paths to increased persistence.

In conclusion, our study expands our understanding of scenarios where the spatial storage effect can be established and uncovers a mechanism by which it promotes population persistence in the face of rapidly changing environmental conditions. This persistence-promoting effect could affect eco-evolutionary dynamics in other cases of environmental change. For example, populations may undergo range expansion or habitat invasions. Range limits are a major concern for populations under the environmental variation caused by climate change (Holt et al., 2022). In addition, previous studies have demonstrated that past invaders and projected future climate migrants are particularly likely to come from habitats with temporal variability (Lee & Gelembiuk, 2008; Stern & Lee, 2020). Studying evo-evolutionary dynamics in small founder populations originating from heterogeneous, varying habitats could provide insights into how invaders establish in a novel habitat. Understanding the role of the storage effect in these other scenarios will become increasingly important as more populations face extreme environmental changes (Fischer et al., 2013; Rahmstorf & Coumou, 2011; Rudgers et al., 2023; Sheridan & Lee, 2018).

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

The code used to generate the results in this study is publicly available on Dryad, DOI: 10.5061/dryad.fqz612k51.

Author contributions

D.G. conceived the study and designed the initial model and simulation code. E.N.R. modified the code and generated the data and figures. D.G. and E.N.R. designed the study and co-wrote the article.

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Conflict of interest

The authors declare no conflict of interest.

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