

Contrasting effects of ecological and evolutionary processes on range expansions and shifts

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Abstract

Research has conclusively demonstrated the potential for dispersal evolution in range expansions
3 and shifts through a process termed spatial sorting. However, the degree of dispersal evolution ob-
served has varied substantially among organisms. Further, it is unknown how the factors influenc-
ing dispersal evolution might impact other ecological processes at play. We use an individual-based
6 model to investigate the effects of the underlying genetics of dispersal and mode of reproduction in
range expansions and shifts. Spatial sorting behaves similarly to natural selection in that dispersal
evolution increases with sexual selection and loci number. Contrary to our predictions, however, in-
9 creased dispersal does not always improve a population's ability to track changing conditions. The
mate finding Allee effect inherent to sexual reproduction increases extinction risk during range
shifts, counteracting the beneficial effect of increased dispersal evolution. Our results demonstrate
12 the importance of considering both ecological and evolutionary processes for understanding range
expansions and shifts.

Introduction

15 Range expansions and shifts have become ubiquitous features of modern biomes. For centuries, humans have facilitated the range expansions of invasive species through travel, commerce, agriculture, and other routes (Elton, 1958), a trend that has only increased with further globaliza-
18 tion (Hulme, 2009). In recent decades, anthropogenic climate change has led to additional range expansions in a wide variety of taxa as species move to track changing climatic conditions (Parmesan, 2006). Further, range expansions are common in conservation settings as successfully reintroduced
21 species expand throughout their former habitats (Smeraldo *et al.*, 2017). Given the widespread occurrences of range expansions and their importance for conservation, dynamics of range expansions have been studied intensively from both ecological (Hastings *et al.*, 2005) and evolutionary (Ex-
24 coffier *et al.*, 2009; Shine *et al.*, 2011) perspectives. How these underlying ecological and evolutionary dynamics interact to shape the outcomes of range expansions remains an open question with great potential to shape our predictions of changes in biodiversity in the coming decades (Miller
27 *et al.*, 2020).

One crucial feature of the evolutionary dynamics of range expansions is the process of spatial sorting, in which individuals aggregate in space according to their dispersal phenotypes (Shine
30 *et al.*, 2011). The expansion edge, by definition, will be composed of individuals which dispersed the greatest distances, while individuals with lower dispersal distances will remain closer to the population core. If dispersal is a heritable trait, then mating among high dispersing individuals
33 at the edge will produce offspring with high dispersal phenotypes (Fronhofer & Altermatt, 2015), leading to a feedback between increased dispersal evolution at the edge and greater rates of expansion (Burton *et al.*, 2010; Ochocki & Miller, 2017; Perkins *et al.*, 2013; Phillips *et al.*, 2006;
36 Weiss-Lehman *et al.*, 2017; Williams *et al.*, 2016). Unlike traditional trait evolution due to natural selection, this evolutionary mechanism does not require differential reproductive success to

act on dispersal (Shine *et al.*, 2011). However, the occurrence of such a differential, for example
39 due to a release from intraspecific competition at the low density range edge, likely accelerates
the process (Perkins *et al.*, 2013). While evidence for this phenomenon has accumulated in both
laboratory and field settings, studies have shown a wide range in the degree to which spatial sorting
42 affects the dynamics of range expansions (Miller *et al.*, 2020).

In laboratory studies that explicitly test the role of spatial evolutionary processes in range ex-
pansions, spatial sorting led to faster range expansions on average (Ochocki & Miller, 2017; Szűcs
45 *et al.*, 2017; Weiss-Lehman *et al.*, 2017; Williams *et al.*, 2016), though the degree to which it ac-
celerated expansions varied among organisms. Increased rates of expansion can be problematic
in the context of invasive species (Phillips *et al.*, 2006), but it could be beneficial to species ex-
48 panding their ranges in response to climate change as increased dispersal abilities allow species to
better track changing climatic conditions (Boeye *et al.*, 2013). However, given the increasing rate
of climate change (Chen *et al.*, 2017) and the substantial gap between current dispersal capabilities
51 and those necessary to keep pace with climate change in some species (Schloss *et al.*, 2012), it is
unclear if dispersal evolution will be enough to rescue faltering populations. Some theoretical mod-
els suggest that dispersal evolution could indeed provide a buffer, allowing populations otherwise
54 doomed to extinction to persist (Boeye *et al.*, 2013), but others show it may be insufficient by itself
to prevent the extinction of struggling populations (Weiss-Lehman & Shaw, 2019). Therefore, it
is critical to understand the factors underlying dispersal evolution in range expansions, and when
57 dispersal evolution will lead to increased spread rates.

The rate of evolution due to natural selection is known to increase with sexual reproduc-
tion (Goddard *et al.*, 2005) and the number of loci defining the trait (Orr & Otto, 1994; Pritchard
60 *et al.*, 2010; Zeyl *et al.*, 2003). Some work suggests that spatial sorting can be regarded as a spa-
tial analogue to natural selection (Phillips & Perkins, 2019), suggesting that dispersal evolution in
range expansions may be affected similarly by mode of reproduction or the number of loci under-

63 lying dispersal. However, spatial sorting is not exactly analogous to natural selection, as it does
not require a fitness differential (Shine *et al.*, 2011). Further, even if sexual reproduction or more
loci contributing to dispersal increase the rate of dispersal evolution, it is unclear how these factors
66 might interact with the ecological processes of range expansion. For example, the serial founding
events of a range expansion could result in mate finding Allee effects in a sexually reproducing
species, potentially limiting expansion speed (Shaw & Kokko, 2015). Such ecological processes
69 are likely even more important in range expansions due to climate change in which there could be
simultaneous range contractions at the opposite range edge. As dispersal evolution has the poten-
tial to be a critical factor in the persistence of species shifting their ranges with climate change, it is
72 imperative to understand how these evolutionary and ecological factors interact to shape dispersal
evolution and expansion dynamics.

To explore the interplay between evolutionary and ecological aspects in shaping dispersal evo-
75 lution and dynamics of range expansions, we constructed an individual-based model to explore
the role of genetic structure (ploidy level and the number of loci defining dispersal) and the mode
of reproduction (asexual vs. sexual and the role of self-fertilization) in dispersal evolution during
78 range expansions. We explored the role of these factors in unbounded range expansions and in
range shifts (range expansion at one edge coupled with range contraction at the opposite edge).
By using a single, common framework to explore these factors, we directly compared the effect
81 of each on the rate of dispersal evolution and related them to the extinction risk faced by popu-
lations shifting their ranges in response to climate change. We predicted that, analogous to traits
evolving via natural selection, spatial sorting would more effectively increase dispersal phenotypes
84 under sexual reproduction and with greater numbers of loci contributing to dispersal. Further, we
hypothesized that this increased rate of dispersal evolution would lead to lower extinction risk in
populations shifting their ranges in response to simulated climate change.

Methods

Model overview

Our model examined population dynamics of a single species within a 1-dimensional landscape consisting of discrete habitat patches. We implemented a life cycle consisting of non-overlapping generations in which individuals first dispersed among patches according to their dispersal trait and then reproduced within their patch. An individual's dispersal trait was defined by a variable number of loci, each contributing additively to the overall trait value. Individuals could be either haploid or diploid and reproduction occurred either asexually or sexually. In sexually reproducing populations, individuals could be either dioecious or monoecious with variable levels of self-fertilization in monoecious populations. For our experimental scenarios, we varied (1) the number of loci defining dispersal, (2) the haploid or diploid nature of the population, (3) the mode of reproduction, and (4) the level of self-fertilization in sexually reproducing monoecious populations. All simulations were performed in R (version 3.5.3 (R Core Team, 2019)) and run on the Teton Computing Environment, Intel x86_64 cluster (Advanced Research Computing Center, 2018). All model code is available through GitHub (<https://github.com/tpweiss06/DispersalEvolution>; upon acceptance of the manuscript we will create a more permanent archive of the model code on Zenodo). Below, we describe each aspect of our model in greater detail.

Environment

Landscapes consisted of linear, 1-dimensional arrays of discrete habitat patches. Environmental conditions in each patch (x) were defined by the carrying capacity $K(x)$, which could range from 0 (uninhabitable) to a maximum value of K_{max} . To simulate range boundaries, we defined two additional parameters: τ defined the width of the range core, in which $K(x) = K_{max}$, and γ was the

rate of decline in $K(x)$ at the range edges. More precisely, the carrying capacity of each patch was given by

$$K(x) = \begin{cases} \max(0, (1 - \gamma(\beta(t) - \tau - x))K_{max}) & \text{if } x < \beta(t) - \tau \\ K_{max} & \text{if } \beta(t) - \tau \leq x \leq \beta(t) + \tau \\ \max(0, (1 - \gamma(x - \beta(t) - \tau))K_{max}) & \text{if } x > \beta(t) + \tau \end{cases} \quad (1)$$

105 in which $\beta(t)$ defined the center of the range. When initiating simulations, $\beta(0) = 0$ but it changed linearly in some scenarios to simulate range shifts due to climate change (see *Experimental scenarios* below).

108

Dispersal

In each generation, individuals first dispersed among the discrete habitat patches making up the landscape. Each individual dispersed according to an exponential dispersal kernel defined by the individual's dispersal trait. The dispersal trait for an individual i was the expected dispersal distance for an individual (d_i), given by

$$d_i = \frac{\hat{d}e^{\rho(\Sigma L - \lambda)}}{1 + e^{\rho(\Sigma L - \lambda)}} \quad (2)$$

where \hat{d} was the maximum expected dispersal distance in terms of discrete patches, ρ and λ were constants determining the slope and location of the transition between 0 and \hat{d} , and the summa-
 111 tion was taken across all L alleles contributing to dispersal. The number of alleles contributing to dispersal in each simulation depended on both the number of loci used in the simulation and the number of chromosomes (i.e. haploid or diploid individuals). Thus, alleles were assumed to
 114 contribute additively with no dominance or epistasis. The expected dispersal distance, d_i , was then used to draw a realized distance from an exponential dispersal kernel and direction (forward or backward in the linear landscape) was chosen by a single draw from a Bernoulli distribution with

117 $p = 0.5$ (i.e. a coin flip).

Population dynamics

Following dispersal, reproduction occurred in each discrete patch according to a stochastic implementation of the classic Ricker model (Melbourne & Hastings, 2008; Ricker, 1954). Importantly, this model can account for asexual reproduction or sexual reproduction with explicit males and females (Melbourne & Hastings, 2008). In the relatively simple case of an asexual population, the expected population size in patch x at time $t + 1$ was given by

$$\hat{N}_{t+1,x} = N_{t,x} R e^{\frac{-\ln(R)N_{t,x}}{K(x)}} \quad (3)$$

where $N_{t,x}$ was the current population size of patch x , R was the intrinsic growth rate, and $K(x)$ was the carrying capacity as defined above. This equation also applies to a sexually reproducing population of monoecious individuals. To expand the model to sexually reproducing populations of dioecious individuals we introduced a new parameter, ψ , defining the expected proportion of females produced each generation (i.e. $\psi = 0.5$ corresponded to an even sex ratio on average). The expected population growth then became

$$\hat{N}_{t+1,x} = F_{t,x} \frac{R}{\psi} e^{\frac{-\ln(R)N_{t,x}}{K(x)}} \quad (4)$$

in which $F_{t,x}$ was the number of females in patch x at time t . To account for demographic stochasticity, these expected population sizes were then used to draw the realized population sizes from a Poisson distribution ($N_{t+1,x} \sim \text{Poisson}(\hat{N}_{t+1,x})$). Similarly, to allow for stochasticity in sex ratios for dioecious populations, the number of females in each generation was drawn from a binomial distribution ($F_{t+1,x} \sim \text{Binomial}(N_{t+1,x}, \psi)$).

For both monoecious and dioecious populations, we assumed a relatively simple mating sys-

tem in which individuals could mate multiple times. Monoecious populations only experienced
 126 a mate finding Allee effect when self-fertilization was prohibited (obligatory outcrossing), mean-
 ing there had to be at least two individuals in a patch for reproduction. In dioecious populations,
 patches had to contain at least one individual of each sex for successful reproduction. However,
 129 as individuals could mate multiple times, if these conditions were met all individuals were able to
 reproduce. Thus, the mate finding Allee effects for both types of sexually reproducing populations
 were minimal.

132 *Inheritance*

For each individual produced for the next generation, parentage was assigned randomly according
 to the mode of reproduction. Under asexual reproduction, a single individual was drawn randomly
 135 (with replacement) from the local population. Under sexual reproduction in dioecious populations,
 a male and female were drawn randomly from the local population. In monoecious populations, a
 single parent was first drawn and then a second was drawn with probability $1 - \omega$ so that ω was the
 138 probability of self fertilization. Once parentage was determined, offspring inherited alleles from
 their parent(s) assuming no linkage among loci and a mutation process defined by two parameters:
 the per allele probability of mutation (ϕ) and the standard deviation of mutational effects (σ).
 141 Thus, when a mutation occurred with probability ϕ , the new allele value was drawn from a normal
 distribution with mean equal to the original allele value and a standard deviation of σ).

Simulation initiation

144 Each simulation began with a burn-in period of 50000 generations to minimize the role of initial
 conditions. Each patch was populated with a number of individuals equal to the patch's carrying
 capacity ($K(x)$). Individuals were assigned random genotypes assuming normally distributed allele
 147 frequencies. The distribution of allele frequencies was adjusted for different simulations so that

the mean and variability of dispersal phenotypes was equivalent regardless of the number of loci defining dispersal or if populations were haploid or diploid. Ranges were stationary during the burn-in period, with $\beta(t) = 0$ for the first 50000 generations of the simulation, after which different experimental scenarios were imposed.

Experimental scenarios

In our simulations, we varied ploidy and mode of reproduction to explore (1) haploid (asexual) populations, (2) diploid dioecious populations, (3) diploid monoecious populations with obligate selfing ($\omega = 1$), (4) diploid monoecious populations with partial selfing ($\omega = 0.5$), and (5) diploid monoecious populations with obligate outcrossing ($\omega = 0$). We also varied the number of loci defining dispersal by powers of 2 (1, 2, 4, 8, 16, or 32 loci), yielding a total of 30 scenarios for our simulations (5 combinations of reproduction and ploidy by 6 possible numbers of loci defining dispersal). After the 50000 generation burn-in period for each simulation, we examined dispersal evolution in two contexts: (1) unbounded range expansions and (2) simultaneous range expansion at one edge and contraction at the opposite range edge (hereafter referred to as range shifts). In unbounded range expansions, the carrying capacities of all patches in the landscape were set to K_{max} in generation 50001 and populations were allowed to expand in both directions. After 200 generations, we recorded the distance spread in both directions and the mean dispersal phenotype and genetic diversity of each patch within 50 patches of the last occupied patch in either direction (equivalent to the number of patches in which $K(x) < K_{max}$ on either end of the stable range; hereafter referred to as the edge population). In range shifts, the center of the range changed linearly with time according to $\beta(t) = vt$ so that v defined the rate of simulated climate change. In these simulations, patch carrying capacities declined away from the range center according to equation 1. Therefore, populations had to expand to track the viable habitat and avoid extinction. Range shifting populations were also tracked for 200 generations, after which mean dispersal phenotype

and genetic diversity were recorded for all patches in extant populations. We also recorded the overall proportion of simulated populations to go extinct during the range shift across all scenarios.

174 Each scenario was explored with 1000 simulations for each population type. For both scenarios, we also performed 1000 simulations in which dispersal evolution was prevented and individuals in each generation were randomly assigned allele values drawn from the population at generation 177 50000 (i.e. from the end of the burn-in period). Thus, we quantified evolutionary changes in dispersal via comparisons between populations before and after 200 generations of either unbounded range expansion or range shift and we further quantified the impact of dispersal evolution on the 180 observed dynamics by comparisons to the respective simulations in which dispersal evolution was prevented. A full list of the parameter values used in our simulations is given in Table 1.

Results

183 As expected, spatial sorting led to increased dispersal phenotypes (on average) in range shifting populations and at the edge of unbounded range expansions (Fig. 1a & 2a). In scenarios with no genetic mixing among individuals (asexual and obligately selfing populations), the increase in 186 dispersal phenotypes was small and constant across different numbers of loci. In scenarios with at least some genetic mixing, on the other hand, increases in average dispersal phenotypes were positively correlated with the number of loci defining dispersal. The magnitude of this relationship 189 depended on the degree to which genetic mixing occurred among individuals in the populations. Dioecious populations experienced the greatest increases in dispersal phenotypes while monoeious populations with partial selfing experienced the lowest increases among this group. However, 192 even in populations with partial self-fertilization, the increase in dispersal phenotypes compared to populations with no genetic mixing among individuals was dramatic.

Genetic diversity was reduced across all simulations as well, consistent with directional evolu- 195 tion of a trait. In unbounded range expansions (Fig. 1b), all scenarios exhibited similar reductions

in genetic diversity of edge populations when dispersal was defined by only a few loci. However, at large numbers of loci, dioecious and asexual populations experienced greater reductions in diversity compared to others while monoecious, obligately outcrossing populations maintained the highest levels of genetic diversity. The reduction in diversity of asexual populations could be due to their haploid nature while all other populations were diploid, and thus individuals had twice the number of alleles for a given number of loci. The reduction in diversity in dioecious populations is likely a result of the stochastic sex ratios in these populations. Deviations from even sex ratios in dioecious populations can reduce the effective population size (Nunney, 1993), thus reducing the genetic diversity these populations can support (Charlesworth, 2009). In range shifts (Fig. 2b), both monoecious, obligately outcrossing and dioecious populations were able to maintain greater levels of genetic diversity as the number of loci defining dispersal increased. However, rather than revealing a fundamental difference between unbounded range expansions and range shifts, this pattern is most likely driven by numerical effects as the number of these populations surviving range shifts also increased with the number of loci (Fig. 4).

Observed increases in average dispersal phenotypes of edge populations in unbounded range expansions corresponded to increases in the distance spread by these populations compared to scenarios in which evolution was prevented (Fig. 3). Following the same trends as the patterns in dispersal phenotypes, populations with no genetic mixing experienced a small and constant increase in distance spread while others showed a positive correlation between the increase in distance spread and the number of loci defining the dispersal trait. However, despite dioecious and monoecious, obligately outcrossing populations experiencing the greatest increases in dispersal phenotypes at the expansion edge, they showed reduced increases in distance spread compared to monoecious, partially selfing populations. This is likely due to the ecological consequences of these mating systems, as individuals that cannot self-fertilize must co-colonize a patch with another individual whereas self-fertilization allows individuals to successfully colonize a new patch

regardless of the presence or absence of a potential mate.

222 These ecological consequences of the different mating systems were even more important for
range shifting populations. Populations with no genetic mixing displayed a constant extinction
probability across different numbers of loci while other populations showed decreasing extinction
225 probability with increasing numbers of loci (Fig. 4). This mirrors the patterns seen in dispersal
phenotypes (Fig. 1a) and distance spread in unbounded range expansions (Fig. 3). Importantly,
though, the difference was stark between monoecious, partially selfing populations and populations
228 with no self-fertilization (monoecious, obligately outcrossing and dioecious populations). The need
for two individuals in reproduction, even under a relatively simple mating system, imposed a mate
finding Allee effect so severe that monoecious, obligately outcrossing and dioecious populations
231 experienced the highest extinction probabilities during range shifts, regardless of the number of loci
defining dispersal. In contrast, monoecious, partially selfing populations experienced the lowest
extinction probabilities, likely because they achieved the benefits of increased dispersal evolution
234 from sexual reproduction without bearing the cost of a mate finding Allee effect.

Importantly, though, all populations still experienced a reduced extinction probability due to
evolution of dispersal compared to no evolution scenarios (Fig. 5). Monoecious, partially selfing
237 populations experienced the largest reduction in extinction risk due to dispersal evolution, and
those reductions increased with the number of loci defining dispersal. When dispersal was defined
by a single locus, monoecious, obligately outcrossing and dioecious populations experienced only
240 a small reduction in extinction risk. However, as the number of loci defining dispersal increased,
these populations experienced greater reductions in extinction risk, eventually matching the modest
reductions seen in populations with no genetic mixing, but also no mate finding Allee effect.

Discussion

Spatial sorting has been implicated in the evolution of dispersal-related traits in a variety of taxa (Duckworth & Badyaev, 2007; Fronhofer & Altermatt, 2015; Léotard *et al.*, 2009; Lombaert *et al.*, 2014; Ochocki & Miller, 2017; Phillips *et al.*, 2006; Weiss-Lehman *et al.*, 2017; Williams *et al.*, 2016). However, the magnitude of the change in dispersal behavior and the degree to which it influences population dynamics in range expansions have been variable across studies (Miller *et al.*, 2020). Here, we demonstrate one reason for this observed variability could be underlying differences in the genetics of dispersal traits and differences in mating systems among taxa. Further, we show the importance of these differences in dispersal evolution to the dynamics of populations undergoing unbounded range expansions and climate-driven range shifts. While sexual reproduction and greater numbers of loci defining the dispersal trait caused larger changes in dispersal due to spatial sorting, the accompanying ecological consequences of sexual reproduction (namely mate finding Allee effects) led to slower than expected spread in range expansions and heightened extinction risk in range shifts.

Sexual reproduction consistently resulted in larger increases to dispersal ability compared to asexual populations in our model (Fig. 1a & 2a). This effect was maximized in dioecious populations and monoecious, obligately outcrossing populations, demonstrating the beneficial effects of genetic mixing achieved through sexual reproduction (Goddard *et al.*, 2005). In monoecious, partially selfing populations, we also saw increased dispersal evolution with increasing numbers of loci, demonstrating the benefits of even partial outcrossing. This result, along with the benefits of sexual vs. asexual reproduction, is in keeping with previous results on evolution of traits under natural selection (Goddard *et al.*, 2005; Orr & Otto, 1994; Pritchard *et al.*, 2010; Zeyl *et al.*, 2003). Thus, our work adds to the growing body of literature suggesting that spatial sorting can be thought of as a spatial analogue to natural selection (Phillips & Perkins, 2019; Shine *et al.*, 2011).

267 Despite the increased magnitude of dispersal evolution, however, monoecious, obligately out-
crossing and dioecious populations consistently spread less far in unbounded range expansions
and experienced higher extinction risk in range shifts compared to monoecious, partially selfing
270 populations (Fig. 3 & 4). These partially self-fertilizing populations essentially gained the ben-
efits of sexual reproduction for dispersal evolution but avoided the costs of mate finding Allee
effects, thus allowing them to benefit the most from dispersal evolution (Fig. 5). Previous work
273 has also demonstrated the importance of mate finding Allee effects in slowing spatial spread (Shaw
& Kokko, 2015), but the degree to which they impact extinction risk in range shifts is surprising.
We assumed a simplistic mating system in which individuals could mate multiple times and only
276 required the presence of one other individual (or one individual of the opposite sex in the case
of dioecious populations) to successfully reproduce. Thus, we expected Allee effects in our sim-
ulations to cause negligible effects and to be overpowered by the benefits of increased dispersal
279 evolution. More complex mating systems and social structures have been shown to lead to higher
extinction risk in stationary populations (Leach *et al.*, 2020), and would likely further exacerbate
the negative impacts of mate finding Allee effects for populations shifting their ranges in response
282 to climate change.

Range shifts have already been documented in a wide variety of taxa, though the degree to
which different species have fully tracked changing climate conditions is quite variable (Chen
285 *et al.*, 2011; Hiddink *et al.*, 2015; Parmesan, 2006). Our results could help explain some of this
variation. For example, bird species in France are shifting their ranges northwards, but are in-
creasingly lagging behind climate indicators (Devictor *et al.*, 2008). Oceanic dinoflagellates, on
288 the other hand, have been able to closely track changing conditions as they shift their ranges with
climate change (Chivers *et al.*, 2017). While many factors are likely to impact such discrepancies
among taxa, including local environmental heterogeneity and dispersal limitations (Velo-Antón
291 *et al.*, 2013) or other functional traits beyond dispersal (Ash *et al.*, 2017), our results suggest that

asexual species like dinoflagellates should more easily track changing conditions compared to sexually reproducing species like birds due to the absence of mate finding Allee effects.

294 As our results demonstrate, ecological and evolutionary processes can have contrasting effects
on the overall dynamics of range expansions and shifts. While we show this specifically for dis-
persal evolution and mate finding Allee effects, it will likely hold true for other ecological and
297 evolutionary processes at play in range expansions and shifts. Further, our model assumed popula-
tions would shift in space in response to climate change, but other responses are possible, including
adaptation to changing conditions (Hoffmann & Sgro, 2011) and shifts in phenology (Cohen *et al.*,
300 2018). Future work should consider the contrasting ecological and evolutionary processes at play
in these other possible responses to climate change as well as how these different responses could
interact with each other. For example, our results suggest self-fertilizing species might be best
303 situated to respond to climate change in the form of a range shift (Fig. 5). However, research has
shown that self-fertilization can reduce the adaptive potential of populations (Noël *et al.*, 2017),
which could limit the ability of such populations to persist in novel conditions after a range shift.
306 Further, while our work demonstrates the importance of simple, mate finding Allee effects in range
shifts, other research has shown the potential for climate change to exacerbate existing Allee effects
through temperature induced changes in metabolism or mating rate (Berec, 2019). Thus, range
309 shifting populations could face the prospect of multiple, compounding Allee effects hindering their
ability to cope with climate change.

Conclusion

312 In this study, we demonstrated the critical interactions between the evolutionary and ecological
consequences of dispersal genetics and reproduction mode during range expansions and shifts. In
particular, we showed that while sexual reproduction can lead to greater increases in dispersal abil-
315 ity, these increases are unable to fully counter the negative impacts of even the most simplistic mate

finding Allee effects on population dynamics during range shifts. Our results suggest a potential strategy to aid many range shifting species could focus on mitigating these mate finding Allee effects. This could be accomplished, for example, through the existing strategy of assisted migration for range shifting species in which the migrants could be transplanted in a manner designed to maximize their ability to find mates in the new habitat Hällfors *et al.* (2017). However, in addition to potentially disrupting local adaptation Montwé *et al.* (2018), such gene flow from the range core to the expanding edge could also interfere with spatial sorting, potentially hindering the evolution of increased dispersal. As our results demonstrate, more work is needed to fully understand the interacting ecological and evolutionary processes at play in species responding to climate change.

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Tables

Parameter	Description	Value
K_{max}	The maximum achievable carrying capacity for a patch	100
R	intrinsic growth rate	2
ψ	expected proportion of females in dioecious populations	0.5
γ	rate of decline in patch carrying capacity at range edges	0.02
τ	range width	15
\hat{d}	maximum dispersal phenotype	6
ρ	slope of the decline from \hat{d} in phenotype space	0.1
λ	constant offset determining the location of the transition between \hat{d} and 0 in phenotype space	10
ϕ	mutation probability	0.02
σ	standard deviation of mutational effects	$\sqrt{0.02}$
nu	rate of simulated climate change	3
ω	probability of self-fertilization	0, 0.5, 1
L	number of loci defining dispersal	1, 2, 4, 8, 16, 32

Table 1: Values and descriptions for model parameters. Most parameters were constant across experimental simulations, but the ones which varied are listed with all their associated values (see text for description of experimental scenarios).

Figures

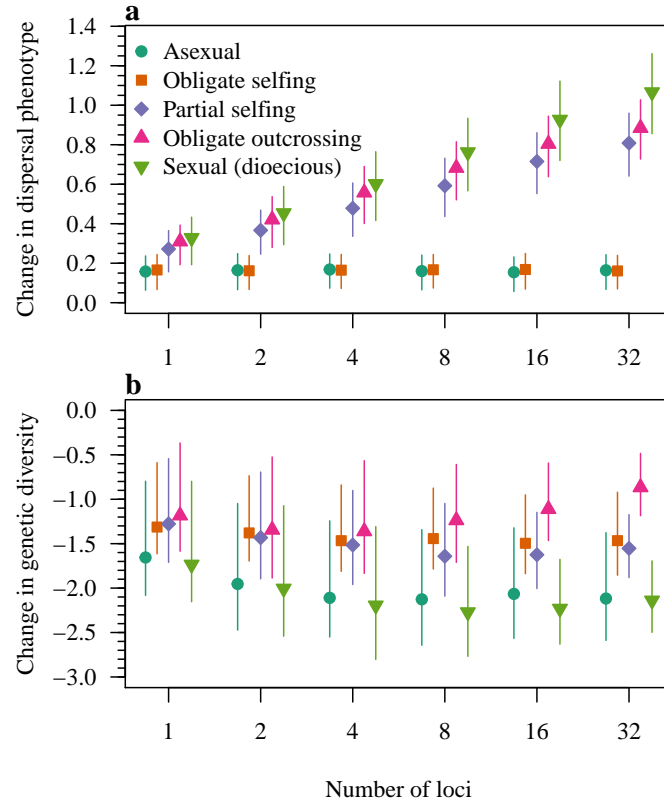


Figure 1: Effects of 200 generations of unbounded range expansion on evolution of the dispersal trait. Panel **a** shows the change in average dispersal phenotype of edge populations after 200 generations compared to the starting population (y axis) across different numbers of loci defining the dispersal trait (x axis). Panel **b** shows the change in average genetic diversity of edge populations on the y axis with loci number again on the x axis. In both panels, the color and shape of points correspond to the population type as indicated in the legend on panel **a**. Points are the means across replicate simulations and line segments show the interquartile ranges.

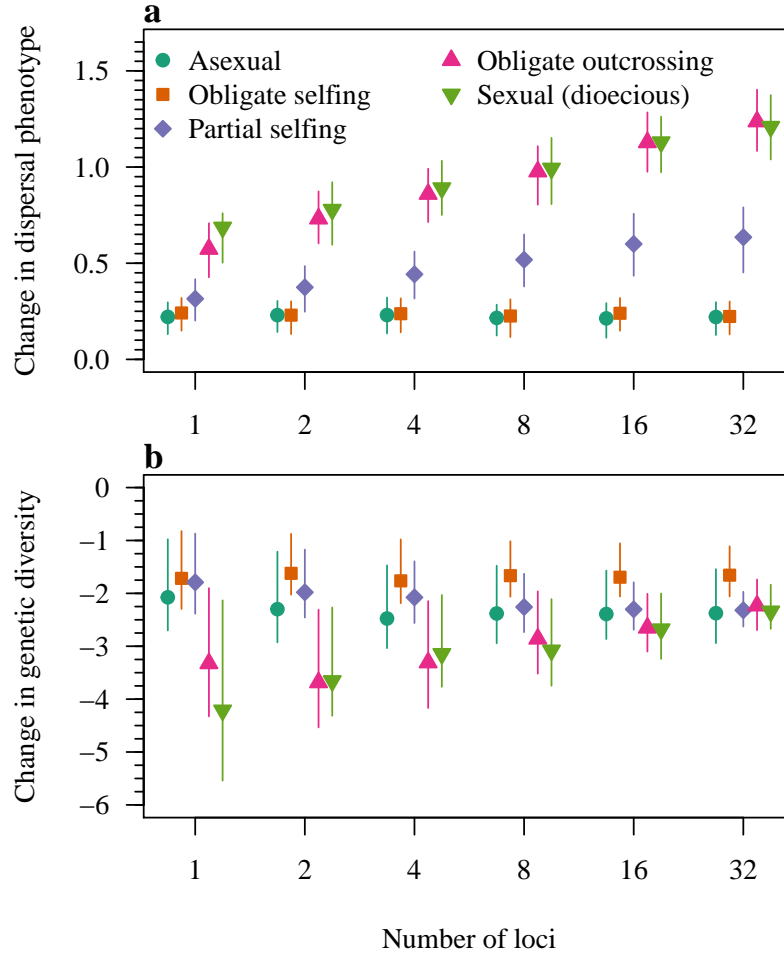


Figure 2: Effects of 200 generations of range shifts on evolution of the dispersal trait. Panel **a** shows the change in average dispersal phenotype of surviving populations after 200 generations compared to the starting population (y axis) across different numbers of loci defining the dispersal trait (x axis). Panel **b** shows the change in average genetic diversity of surviving populations on the y axis with loci number again on the x axis. In both panels, the color and shape of points correspond to the population type as indicated in the legend on panel **a**. Points are the means across replicate simulations and line segments show the interquartile ranges.

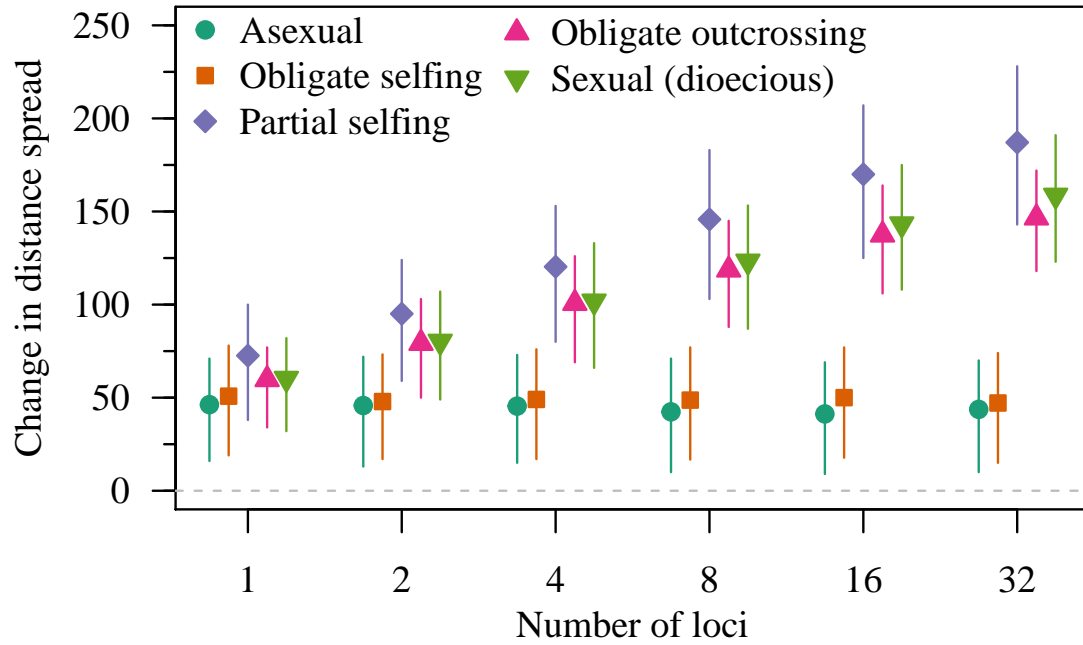


Figure 3: Effect of evolution on distance spread in unbounded range expansions. The y axis shows the change in distance spread between simulations with evolution compared to simulations without evolution in units of discrete patches. Positive values indicate an increased distance spread due to evolution. The dashed grey line at 0 corresponds to no change in distance spread due to evolution. The x axis shows the number of loci defining dispersal in each simulation. As in previous graphs, the color and shape of points correspond to the population type as indicated in the legend. Points are the among simulation means and line segments show the interquartile ranges.

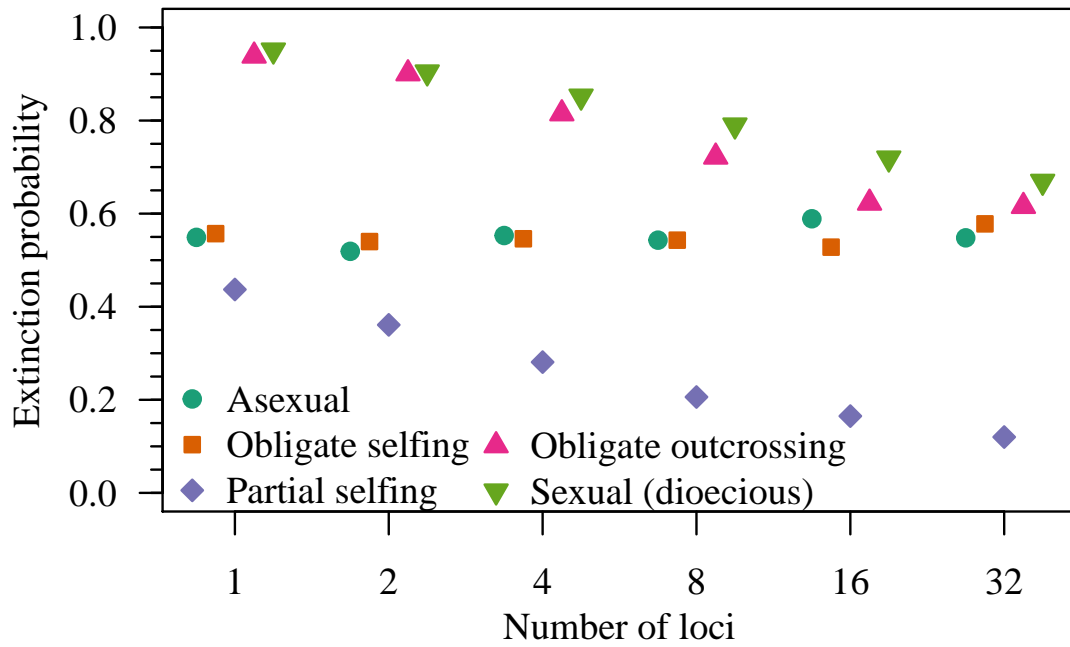


Figure 4: Extinction risk of evolving populations undergoing climate driven range shifts for 200 generations. The y axis shows the proportion of replicate simulations in each category to go extinct during the 200 generations. The x axis shows the number of loci defining dispersal in each simulation. As in previous graphs, the color and shape of points correspond to the population type as indicated in the legend.

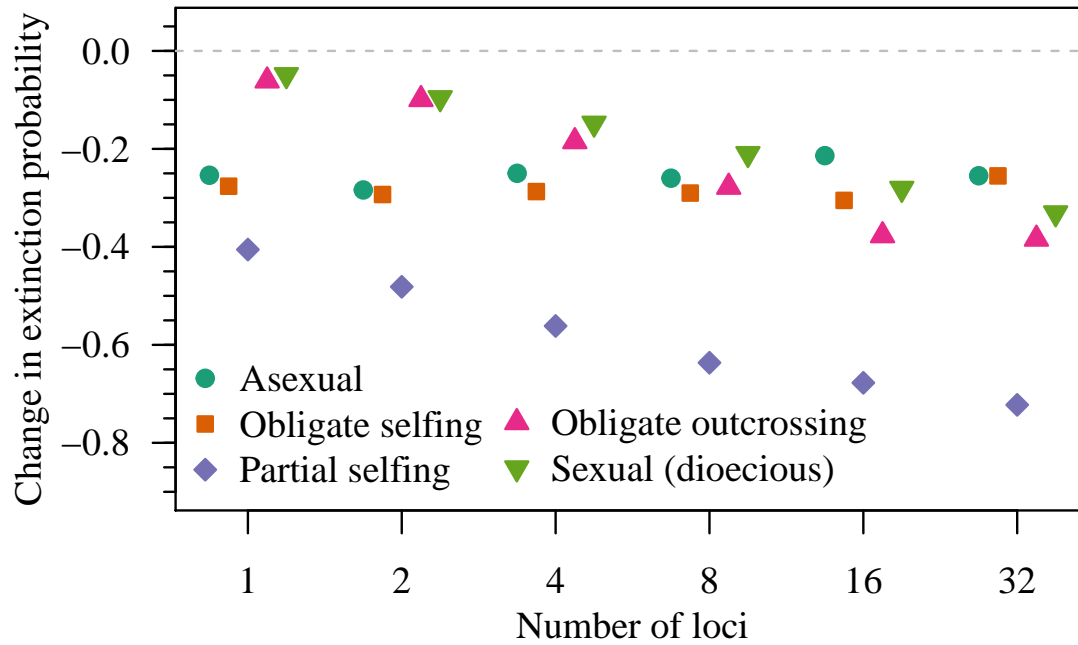


Figure 5: Change in extinction risk due to evolution in climate driven range shifts. The y axis shows the change in the proportion of replicate simulations to go extinct in scenarios with evolution compared to scenarios without evolution. Negative values indicate a reduced extinction risk due to evolution. The dashed grey line at 0 corresponds to no change in extinction risk due to evolution. The x axis shows the number of loci defining dispersal in each simulation. As in previous graphs, the color and shape of points correspond to the population type as indicated in the legend.