The Effect of Habitat Choice on Evolutionary Rescue in Subdivided Populations

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abstract: Evolutionary rescue is the process by which a population, in response to an environmental change, successfully avoids extinction through adaptation. In spatially structured environments, dispersal can affect the probability of rescue. Here, we model an environment consisting of patches that degrade one after another, and we investigate the probability of rescue by a mutant adapted to the degraded habitat. We focus on the effects of dispersal and of immigration biases. We identify up to three regions delimiting the effect of dispersal on the probability of evolutionary rescue: (i) starting from low dispersal rates, the probability of rescue increases with dispersal; (ii) at intermediate dispersal rates, it decreases; and (iii) at large dispersal rates, it increases again with dispersal, except if mutants are too counterselected in not-yet-degraded patches. The probability of rescue is generally highest when mutant and wild-type individuals preferentially immigrate into patches that have already undergone environmental change. Additionally, we find that mutants that will eventually rescue the population most likely first appear in nondegraded patches. Overall, our results show that habitat choice, compared with the often-studied unbiased immigration scheme, can substantially alter the dynamics of population survival and adaptation to new environments.

Keywords: evolutionary rescue, local adaptation, source-sink dynamics, dispersal, gene flow, habitat choice.

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Introduction

Current anthropogenic environmental changes, such as deforestation, soil and water contamination, and rising temperatures, contribute to the decline of populations of many species that might eventually become extinct (Diniz-Filho et al. 2019). Pests and pathogens experience similarly strong selective pressures as a result of consumption of antibiotics and use of pesticides (Ramsayer et al. 2013; Kreiner et al. 2018). The process of genetic adaptation that saves populations from extinction is termed "evolutionary rescue." This process is characterized by an initial population decline (which, without adaptation, would result in population extinction) followed by recovery due to the establishment of adapted genotypes, classically resulting in a U-shaped demographic trajectory over time (Gomulkiewicz and Holt 1995). In recent years, empirical examples of evolutionary rescue have accumulated (as reviewed in Alexander et al. 2014; Carlson et al. 2014; Bell 2017). Laboratory experiments have provided direct evidence of evolutionary rescue (e.g., Bell and Gonzalez 2009; Agashe et al. 2011; Lachapelle and Bell 2012; Lindsey et al. 2013; Stelkens et al. 2014). In the wild, however, demographic and genotypic data are rarely monitored together at the same time, which impedes direct observation of evolutionary rescue. Still, evolutionary rescue has been suggested as a mechanism that has saved a few wild populations from extinction (e.g., Vander Wal et al. 2012; Di Giallonardo and Holmes 2015; Gignoux-Wolfsohn et al. 2018).

Here, we study the effect of dispersal and habitat choice on evolutionary rescue in a subdivided population. We assume that dispersal intensity and habitat choice are fixed and do not evolve. In general, the traits involved in adaptation in models of evolutionary rescue can be continuous (e.g., Bürger and Lynch 1995; Gomulkiewicz

and Holt 1995; Boulding and Hay 2001; Osmond et al. 2017) or discrete (e.g., Orr and Unckless 2008; Martin et al. 2013; Uecker et al. 2014). We consider genetic adaptation mediated by a discrete trait, and we assume that fitness of individuals is determined by a single haploid locus.

Evolutionary rescue is often studied in a spatially homogeneous situation where the whole population experiences a sudden decrease in habitat quality. In this setting, a large number of theoretical results have been established, for example, on the effects of recombination (Uecker and Hermisson 2016) and horizontal gene transfer (Tazzyman and Bonhoeffer 2014), mode of reproduction (Glémin and Ronfort 2013; Uecker 2017), intra- and interspecific competition (Osmond and de Mazancourt 2013), predation pressure (Yamamichi and Miner 2015), bottlenecks (Martin et al. 2013), different genetic pathways (Osmond et al. 2019), and the context-dependent fitness effects of mutations (Anciaux et al. 2018). In contrast to these abrupt-change scenarios, evolutionary rescue can also be studied in a gradually changing environment (e.g., Bürger and Lynch 1995; Osmond et al. 2017).

In fragmented environments, habitat deterioration is not necessarily synchronized across patches: there can be a transient spatially heterogeneous environment consisting of a mosaic of old- and degraded-habitat patches, until eventually the whole environment has deteriorated. If individuals that populate different patches are able to move between those, the effect of dispersal on evolutionary rescue needs to be taken into account (Uecker et al. 2014; Tomasini and Peischl 2020). The intensity of dispersal among patches tunes how abruptly environmental change is experienced. With very low dispersal, patches are essentially isolated from each other, and the local population of each patch undergoes an abrupt change independently of the other patches. With higher dispersal, asynchronous deterioration among patches is experienced as a more gradual change overall. Experiments that study the effect of dispersal on evolutionary rescue are rare, but, for instance, Bell and Gonzalez (2011) found that dispersal can increase the probability of successful genetic adaptation.

The transient mosaic of degraded and nondegraded patches that results from asynchronous degradation in a fragmented habitat is similar to the setting of models of source-sink dynamics. These models represent a spatially heterogeneous environment, constant in time, in which wild-type populations in unfavorable habitats can be maintained only thanks to recurrent immigration from favorable habitats. Experimental and theoretical studies have found that an increase in dispersal can have a positive or negative effect on genetic adaptation in a heterogeneous environment (see, e.g., Holt and Gomulkiewicz [1997] for studies of discrete traits; Gomulkiewicz et al. [1999] for positive effects; Nagylaki [1978], Karlin and Campbell [1981], and Storfer and Sih [1998] for negative effects; and Kawecki [2000] and Gallet et al. [2018] for both positive and negative effects).

In theoretical studies of local adaptation and evolutionary rescue, dispersal is typically assumed to be unbiased; that is, dispersing individuals are distributed uniformly among patches. Only a few investigations in the context of local adaptation in source-sink systems have taken into account nonuniform dispersal patterns (e.g., Kawecki 1995; Holt 1996; Kawecki and Holt 2002; Amarasekare 2004). This analytical focus on unbiased dispersal is in stark contrast to dispersal schemes observed in nature (Edelaar et al. 2008; Clobert et al. 2009; Edelaar and Bolnick 2012).

One of the best documented modes of nonuniform dispersal is density-dependent dispersal. Density dependence can be positive or negative: individuals either prefer to settle or stay in large groups (positive density dependence) or choose to remain in or move to less populated regions (negative density dependence). Density-dependent dispersal, of either form, is ubiquitously found in nature and has been reported in many species across the tree of life, including insects (Endriss et al. 2019), spiders (De Meester and Bonte 2010), amphibians (Gautier et al. 2006), birds (Wilson et al. 2017*b*), fishes (Turgeon and Kramer 2012), and mammals (Støen et al. 2006).

Another well-established dispersal scheme is a type of habitat choice whereby individuals tend to immigrate into habitats to which they are best adapted. This mechanism has, for example, been reported in lizards (Bestion et al. 2015), birds (Dreiss et al. 2011; Benkman 2017), fishes (Bolnick et al. 2009), worms (Mathieu et al. 2010), and ciliates (Jacob et al. 2017, 2018).

Dispersal biases can affect the different steps of dispersal (the probability of emigration, the vagrant stage, and immigration; Bowler and Benton 2005; Ronce 2007). In this work, we focus on effects on the immigration step.

We model an environment that consists of various patches with one of two possible habitats: the "old" habitat, in which both types, wild type and mutant, have sufficient offspring on average to ensure survival of the population; and the degraded "new" habitat, where in the absence of immigration the wild-type population will eventually become extinct. We study four biologically motivated dispersal schemes, which correspond to the four combinations of biases toward old versus new patches for wild types and mutants, and we compare these dispersal schemes to unbiased dispersal. Our analysis is carried out stepwise. We first consider a temporally constant but spatially heterogeneous environment with two (old and new) patch types. In this setting, we first study the probability of establishment of a single mutant, assuming there are no further mutations between types. We then relax the assumption of no

further mutations and compute a probability of adaptation, that is, of emergence and successful establishment of the mutant lineage. Finally, we let habitat degradation proceed, assuming that patches, one after another, deteriorate over time until all locations contain the new habitat. Using the previous results, we approximate the probability of evolutionary rescue—that is, that a mutation appears and establishes, thereby allowing the population to persist in spite of environmental degradation. We find that dispersal biases affect the probabilities of establishment and of evolutionary rescue.

Model and Methods

Main Assumptions and Life Cycle

We consider a spatially structured environment consisting of M patches all connected to each other. The habitat of a patch is either in the old or in the new state, corresponding to habitat quality before and after environmental deterioration, respectively. One after another every τ generations, the habitat of a patch deteriorates, from the old to the new state, with the transition being irreversible. Initially (time $t < 0$), all patches are of the old-habitat type. At time $t = 0$, the first patch deteriorates. After $(M - 1)\tau$ generations, all patches are of the new-habitat type. We denote the time-dependent frequency of old-habitat patches by f_{old}. It equals 1 before the first environmental change takes place ($t < 0$) and decreases by $1/M$ after each environmental deterioration event until it eventually hits zero, when all patches have undergone the environmental change. This setting corresponds to the one analyzed by Uecker et al. (2014) and more recently by Tomasini and Peischl (2020) in the special case of just two patches. The maximum numbers of individuals that can live in a patch of a given habitat type (i.e., the carrying capacities) are denoted K_{old} and K_{new} for old- and new-habitat patches, respectively; K_{old} and K_{new} may differ. We view these carrying capacities as a number of territories or nesting sites; all of these sites are assumed to be accessible to individuals of both types, so that K_{old} and K_{new} are the same for both types of individuals.

The population living in this environment consists of asexually reproducing haploid individuals; generations are discrete and nonoverlapping. There are two possible types of individuals: wild types and mutants. The individuals go through the following life cycle.

Step 1: dispersal. Individuals may move between patches. Further details about this step are given below.

Step 2: reproduction. Individuals reproduce within patches. The number of offspring produced by an individual of type i (before density regulation, if any)—that is, its fecundity—is drawn from a Poisson distribution with expectation ω_i^{old} and ω_i^{new} in old- and new-habitat patches, respectively. The index i specifies the type of the individual: "w" for wild type, "m" for mutant. Having fewer than 1 offspring in expectation means that the local subpopulation will become extinct in the absence of immigration because the deaths of the parents at each generation are not compensated by enough births on average. On the contrary, the local population is viable (i.e., has a chance not to become extinct) if the expected fecundity is greater than 1. In most figures, we assume that both wild-type and mutant individuals have an expected fecundity greater than 1 in old-habitat patches and that the mutant's expected fecundity there is lower than the wild type's (i.e., $1 < \omega_{\text{m}}^{\text{old}} < \omega_{\text{w}}^{\text{old}}$); but we also consider the extreme scenario $\omega_{\text{m}}^{\text{old}} = 0$. In new-habitat patches, a wild-type population will eventually become extinct, while a mutant one would persist (hence the term "rescue mutant"): $\omega_{\text{w}}^{\text{new}} < 1 < \omega_{\text{m}}^{\text{new}}$. All parents die at the end of this step.

Step 3: mutation. Wild-type offspring mutate to the rescue mutant type with probability θ. Back mutations from the mutant to the wild type are neglected.

Step 4: density regulation. If the number of offspring produced locally exceeds the local carrying capacity K_k (where k refers to the habitat type, old or new), the population size is down-regulated to K_k by randomly removing individuals until the local population size is equal to K_k (this corresponds to ceiling density regulation). Mutant offspring have the same chance of being removed as wild-type offspring; that is, we assume that wild-type and mutant individuals are competitively equivalent. If the number of offspring is below the carrying capacity, the regulation step is unnecessary. We write "surviving offspring" for offspring that survive the density regulation step and become adults at the next generation. At the end of this step, all offspring become adults, and a new cycle begins.

Dispersal Mechanisms

We split the dispersal step into emigration and immigration. Emigration is type independent: all individuals have the same probability m of leaving the patch they were born in. We assume that dispersal biases affect the immigration step. We denote by π_i the bias for immigration to an old-habitat patch, where the index i refers to the type of the dispersing individual. If $\pi_i < 0$, individuals of type i are relatively more likely to settle in new-habitat patches than in old-habitat patches; conversely, their bias is toward old-habitat patches if $\pi_i > 0$. The case $\pi_i = 0$ corresponds to unbiased dispersal. For simplicity, we assume that dispersal is cost-free. While local population sizes may be affected by dispersal, the global size of the metapopulation remains the same before and after dispersal. Note that our methods can be readily applied to costly dispersal (including to costs that differ among wild-type and mutant

individuals) as well as to type- and habitat-dependent emigration probabilities.

The probability that a dispersing individual of type i settles in a patch of the new-habitat type is

$$\mu_i^{\text{new}} = \frac{1 - f_{\text{old}}}{1 - f_{\text{old}} + e^{\pi_i} f_{\text{old}}} = 1 - \mu_i^{\text{old}}, \qquad (1)$$

where, as defined above, f_{old} is the frequency of old-habitat patches and π_i is the dispersal bias into old-habitat patches. The use of an exponential e^{π_i} ensures that the fraction in equation (1) is positive and between 0 and 1.

Qualitatively, there are four possible combinations of dispersal biases. We name them according to the preferences of wild type and then of the mutant (e.g., "old-new" scheme: wild-type individuals have a bias toward old-habitat patches, and mutant individuals have one toward new-habitat patches). We add to these four dispersal schemes the case of unbiased dispersal. Figure 1 provides an overview of the different schemes, together with the parameter values used in the numerical simulations.

Each of these dispersal schemes can be related to a biological illustration.

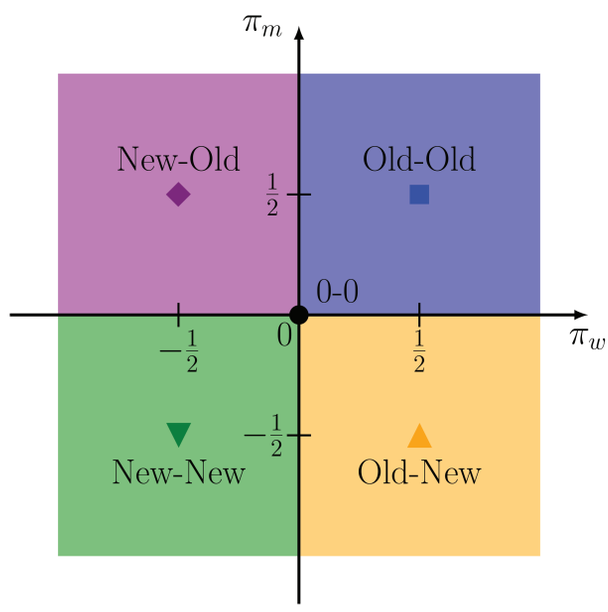


Figure 1: Parameter sets and legends for the different dispersal schemes. The colors and markers are the same across all figures. The horizontal axis is the dispersal bias of the wild type, π_w (positive values correspond to preferential immigration into old-habitat patches), and the vertical axis is that of the mutant, π_m. The markers are located at the parameter values used in the simulations.

Old-old scheme ($\pi_w > 0$, $\pi_m > 0$): Both types of individuals have a bias toward old-habitat patches. If we assume that mutant individuals have a higher fecundity in old-habitat patches than in new-habitat patches (i.e., $\omega_m^{\text{old}} > \omega_m^{\text{new}}$, which is the case in our numerical examples), then this dispersal scheme corresponds to biases toward the habitat where individuals have the highest fecundity. This type of dispersal, which can be described as matching habitat choice, has, for example, been observed with common lizards (*Zootoca vivipara*; Bestion et al. 2015), threespine sticklebacks (*Gasterosteus aculeatus*; Bolnick et al. 2009), and barn owls (*Tyto alba*; Dreiss et al. 2011).

With population densities being high in the old-habitat patches, this dispersal scheme can also be interpreted as positive density-dependent immigration. For prey species, highly populated locations can be an indication for a safe shelter or of a place with numerous mating opportunities. This type of positive density-dependent immigration (also called conspecific attraction) is, for example, found in several amphibians, such as the salamander species *Mertensiella luschani* (Gautier et al. 2006) and *Ambystoma maculatum* (Greene et al. 2016) as well as the frogs *Oophaga pumilio* (Folt et al. 2018).

Old-new scheme ($\pi_w > 0$, $\pi_m < 0$): Wild-type individuals preferentially immigrate into old-habitat patches, while mutants prefer new-habitat patches. This corresponds to immigration to patches where the focal type is fitter than the other type (since $\omega_w^{\text{old}} > \omega_m^{\text{old}}$ and $\omega_m^{\text{new}} > \omega_w^{\text{new}}$). A similar dispersal scheme was recently observed for the ciliates *Tetrahymena thermophila* with a specialist and generalist type (Jacob et al. 2018), where the specialist disperses to its preferred habitat while the generalist prefers to immigrate to a suboptimal habitat, where it outcompetes the specialist.

New-new scheme ($\pi_w < 0$, $\pi_m < 0$): Both types of individuals preferentially immigrate into new-habitat patches. With population densities being on average lower in new-habitat patches and, in particular, because the carrying capacity is not typically reached in new-habitat patches during the initial phase of evolutionary rescue, this dispersal scheme can be interpreted as negative density-dependent immigration, whereby individuals are more likely to move to less populated patches. In nature, such a bias may exist because in less populated locations, resources might be more abundant, intraspecific

competition alleviated, and the chance of infection transmission decreased, which may compensate for the potentially reduced habitat quality. Density-dependent immigration effects as described here are, for example, found in the damselfish species *Stegastes adustus* (Turgeon and Kramer 2012) and the migratory birds *Setophaga ruticilla* (Wilson et al. 2017*b*).

New-old scheme ($\pi_w < 0$, $\pi_m > 0$): Wild-type individuals preferentially immigrate into new-habitat patches, while mutants prefer old-habitat patches. This dispersal scheme is considered mostly for completeness, because it is biologically quite unlikely. It can be related to the concept of an "ecological trap," wherein individuals tend to immigrate into patches that cannot sustain a population, in its most extreme form resulting in the extinction of the species (Battin 2004).

Unbiased dispersal scheme (0-0) ($\pi_w = 0$, $\pi_m = 0$): Neither type has a dispersal bias. Most theoretical results examining the interplay of dispersal and establishment have used this dispersal scheme. We therefore use it as a benchmark to which we compare the biased dispersal schemes.

All of the model parameters are summarized in table 1, along with the default parameter values and ranges. If not stated otherwise, the default parameter values are used for the stochastic simulations.

Simulations

The simulation algorithm implements the life cycle described above. We specify here the sampling distributions that we use in our stochastic simulations.

Dispersal. For each patch, a random number of dispersing individuals is drawn from a binomial distribution with success probability m. The dispersing individuals from all patches are pooled together and redistributed into patches according to their type and dispersal pattern. For each type of individual (wild type and mutant), immigration patches are assigned by first drawing the number of individuals that immigrate into old-habitat patches from a binomial distribution with success probability μ_i^{old} (eq. [1]) and then distributing these individuals uniformly at random over the old-habitat patches. The remaining dispersing individuals are then distributed uniformly at random into the new-habitat patches.

Reproduction. In each patch, reproduction is simulated by drawing a Poisson-distributed number of offspring for each type. The mean of the Poisson distribution is the product of the number of individuals of type i in that patch times ω_i^k, the mean number of offspring of a single individual of type i in a patch of habitat k (old or new). All adults are then removed.

Mutation. The number of wild-type offspring mutating into the mutant type is drawn from a binomial distribution, with success probability θ, the mutation probability.

Density regulation. If the number of offspring in a patch is higher than the local carrying capacity (K_k for a patch of habitat-type k [old or new]), we sample K_k individuals uniformly at random without replacement from the offspring population of the patch (hypergeometric

Table 1: Model parameters and variables

Notation	Interpretation	Range	Default value
K_k	Carrying capacity in a patch of type k	$0 < K_{\text{new}} < K_{\text{old}}$	$K_{\text{old}} = 1{,}000$, $K_{\text{new}} = 500$
ω_w^{old}	Fecundity of wild-type individuals in old-habitat patches	$1 < \omega_w^{\text{old}}$	1.5
ω_m^{old}	Fecundity of mutant individuals in old-habitat patches	$1 < \omega_m^{\text{old}} < \omega_w^{\text{old}}$	1.45 or 1.35
ω_w^{new}	Fecundity of wild-type individuals in new-habitat patches	$0 \le \omega_w^{\text{new}} < 1$	.75
ω_m^{new}	Fecundity of mutant individuals in new-habitat patches	$1 < \omega_m^{\text{new}}$	1.02
m	Emigration probability	$0 \le m \le 1$	.06
π_i	Type i bias toward the old habitat	$\pi_i \in \mathbb{R}$	Fig. 1
M	Number of patches	$2 \le M$	10
f_{old}	Frequency of old-habitat patches	$0 \le m \le 1$	.5
θ	Mutation probability	$0 < \theta$	$1/25MK_{\text{new}}$
τ	Time interval between two consecutive deterioration events	$0 < \tau$	100
a_{old}	Growth rate of the mutant in the old habitat	$-1 \le a_{\text{old}}$	Eq. (2)
a_{new}	Growth rate of the mutant in the new habitat	$-1 \le a_{\text{new}}$	Eq. (3)
$\hat{N}_i^k$	Number of type i individuals in type k habitat patches at stationary	$0 \le \hat{N}_i^k \le K_i$	Eq. (S4), fig. S1
$\tilde{N}_i^k$	Number of type i individuals in type k habitat patches at dispersal	$0 \le \tilde{N}_i^k$	Eq. (S5), fig. S2

sampling); all individuals have the same chance of survival at this step. Otherwise, the local population is left unchanged.

We consider the mutant population to be established if its total population size in patches of either the old- or the new-habitat type is greater than 60% the total carrying capacity of patches of that type ($(0.6 \times K_{\text{new}} \times M(1 - f_{\text{old}}))$ for new-habitat patches, $(0.6 \times K_{\text{old}} \times Mf_{\text{old}})$ for old-habitat patches).

Unless stated otherwise, the simulation results are averages of 10^5 independent runs. All simulations are written in the C++ programming language and use the Gnu Scientific Library. Code and data to generate the figures have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.rv15dv47j; Czuppon et al. 2021).

Analysis Steps

We decompose our analysis into several steps of increasing complexity.

Step 1. We first consider an environment that is constant over time and heterogeneous in space, with a fraction f_{old} of old-habitat patches and $1 - f_{\text{old}}$ of new-habitat patches. The population is initiated with wild-type individuals at carrying capacity in old-habitat patches and at the migration-selection equilibrium $\hat{N}_{\text{w}}^{\text{new}}$ in new-habitat patches (for details, see sec. S1 in the supplemental PDF, available online) and with a single mutant individual, in either an old- or a new-habitat patch. There are no further mutations ($\theta = 0$), and we compute the probability of establishment of a mutant lineage.

Step 2. We then consider the same environmental setting but initialize the population with only wild-type individuals. Mutants can appear by mutation during the simulation ($\theta > 0$). We compute the probability of adaptation (i.e., the probability that during a fixed time interval, a mutant appears by mutation and then establishes).

Step 3. Finally, we consider the full scenario where each patch degrades one after another, as described above. The environment is spatially and temporally variable. The population is initialized with only old-habitat patches, all at carrying capacity, with wild-type individuals only. We compute the probability of evolutionary rescue (i.e., the probability that a mutant appears by mutation and establishes before the population becomes extinct).

To study the effect of standing genetic variation on evolutionary rescue, we will later relax the assumption that there are only wild-type individuals in the population when environmental degradation begins. These simulations are started long enough before the degradation of the first patch takes place, so that local populations are close to mutation-selection equilibrium.

Additional Assumptions for the Mathematical Analysis

We make a few additional assumptions for the mathematical analysis of the three probabilities. These assumptions are relaxed in the stochastic simulations.

A key assumption is that the mutant individuals are rare enough that their dynamics do not affect the wild-type population during the establishment phase of the mutant lineage. Because of their rareness, we can also consider that all mutants reproduce, disperse, and die independently of each other. The wild-type population sets a demographic context that affects mutant dynamics. The mathematical analysis therefore focuses on the population dynamics of the mutant population, considering the wild-type population as constant over time (except in the rescue scenario).

We assume that the subpopulations in old-habitat patches are always at carrying capacity (i.e., that there are always enough offspring produced to at least replace all of the parents). Denoting by $\tilde{N}_i^k$ the number of type i individuals in a k-habitat patch right after dispersal, the expected number of surviving offspring of mutant individuals in this old-habitat patch (i.e., of offspring that survive density regulation and become adults in the next generation) is

$$K_{\text{old}} \frac{\omega_{\text{m}}^{\text{old}} \tilde{N}_{\text{m}}^{\text{old}}}{\omega_{\text{w}}^{\text{old}} \tilde{N}_{\text{w}}^{\text{old}} + \omega_{\text{m}}^{\text{old}} \tilde{N}_{\text{m}}^{\text{old}}} \approx K_{\text{old}} \frac{\omega_{\text{m}}^{\text{old}} \tilde{N}_{\text{m}}^{\text{old}}}{\omega_{\text{w}}^{\text{old}} \tilde{N}_{\text{w}}^{\text{old}}} \stackrel{\text{def}}{=} (1 + a_{\text{old}}) \tilde{N}_{\text{m}}^{\text{old}}. \tag{2}$$

The approximation results from the assumption that mutants are rare compared with wild-type individuals in old-habitat patches. Equation (2) defines the per capita expected growth rate of mutants in old-habitat patches, α_{old}. It depends on $\tilde{N}_{\text{w}}^{\text{old}}$, the size of the local wild-type population right after dispersal, which is calculated in section S1 of the supplemental PDF (eq. [S5a]).

In new-habitat patches, the situation is a bit more involved. Either the local population size after reproduction exceeds the carrying capacity, in which case density regulation is necessary, or it is below the carrying capacity. In the latter case, the expected number of offspring per mutant is simply given by their fecundity, $\omega_{\text{m}}^{\text{new}}$. In the former case, where the population after reproduction exceeds the carrying capacity K_{new}, an argument similar to the one in old-habitat patches allows us to approximate the per capita number of surviving offspring, as in equation (2). These two cases yield the following definition of the per capita growth rate of mutants in new-habitat patches, α_{new}:

$$1 + a_{\text{new}} = \begin{cases} K_{\text{new}} \dfrac{\omega_{\text{m}}^{\text{new}}}{\omega_{\text{w}}^{\text{new}} \tilde{N}_{\text{w}}^{\text{new}}} & \text{if } \tilde{N}_{\text{w}}^{\text{new}} \geq \dfrac{K_{\text{new}}}{\omega_{\text{w}}^{\text{new}}}, \\ \omega_{\text{m}}^{\text{new}} & \text{if } \tilde{N}_{\text{w}}^{\text{new}} < \dfrac{K_{\text{new}}}{\omega_{\text{w}}^{\text{new}}}. \end{cases} \tag{3}$$

Note that the first line is obtained using the same rare-mutant approximation as in equation (2).

We finally combine the different steps of the life cycle. The expected per capita numbers of surviving mutant offspring in habitat k' of an individual in a k-habitat patch at the beginning of the generation, $\lambda_{k,k'}$, are the following:

$$\begin{aligned}\lambda_{\text{old,old}} &= (1 - m\mu_{\text{m}}^{\text{new}})(1 + a_{\text{old}}),\\ \lambda_{\text{old,new}} &= m\mu_{\text{m}}^{\text{new}}(1 + a_{\text{new}}),\\ \lambda_{\text{new,old}} &= m\mu_{\text{m}}^{\text{old}}(1 + a_{\text{old}}),\\ \lambda_{\text{new,new}} &= (1 - m\mu_{\text{m}}^{\text{old}})(1 + a_{\text{new}}).\end{aligned} \tag{4}$$

Our final assumption for the mathematical analysis is that the distributions of numbers of surviving offspring are Poisson, with means $\lambda_{k,k'}$ (counting the surviving offspring in habitat k' of a parent in a k-habitat patch at the beginning of the generation). In reality, only the production of offspring before density regulation is Poisson; here we lump in the effects of dispersal and of density regulation. These mean values are treated as (piecewise) constant over time. This way, the dynamics of the mutant population can be described by a two-type branching process, for which an established methodology exists (Haccou et al. 2005). (In our context, the two "types" in the name of the method, "two-type branching process," correspond to the two habitat types.)

Results

We proceed stepwise, as outlined above, toward the computation of the probability of evolutionary rescue. For each step, we first present a mathematical analysis and then compare our results to the output of simulations that relax the assumptions made for mathematical purposes. First, we compute the establishment probability of a single mutant individual, depending on whether the mutation appeared in an old- or a new-habitat patch, in an environment where the numbers of old- and new-habitat patches are fixed. Second, we derive an expression for the probability of adaptation (i.e., the probability for a mutation to appear in a given time interval and establish), again in a fixed environmental configuration. In this context, we also investigate the habitat of origin of the mutant lineages that eventually establish. Third, we study the time-varying scenario where patches, one after another, deteriorate, and we study the probability of evolutionary rescue. We again investigate the habitat of origin of the rescue mutant, and we compare the contributions to evolutionary rescue of standing genetic variation (i.e., mutations that are present before the environment starts deteriorating) and de novo mutations (i.e., mutations that appear while the environment is deteriorating).

Establishment Probability in a Heterogeneous Environment

In this first step, we consider that there is initially a single mutant individual in the population, located in either an old- or a new-habitat patch, and we compute the probability of establishment of the mutant population. In this step, we ignore further mutations and are only concerned with the fate of this single mutant lineage.

Mathematical Analysis. We denote by φ_{old} (resp. φ_{new}) the probability of establishment of this two-type branching process when the mutant is initially located in an old-habitat (resp. new-habitat) patch. This probability is computed by considering all possible ways of becoming extinct: the initial individual having j surviving offspring in a patch of type k, but all lineages descending from these j offspring eventually become extinct; then summing over k and j. Denoting by $\mathbb{P}_{k,k'}(j)$ the probability that an individual in a k-habitat patch at the beginning of the generation has j surviving offspring in a k'-habitat patch after density regulation, the following system of equations holds:

$$1 - \varphi_{\text{old}} = \sum_{j=0}^{\infty}\sum_{j'=0}^{\infty}(\mathbb{P}_{\text{old,old}}(j)(1 - \varphi_{\text{old}})^{j} \times \mathbb{P}_{\text{old,new}}(j')(1 - \varphi_{\text{new}})^{j'}), \tag{5a}$$

$$1 - \varphi_{\text{new}} = \sum_{j=0}^{\infty}\sum_{j'=0}^{\infty}(\mathbb{P}_{\text{new,old}}(j)(1 - \varphi_{\text{old}})^{j} \times \mathbb{P}_{\text{new,new}}(j')(1 - \varphi_{\text{new}})^{j'}). \tag{5b}$$

As mentioned previously, we assume for our mathematical analysis that the numbers of surviving offspring per parent over the whole life cycle are Poisson distributed with means $\lambda_{k,k'}$ given in equation (4):

$$\mathbb{P}_{k,k'}(j) = \frac{\lambda_{k,k'}^{j}}{j!}e^{-\lambda_{k,k'}}. \tag{6}$$

Inserting these expressions into system (5) and simplifying, we obtain

$$1 - \varphi_{\text{old}} = \exp[-(1 - m\mu_{\text{m}}^{\text{new}})(1 + a_{\text{old}})\varphi_{\text{old}} - m\mu_{\text{m}}^{\text{new}}(1 + a_{\text{new}})\varphi_{\text{new}}], \tag{7a}$$

$$1 - \varphi_{\text{new}} = \exp[-m\mu_{\text{m}}^{\text{old}}(1 + a_{\text{old}})\varphi_{\text{old}} - (1 - m\mu_{\text{m}}^{\text{old}})(1 + a_{\text{new}})\varphi_{\text{new}}]. \tag{7b}$$

The establishment probabilities φ_{old} and φ_{new} are then given by the unique positive solution of system (7) (Haccou et al.

2005, chaps. 5.3 and 5.6). This system of equations can be solved numerically. An analytical approximate solution is available in the case of weak selection and weak dispersal (i.e., a_{old}, a_{new}, $\text{m} \ll 1$); we refer readers to Haccou et al. (2005, theorem 5.6) for the general theory and to Tomasini and Peischl (2018) for an application in a similar setting. The detailed derivation is presented in section S2 of the supplemental PDF. We find

$$\begin{aligned}\varphi_{\text{old}} \approx a_{\text{old}} &+ a_{\text{old}} \frac{1 - f_{\text{old}} + e^{\pi_{\text{m}}} f_{\text{old}}}{\sqrt{C}} (a_{\text{old}} - a_{\text{new}}) \\ &+ \frac{m}{\sqrt{C}} (a_{\text{new}}(1 - f_{\text{old}}) + a_{\text{old}} e^{\pi_{\text{m}}} f_{\text{old}} \\ &- (a_{\text{old}} - a_{\text{new}})(1 - f_{\text{old}})),\end{aligned} \tag{8a}$$

$$\begin{aligned}\varphi_{\text{new}} \approx a_{\text{new}} &+ a_{\text{new}} \frac{1 - f_{\text{old}} + e^{\pi_{\text{m}}} f_{\text{old}}}{\sqrt{C}} (a_{\text{new}} - a_{\text{old}}) \\ &+ \frac{m}{\sqrt{C}} (a_{\text{new}}(1 - f_{\text{old}}) + a_{\text{old}} e^{\pi_{\text{m}}} f_{\text{old}} \\ &- (a_{\text{new}} - a_{\text{old}}) e^{\pi_{\text{m}}} f_{\text{old}}),\end{aligned} \tag{8b}$$

with

$$\begin{aligned}C = &(1 - f_{\text{old}} + e^{\pi_{\text{m}}} f_{\text{old}}) \\ &\times ((1 - f_{\text{old}})(a_{\text{new}} - a_{\text{old}} + m)^2 \\ &+ e^{\pi_{\text{m}}} f_{\text{old}} (a_{\text{new}} - a_{\text{old}} - m)^2).\end{aligned}$$

Recall that both a_{old} and a_{new}, while considered constant in time, depend on the model's parameters, and in particular on the dispersal probability m. The establishment probabilities φ_{old} and φ_{new} in equations (8) are therefore not affine functions of m (although they look so in eqq. [8]).

If the emigration probability is zero ($m = 0$), the subpopulations in each habitat evolve in isolation from each other. The establishment probabilities in equations (8) become

$$\varphi_{\text{old}}(m = 0) = 0, \tag{9a}$$

$$\varphi_{\text{new}}(m = 0) = 2a_{\text{new}}. \tag{9b}$$

Equation (9b) corresponds to Haldane's classical result for the establishment probability of a slightly advantageous mutant (Haldane 1927). The mutation being counter-selected in old-habitat patches, its probability of establishment is null (eq. [9a]).

When the emigration probability is strictly positive ($m > 0$), in the case of unbiased dispersal ($\pi_{\text{w}} = \pi_{\text{m}} = 0$) and for equal numbers of old- and new-habitat patches ($f_{\text{old}} = 1/2$), we recover the approximation found in Tomasini and Peischl (2018; compare system [8] with their eqq. [4] and [5]). Note that the approximation is independent of the actual number of patches (there are two patches in total in Tomasini and Peischl 2018): the approximation depends only on the environmental configuration determined by the frequency of old-habitat patches f_{old}.

Comparison to Simulations and Qualitative Behavior. Our mathematical analysis provided two kinds of results for the establishment probability: an implicit solution in equations (7), which we solve numerically, and an explicit but approximate solution in equations (8). In figure 2, we compare these solutions to simulation results for different values of the emigration rate m. We find good agreement with the numerical solution of equations (7) (solid lines). The approximation given in equations (8) (dashed lines) deviates slightly from the simulation results in regions where m is not small, that is, when the assumptions made in the derivation of the approximation in equations (8) do not hold.

We identify up to three different regions that define how the probability of establishment of a single mutant initially in an old-habitat patch (φ_{old}) changes with the emigration probability m (fig. 2*a*). This is in line with previous observations in the context of local adaptation (e.g., Kawecki 1995; Tomasini and Peischl 2018) and evolutionary rescue (Uecker et al. 2014). We define the regions as follows: (i) at low dispersal rates m, an initial increase in the establishment probability with m; (ii) a local maximum with a subsequent decrease of the establishment probability; and (iii) at high dispersal rates m, an increase in the establishment probability with m.

In region (i), the beneficial effect of dispersal on the establishment probability φ_{old} is due to mutants dispersing from old- to new-habitat patches, where they are fitter than the wild type. While this effect is still present in region (ii), the establishment probability φ_{old} now decreases with dispersal because the offspring of individuals that dispersed to a new-habitat patch can disperse back into old-habitat patches. More precisely, the expected per capita number of surviving offspring in the new habitat of an adult in a new-habitat patch is $\lambda_{\text{new,new}} = (1 - m\mu_{\text{m}}^{\text{old}})(1 + a_{\text{new}})$. This product can, for large emigration probabilities m, be smaller than 1 (i.e., a mutant in a new-habitat patch has on average less than one offspring in a new-habitat patch). This is detrimental to the mutant because it means that mutants do not efficiently reproduce in the habitat where they are fitter. Finally, in region (iii) at high dispersal, so many wild-type individuals leave old-habitat patches that competitive pressure in old-habitat patches is substantially decreased. The post-dispersal size of the wild-type population $\tilde{N}_{\text{w}}^{\text{old}}$ is then low enough that the local growth rate of the mutant in these

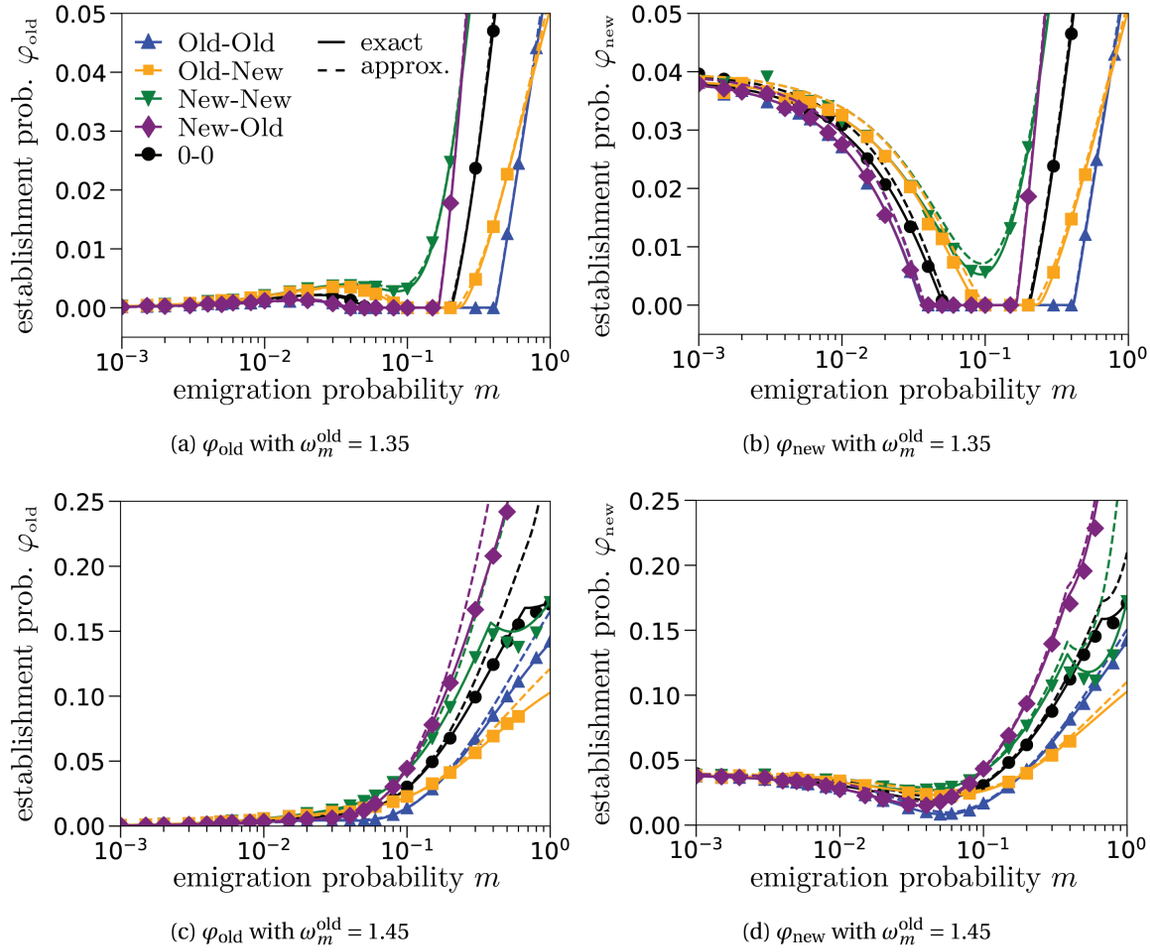


Figure 2: Establishment probability as a function of the emigration rate. *a* and *c* show the establishment probabilities when the mutant arises in an old-habitat patch (φ_{old}) and *b* and *d* show the establishment probabilities when the mutant arises in a new-habitat patch (φ_{new}), for mutant fecundity in old-habitat patches $\omega_m^{old} = 1.35$ in *a* and *b* and $\omega_m^{old} = 1.45$ in *c* and *d*. Markers: simulations; full lines: numerical solution of equations (7); dashed lines: approximate solution shown in equations (8). The colors and marker shapes correspond to the different dispersal schemes, with the same parameters as in figure 1. For a mutant emerging in old-habitat patches (*a*, *c*), the establishment probability φ_{old} is zero in the absence of dispersal ($m = 0$); it then increases with emigration m, which gives mutants a chance to settle in new-habitat patches, where they are selectively favored; φ_{old} may still decrease at intermediate emigration probability (in *a*). For a mutant emerging in new-habitat patches (*b*, *d*), the establishment probability φ_{new} is approximately $2a_{new} = 0.04$ in the absence of dispersal ($m = 0$). Increased dispersal is initially detrimental because mutants can land in old-habitat patches, where they are selectively disfavored, but φ_{new} eventually increases with m thanks to competitive release in old-habitat patches. Large dispersal and a bias of the wild type toward the new habitat may inhibit the establishment of the mutant (new-new dispersal scheme in *c* and *d*) because of gene swamping. For even larger m, competitive release becomes more important, and the establishment probability reincreases.

patches, a_{old} (the first term in eqq. [8]), becomes positive (fig. S3; figs. S1–S9 are available online). This effect is called "relaxed competition" (Uecker et al. 2014). The onset of this effect, in terms of the emigration probability m, is strongly dependent on the difference in fecundity of the mutant and the wild type in the old habitat. The smaller the difference in fecundity is, the "earlier" (i.e., for smaller emigration rates m) relaxed competition becomes relevant (compare fig. 2*a* with fig. 2*c*) to a point that region (ii) vanishes (fig. 2*c*) and there is no decrease of φ_{old} with m any longer. In contrast, for lower mutant fecundity values ω_m^{old}, region (iii) might vanish (see fig. S4), because the mutant's fecundity in old-habitat patches is too low compared with the wild type's, so the mutant does not benefit from relaxed competition in old-habitat patches.

The qualitative behavior of the establishment probability of a mutant emerging in the new habitat, φ_{new}, can be interpreted in a similar way (fig. 2*b*, 2*d*). The

establishment probability φ_{new} decreases with the emigration probability m at low m because the mutant appeared in a new-habitat patch, where it fares better than the wild type, so there is no initial benefit due to dispersal. When the emigration probability is higher, mutants can back emigrate to new-habitat patches, while those that land in old-habitat patches can enjoy relaxed competition when m is high. This is why φ_{new} increases with m at higher m.

An additional effect can take place at high dispersal and reduce mutant establishment probabilities, in particular when the wild type is biased toward new-habitat patches (see, e.g., the new-new scheme in fig. 2*c*, 2*d*). The high dispersal of wild-type individuals lets the local population in new-habitat patches exceed the carrying capacity K_{new}, inhibiting the establishment of a locally better-adapted type (mutant). Note that the lower carrying capacity in new-habitat patches than in old-habitat patches ($K_{\text{new}} < K_{\text{old}}$) creates a favorable setting to this effect, also referred to as "gene swamping" (Nagylaki 1978; Lenormand 2002). Further increasing the emigration probability m results in relaxed competition in the old habitat, which explains the reincrease of the new-new dispersal scheme.

Comparison of Dispersal Schemes. We now compare the establishment probabilities across the different dispersal schemes. Mostly, a general bias toward the new habitat (new-new scheme in fig. 2) enhances mutant establishment compared with the unbiased dispersal scheme (0-0). This can be attributed to two reasons. First, the mutant is more likely to disperse to the new habitat, where it outcompetes the wild type. Second, competition in old-habitat patches is relaxed starting at low emigration probabilities m because the wild type preferentially disperses to new-habitat patches. Conversely, a bias toward the old habitat (old-old scheme) lowers mutant establishment probabilities compared with the unbiased dispersal scheme.

The rankings of the type-dependent dispersal schemes (old-new and new-old schemes) compared with the unbiased scheme (0-0) depend on the amount of dispersal (compare the orange, purple, and black curves in fig. 2). As explained above, at low dispersal probabilities m, the prevalent force is the dispersal of mutants to new-habitat patches. The establishment probability of the mutant is therefore higher for the old-new scheme, where mutants preferentially disperse to new-habitat patches compared with random dispersal, while the opposite is true for the new-old scheme. At high dispersal probabilities m, however, an important force is competitive release in old-habitat patches. The establishment probability of the mutant is therefore higher in the scheme where wild-type individuals preferentially disperse out of old-habitat patches, releasing competition there (new-old scheme).

Probability of Adaptation in a Heterogeneous Environment

We now study the probability of adaptation when mutations occur recurrently. As in the previous section, we consider a heterogeneous environment with a fixed number of old- and new-habitat patches. This is effectively a source-sink system (Holt 1985; Pulliam 1988), where old- and new-habitat patches correspond to sources and sinks for the wild type, respectively. In the previous section, we initialized the system with one mutant in either an old- or a new-habitat patch and computed the establishment probability. Now, we let mutants appear randomly within a certain time frame. The last time point at which a mutation can occur is denoted by t_{fin}.

In this setting, the probability of adaptation P_{adapt} is approximated by

$$P_{\text{adapt}} = 1 - \exp\left(-\theta t_{\text{fin}} M\left(\underbrace{\varphi_{\text{old}} f_{\text{old}} K_{\text{old}}}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}}(1 - f_{\text{old}})\hat{N}_{\text{w}}^{\text{new}}}_{\text{new habitat contribution}}\right)\right). \tag{10}$$

This is 1 minus the probability that no mutant establishes within the $[0, t_{\text{fin}}]$ time interval, given by the probability of zero successes of a Poisson distribution. The rate of this Poisson distribution is the expected number of successfully emerging mutant lineages until time t_{fin}. Mutants arise with probability θ; $Mf_{\text{old}}K_{\text{old}}$ is the total number of wild-type individuals in old-habitat patches, and $M(1 - f_{\text{old}})\hat{N}_{\text{w}}^{\text{new}}$ is the total number of wild-type individuals in new-habitat patches. A mutant arising in a k-habitat patch has a probability φ_k of establishing in the population; we assume that mutants establish independently of one another. Assuming a Poisson distribution for the number of successful mutant lineages is an approximation of a binomial distribution with a large sample size (the wild-type population size) and a small success probability (the establishment probabilities φ_k times the mutation probability θ). Note also that for t_{fin} tending to infinity, there will almost surely be a successful mutant, so that $P_{\text{adapt}} = 1$.

The probability of adaptation P_{adapt} calculated with equation (10) is compared with simulation results in figure 3. In spite of our approximations, the fit to simulation results is still very good. As P_{adapt} includes the probabilities of establishment φ_k, here again the shapes of the curves as a function of the emigration probability m depend on the fecundity of the mutant in old-habitat patches, $\omega_{\text{m}}^{\text{old}}$ (fig. 3*a*, 3*c*). Likewise, the rankings of the different dispersal schemes are comparable to the ones observed for the establishment probability.

Figure 3*b* and figure 3*d* show the probability of adaptation as a function of the frequency of old-habitat

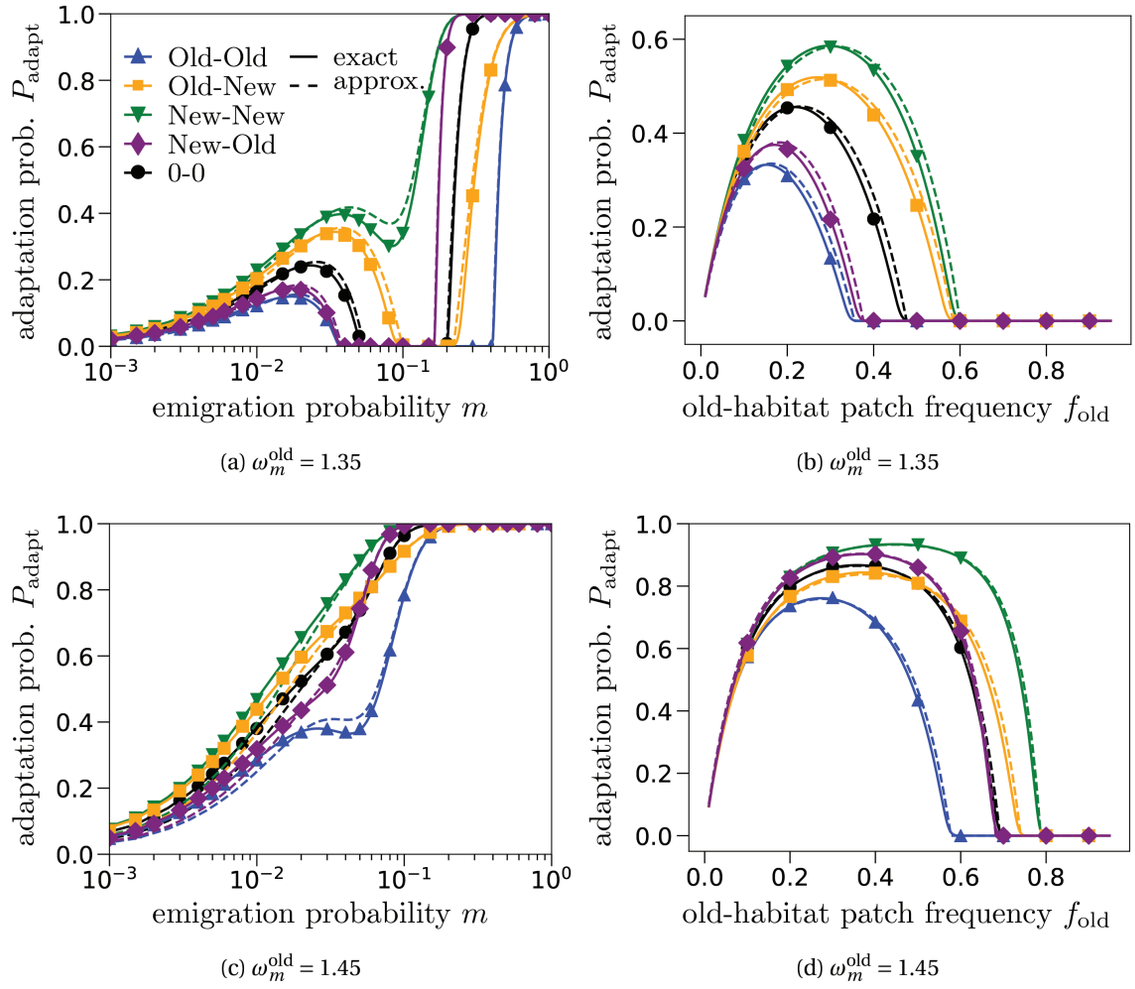


Figure 3: Probability of adaptation in a heterogeneous environment. In *a* and *c*, we vary the emigration rate m and observe a similar qualitative behavior as for the establishment probability φ_k in figure 2. In *b* and *d*, we vary the frequency of old-habitat patches. The maximum is the result of two counteracting processes. The higher the number of old-habitat patches (the greater f_{old}), the larger the wild-type population. As a consequence, more mutants appear in the studied time frame. In contrast, the fewer old-habitat patches there are in the environment (the lower f_{old}), the higher the probability of successful establishment of a mutant population. The curves are given by equation (10); approximate curves use the approximate solution for φ_k given in equations (8), while exact curves are obtained by numerically solving equations (7) for φ_k. In all panels, the mutation probability is $u = 1/(MK_{\text{new}})$, and the final time for a mutant to appear is $t_{\text{fin}} = 100$.

patches f_{old}. The maximum of P_{adapt} at intermediate f_{old} is the result of two antagonistic effects: (1) the likelihood that a mutation appears increases with the number of wild-type individuals present in the system, which is highest for high frequencies of old-habitat patches f_{old}, and (2) the probability of establishment of a mutant decreases with the number of old-habitat patches.

The different dispersal schemes alter both effects. The probability of adaptation is highest when there is a general bias toward the new habitat (new-new scheme), because of a combination of high establishment probabilities (fig. 2) and high local population sizes thanks to the bias (fig. S1). Conversely, a general preference for old-habitat patches (old-old scheme) yields lower probabilities of adaptation.

Habitat of Origin of the Adaptive Mutation. We now ask in which habitat mutations leading to successful establishment appear. To do so, we distinguish in the simulations between mutants that appear in old-habitat patches and mutants that appear in new-habitat patches, and we identify the habitat of origin of the mutation by considering the composition of the mutant population after establishment. We, however, do not distinguish between separate

mutations that appear in the same type of habitat, meaning that we cannot rule out the presence of multiple lineages if they all appeared in the same type of patch: there may be soft selective sweeps (for a review, see Hermisson and Pennings 2017). With this implementation, we can be sure that multiple lineages contributed only when the established mutant population contains mutants that appeared in both old- and new-habitat patches.

Analytically, we approximate the probability of observing a mutant population that can be traced back to mutants from old-habitat patches only by

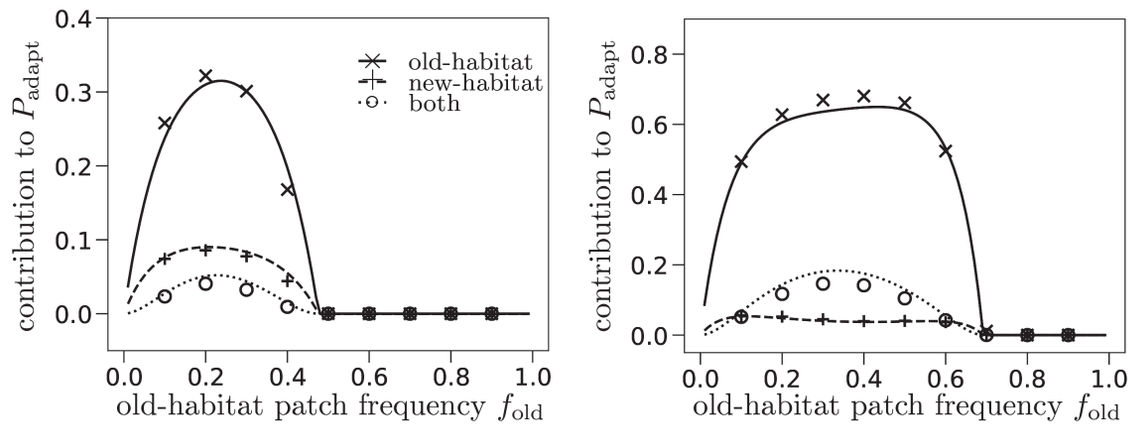
$$\begin{aligned}&\mathbb{P}(\text{successful adaptation from old habitat})\\&\quad\times(1-\mathbb{P}(\text{successful adaptation from new habitat}))\\&\approx(1-\exp(-\theta t_{\text{fin}}M\varphi_{\text{old}}f_{\text{old}}K_{\text{old}}))\\&\quad\times(\exp(-\theta t_{\text{fin}}M\varphi_{\text{new}}(1-f_{\text{old}})\hat{N}_{\text{w}}^{\text{new}})).\end{aligned}\tag{11}$$

The corresponding probabilities for the other two scenarios can be computed analogously. The approximation uses our key assumption that different mutant individuals and their offspring do not affect each others' dynamics (branching process). In the simulations, we turn off mutations after generation $t_{\text{fin}} = 100$ and sample the population after 1,000 generations. Compared with counting the number of successful lineages right after the mutant population size has crossed the establishment threshold, this method lowers the likelihood of counting mutant lineages that appeared just before the total mutant population exceeds the establishment threshold but are themselves not established. We label a run as having established lineages originated from different habitat types ("both" in fig. 4) if these lineages are still alive at the end of the simulation. Simulations where established lineages arose exclusively in old- or new-habitat patches are labeled "old-habitat patch" and "new-habitat patch," respectively.

We compare our calculations to simulation results in figure 4, varying the frequency of old-habitat patches f_{old}. Most successful mutations arise in old-habitat patches, with a much smaller contribution to the probability of adaptation for lower numbers of mutant offspring in old habitats (fig. 4*a*) than for larger numbers of offspring (fig. 4*b*). The contributions of old- versus new-habitat patches depend on the product $\varphi_k\hat{N}_{\text{w}}^{k}f_k$, which we decompose in figure S5. Even though the establishment probability from old-habitat patches is lower ($\varphi_{\text{old}} < \varphi_{\text{new}}$), the total population size of the wild type in old-habitat patches is larger than that in new-habitat patches, so that more mutants appear in old-habitat patches than in new-habitat patches, which compensates for their lower establishment probability.

Evolutionary Rescue

Finally, we assume that patches deteriorate one after another at regular time intervals τ, until all patches have



(a) $\omega_m^{\text{old}} = 1.35$ (b) $\omega_m^{\text{old}} = 1.45$

Figure 4: Origin of the adaptive mutant, depending on mutant fecundity in old-habitat patches $\omega_{\text{m}}^{\text{old}}$ (recall that $\omega_{\text{w}}^{\text{old}} = 1.5$). The points correspond to simulations, where mutants arising in old- versus new-habitat patches are differently labeled and where we consider the composition of the mutant population at the end of the simulation. The labels "old-habitat" and "new-habitat" correspond to established mutant lineages from exclusively that habitat type, and "both" refers to mutant populations that can be traced back to both habitat types. The solid lines are given by equation (11) (dashed and dotted lines are obtained analogously) under the unbiased dispersal scheme ($\pi_{\text{w}} = \pi_{\text{m}} = 0$). Mutants that establish predominantly appeared in old-habitat patches: the lower establishment probability for mutants emerging in old-habitat patches is compensated by the larger number of mutants appearing in these patches, because of a higher local population size. Note the different scalings on the *Y*-axes.

switched to the new habitat. If the wild-type population fails to generate a successful mutant, the population will inevitably become extinct, because the entire environment will consist of new-habitat patches and because a wild-type population is assumed not to be viable there. We first focus on evolutionary rescue due to de novo mutations. Because the configuration of the environment changes over time, we denote by $f_{\text{old}}(i) = (M - i)/M$ the proportion of old-habitat patches after the ith deterioration event. We also explicitly write the dependency of the establishment probabilities on the proportion of old-habitat patches, $\varphi_k(f_{\text{old}}(i))$—this is only a notation change, as the formulas presented before still apply (eqq. [7], [8]). We approximate the probability of evolutionary rescue, denoted by P_{rescue}, as

$$P_{\text{rescue}} \approx 1 - \exp\left(-\theta \sum_{i=1}^{M-1} \left(\underbrace{\varphi_{\text{old}}(f_{\text{old}}(i)) \sum_{j=(i-1)\tau}^{i\tau-1} N_{\text{w}}^{\text{old}}(j)}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}}(f_{\text{old}}(i)) \sum_{j=(i-1)\tau}^{i\tau-1} N_{\text{w}}^{\text{new}}(j)}_{\text{new habitat contribution}} \right) - \underbrace{\theta \varphi_{\text{new}}(0) \sum_{j=\tau(M-1)}^{\infty} N_{\text{w}}^{\text{new}}(j)}_{\text{contribution after the last patch deteriorated}} \right), \tag{12}$$

where $N_{\text{w}}^{k}(j)$ denotes the overall number of wild-type individuals living in habitat k (old or new) in generation j (see the supplemental PDF, sec. S1.4, eq. [S8]). The interpretation of this equation is the same as for the probability of adaptation in equation (10). The only difference is that we now need to account for a changing environment. In the formula, these changes are accounted for by the sums that iterate through the (discrete) time steps and by the time dependence of the corresponding quantities. We further note that we follow the expected value of the wild-type population size deterministically over time ($N_{\text{w}}^{k}(j)$), instead of assuming it to be already in its steady state, as in equation (10). The establishment probabilities $\varphi_k(f_{\text{old}}(i))$ are, however, still computed using stationary population sizes, calculated at each time step using equations (7) and (8) (i.e., they are considered as a piecewise constant).

Comparison to simulated data indicates that the approximation in equation (12) correctly predicts the ranking of dispersal schemes; the actual fit to data is, however, less good than for the previous steps of our analysis. This discrepancy can be explained: our mathematical analysis assumes that for a mutant born in a certain patch configuration, say with i old-habitat patches, the environment does not change anymore. That is, a mutant born in a k-habitat patch in this environment contributes $\varphi_k(i/M)$ to the probability of evolutionary rescue despite further patches deteriorating—while having more new-habitat patches increases the probability of establishment (see, e.g., fig. S5). Thus, the probability of establishment is underestimated. This is especially true for mutants that emerge just before a deterioration event. Additionally, $\varphi_k(i/M)$ assumes stationary wild-type population sizes and therefore does not reflect the decreasing wild-type population size right after the deterioration of a patch. A time-dependent establishment probability could account for these effects but unfortunately is not amenable to approximations in our framework. Uecker et al. (2014) were able to find a time-dependent solution by focusing on specific scenarios: situations with either full mixing of the global population ($m = 1$) or a sterile mutant in old-habitat patches ($\omega_{\text{m}}^{\text{old}} = 0$). In these extreme cases, the branching process becomes one dimensional and an analytical, time-dependent solution can be obtained, which is not the case with a two-dimensional branching process like ours.

The ranking of the different dispersal schemes is overall conserved from the previous steps of our analysis (fig. 3). Differences between the dispersal schemes are more marked when the fecundity of the mutant in old-habitat patches is lower (fig. 5*c*, 5*d*), including when the mutant cannot reproduce at all in old-habitat patches ($\omega_{\text{m}}^{\text{old}} = 0$). It is comparatively better for rescue that the mutant preferentially disperses into new-habitat patches, where it is relatively fitter, and for the wild type to also preferentially disperse into new-habitat patches, thereby releasing competition in old-habitat patches.

When mutant fecundity in old-habitat patches is comparatively low (fig. 5*c*, 5*d*), the probability of evolutionary rescue often reaches a local (or global) maximum at intermediate emigration probabilities. This finding extends previous results (Uecker et al. 2014; Tomasini and Peischl 2020) to arbitrary dispersal schemes affecting the immigration process.

Habitat of Origin of the Rescue Mutant and Standing Genetic Variation. Similar to what we found for the probability of adaptation, rescue mutants mainly originate from old-habitat patches (fig. 6*a*). Mutations are more likely to appear in the more populated patches (old habitat). However, a low mutant fecundity in old-habitat patches $\omega_{\text{m}}^{\text{old}}$ decreases the chance of establishment of the mutants that appear in old-habitat patches (compare black and yellow symbols in fig. 6*a*). Here again, we cannot rule out that multiple mutant lineages having appeared in the same habitat type established. Only when mutants from both habitat types are present can we be sure that at least two

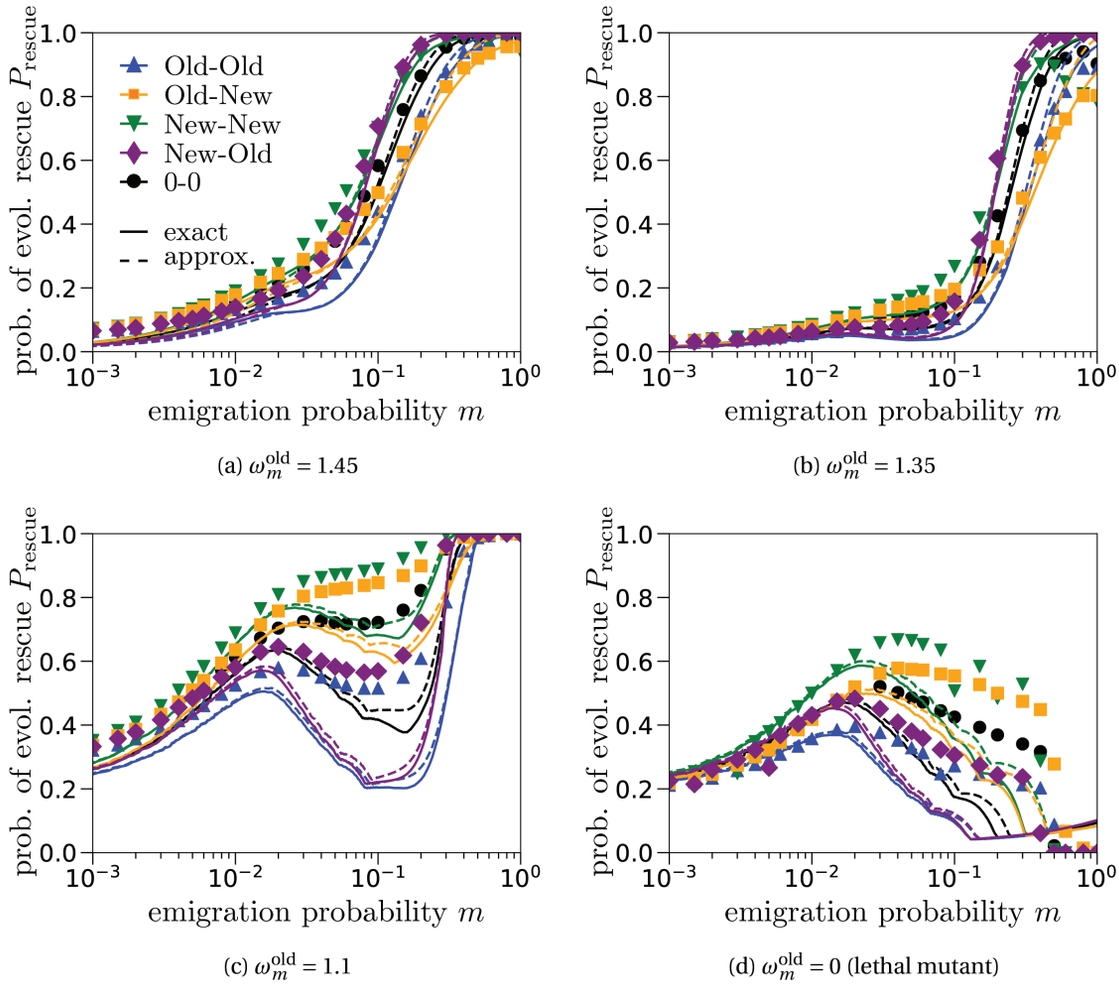
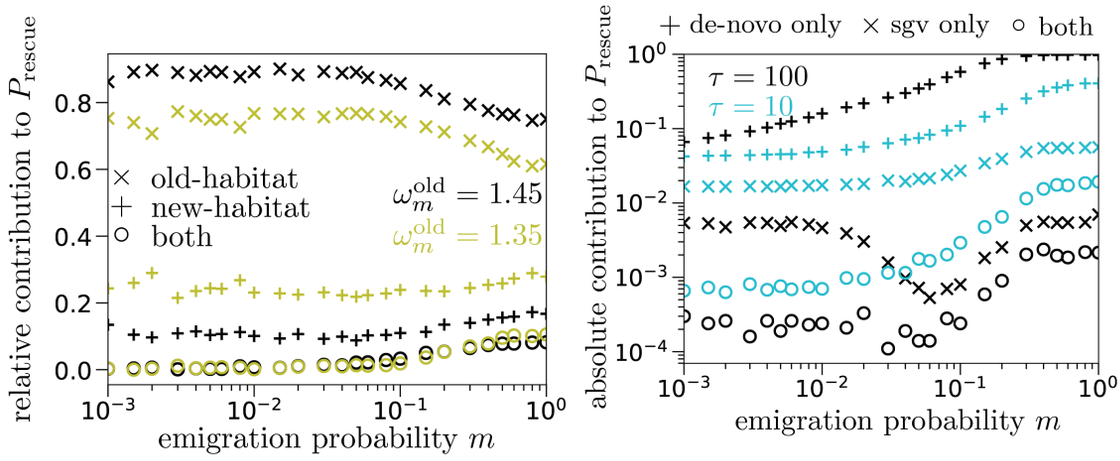


Figure 5: Probability of evolutionary rescue compared with simulation results. Our predictions, computed with equation (12), match the qualitative behavior of the simulated data for the probability of evolutionary rescue. All rankings of the dispersal schemes align well. Quantitatively though, we find that our predictions tend to underestimate the simulated data. In *a* and *b*, the mutation probability is set to $\theta = 1/(25MK_{\text{new}})$; in *c* and *d*, it is $\theta = 1/(MK_{\text{new}})$. For the establishment probabilities φ_k in equation (12), the solid lines show the exact solution of equations (7), and the dashed lines show the approximated ("approx.") solution from equations (8).

lineages contributed to establishment (i.e., there was a soft sweep). In our parameter set, the probability of rescue with a mix of origins was very low in our simulations (circles in fig. 6*a*). Note that our choice of a small mutation rate corresponds to a hard selective sweep regime ($\theta K_{\text{old}}M = 0.08 < 1$; Wilson et al. 2017*a*; Hermisson and Pennings 2017).

So far, we have considered settings where evolutionary rescue is exclusively due to de novo mutations. To explore the role of standing genetic variation, we ran simulations where we let the system evolve for 1,000 generations before the first degradation event happened—we were not able to find a theoretical prediction for the contribution of standing genetic variation. Mutants that appeared before the first degradation event (i.e., at times $t < 0$ when $f_{\text{old}} = 1$) were labeled "sgv-mutants." Mutants appearing after $t = 0$ are labeled "de novo mutants." Figure 6*b* shows the contributions of de novo mutations and of standing genetic variation to the probability of evolutionary rescue. Rescue events involving mutants from standing genetic variation are much rarer than rescue events from de novo mutants (note the log scale in fig. 6*b*). The number of rescue events due to standing genetic variation decreases when the interval between two degradation events, τ, increases (compare blue and black cross marks in fig. 6*b*; see also fig. S6 in sec. S5 of the supplemental PDF for more details). This is because mutants that were present at time $t = 0$ (sgv-mutants) needed



(a) Habitat of origin of the rescue mutants

(b) Contribution of de-novo mutations compared to standing genetic variation

Figure 6: Habitat of origin of the rescue mutation and the impact of standing genetic variation. *a*, We compare the origin of successful mutations for different mutant fecundity in the old-habitat patches (black vs. yellow). Comparatively more established mutants originated from new-habitat patches when the mutant fecundity in old-habitat patches ω_m^{old} is lower (compare black and yellow plus signs). Dispersal is unbiased ($\pi_m = \pi_w = 0$). *b*, The larger the time interval τ between two degradation events, the smaller the influence of standing genetic variation on the probability of evolutionary rescue (compare black and blue cross marks). For large emigration probabilities, the probability of evolutionary rescue due to de novo mutants increases (fig. 5). This is also true for rescue events due to standing genetic variation (see blue cross marks). The simulations are done by letting the system evolve for 1,000 generations before the first deterioration event happens. Parameters: $\pi_m = \pi_w = 0$ in both scenarios and $\omega_m^{\text{old}} = 1.45$. Note the log scale on the *Y*-axis.

to survive for sufficiently many patch deterioration events before their growth rate turned positive, giving them a chance to establish. The longer this time (higher τ), the less likely their establishment. As already shown, the probability of evolutionary rescue by de novo mutation increases with emigration probability m when m is large (fig. 5). This is also the case for sgv-mutants (fig. 6*b*), for the same reasons (relaxed competition in old-habitat patches when m is large).

Discussion

We have studied the effect of four dispersal schemes on the probabilities of establishment, adaptation, and evolutionary rescue and compared them with unbiased dispersal, which is the dispersal scheme predominantly considered in models so far. For all biased dispersal schemes, the probabilities deviate from the ones obtained for unbiased dispersal. The highest probabilities of establishment, adaptation, and evolutionary rescue are typically found for a general bias toward degraded patches (new-new dispersal scheme), and the lowest are typically found for a general bias toward nondegraded patches (old-old scheme). We find that all of the probabilities can be a nonmonotonic function of dispersal. This nonmonotonicity is explained by the multiple effects of dispersal: bringing mutants to degraded patches, but also back to nondegraded patches, and relaxation of competition in nondegraded patches by distributing individuals more evenly across the patches. Last, we found that successful mutant lineages mostly emerge in old-habitat patches and that standing genetic variation prior to the degradation of the first patch contributes only a little to evolutionary rescue in a subdivided population.

Dispersal and Adaptation

Theoretical studies that investigated the effects of spatial subdivision on the adaptation of a population in a heterogeneous environment can be classified into two types depending on how they treat demography. One type of models, classically analyzed in a population genetics framework, assumes constant population sizes in all patches, independent of their local habitat type and of dispersal strength (a feature that we later call "implicit demography"). Results obtained in this framework show one notable difference compared with our model with demography: in these models, the probability of successful establishment of a rare mutant favored in some part of the environment decreases at larger dispersal rates (e.g., Nagylaki 1978; Bürger and Akerman 2011). This gene

swamping effect is due to the dispersal of nonadapted individuals into the habitat type where the rare mutant is beneficial, decreasing the local frequency of the mutant (Lenormand 2002; Tomasini and Peischl 2018).

The second type of models explicitly takes into account demographic effects due to dispersal, often in the context of source-sink systems (Holt 1985; Pulliam 1988). Here, the effect of dispersal on adaptation depends on the growth rate differences of the mutant and the wild type in the two habitats (Kawecki 2000), which we also observe. When the mutant is just slightly less fit than the wild type in the old habitat (fig. 2*c*), the probability of adaptation monotonically increases with dispersal. When the mutant's fecundity is lower, establishment probabilities reach a local maximum at intermediate dispersal rates and increase again at large dispersal rates as a result of relaxed competition (fig. 2*a*). When the fecundity of the mutant is even smaller, the local maximum remains but relaxed competition no longer occurs (cf. fig. S4).

To compare the effects of explicit versus implicit demographic dynamics, we provide in the supplemental PDF a version of our model with implicit demographic dynamics (sec. S6, fig. S7), that is, where all patches are at carrying capacity at the end of the life cycle. The two models are most different when dispersal is high. With explicit demographic dynamics, we found that with high dispersal, adaptation is most likely if the wild type preferentially disperses into degraded patches (new-new dispersal scheme). With implicit demographic dynamics, on the contrary, this is the case if the wild type remains in nondegraded patches (old-new scheme). Relaxed competition can also happen in models with implicit demography, but only if the dispersal preference is type dependent (new-old or old-new scheme; fig. S7). This is because for large emigration probabilities type-dependent dispersal preferences cause a quasi separation of the mutant and the wild type into different patch types, so they are less directly competing.

Standing Genetic Variation and Evolutionary Rescue

We also studied the contribution of standing genetic variation to evolutionary rescue. This contribution increases with the speed of environmental change since with smaller intervals between degradations τ, sgv-mutant lineages only need to survive for a shorter time until they experience a favorable environment with more degraded patches, where establishment becomes more likely (figs. 6*b*, S6). This observation has also been made in a quantitative genetics setting, where the adaptive trait is continuous (and not discrete, as in our model; Matuszewski et al. 2015). Experimental results with *Caenorhabditis elegans* also indicate that the impact of standing genetic variation is small under slow environmental change (Guzella et al. 2018).

The Effect of Biased Dispersal Patterns on Adaptation and Evolutionary Rescue

The importance of considering dispersal schemes other than unbiased dispersal has been highlighted in several papers (Edelaar et al. 2008; Clobert et al. 2009; Edelaar and Bolnick 2012). This has led to a number of simulation studies exploring the effect of various dispersal schemes on (local) adaptation (e.g., Vuilleumier et al. 2010; Holt and Barfield 2015; Mortier et al. 2018; Pellerin et al. 2018). These cited studies examined the effect of matching habitat choice on adaptation in a heterogeneous environment and observed that it increases the probability of adaptation compared with unbiased dispersal.

We identified two types of effects of the different dispersal schemes. First, by changing population densities in both habitat types, the dispersal schemes change the growth rate of the mutant in both patch types (fig. S3) by altering the strength of local density regulation. This is the primary reason for the ranking of the dispersal schemes, with a general immigration bias into new habitats (new-new scheme) promoting evolutionary rescue the most and a general immigration bias into old habitats (old-old scheme) promoting it the least. Second, the different dispersal schemes affect the number of mutations arising in either habitat type. This affects the probability of evolutionary rescue and is also relevant for the origin of the successful mutant lineage (fig. S8). As the genetic background may vary across patches, the origin of a successful mutation will also determine which mutations will hitchhike with it. Similarly, with polygenic rescue or under recombination (e.g., Schiffers et al. 2013; Uecker and Hermisson 2016), the origin of a mutant is likely to affect its success, as is the case in our model.

Generality of Our Theoretical Analysis and Future Directions

Our mathematical analysis relies on the simplifications that the wild-type population does not change over time and that the mutant is rare enough that mutants live independently of each other and do not affect wild-type individuals. This allows us to summarize mutant population dynamics with the λ terms presented in equation (4). Furthermore, for our approximation in equation (8) to generate accurate predictions, it is essential that growth rate differences between the wild type and the mutant are weak and dispersal is low—these conditions are, however, not needed when we numerically solve system (7) (see also sec. S8 in the supplemental PDF, where we relax the condition of small mutant fecundity in the new habitat).

Our approach can account for various dispersal schemes and local type-dependent population dynamics

(i.e., different reproduction and competitive parameters for the wild type and the mutant). However, it cannot account for type-dependent carrying capacities, explicit spatial structure, or rapidly changing environments.

Last, our model can readily be extended and include a cost of dispersal or a different life cycle. In particular, different life cycles could yield different results regarding adaptation. For example, juvenile dispersal—that is, dispersal right before density regulation—has been found to facilitate adaptation to a sink environment more than adult dispersal (dispersal right before reproduction; Holt and Barfield 2015). In the context of local adaptation in a heterogeneous environment, Débarre and Gandon (2011) found that stronger adult dispersal than juvenile dispersal creates favorable conditions for local adaptation and maintenance of a polymorphism. More generally, the life cycle has also been found to affect the evolution of dispersal (Massol and Débarre 2015).

Conclusion

In conclusion, we studied the effect of dispersal and habitat choice on the probability of establishment, adaptation, and evolutionary rescue in a subdivided population under divergent selection. We recover previous results on adaptation and, using results from the theory of multitype branching processes, provide a general framework for studying the evolutionary dynamics of a subdivided population in heterogeneous environments in discrete time. This unifying approach allows us to identify the forces responsible for the different predictions obtained in the population genetics literature and under source-sink dynamics. We find that including population demography substantially alters the results for high dispersal rates. For constant population sizes and type-independent dispersal schemes, high dispersal rates have a negative effect on establishment, while with explicit demography the effect is largely positive. The latter is a result of relaxed competition in old-habitat patches. Most importantly, we extend the existing literature by comparing different dispersal schemes and studying their effects on adaptation and evolutionary rescue. We find that a general dispersal bias toward degraded patches results in the highest probability of adaptation and evolutionary rescue. The lowest values are obtained for a general bias toward nondegraded patches. These results show that nonuniform dispersal patterns can have a strong influence on population survival and adaptation in a heterogeneous environment.

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Statement of Authorship

P.C.: conceptualization; model analysis; coding simulations; data analysis; writing, original draft; writing, review and editing. F.B.: conceptualization; data analysis; supervision; writing, review and editing. H.U.: conceptualization; data analysis; writing, review and editing. F.D.: conceptualization; data analysis; funding acquisition; supervision; writing, original draft; writing, review and editing.

Data and Code Availability

All code and simulation data have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.rv15dv47j; Czuppon et al. 2021).

Literature Cited

Agashe, D., J. J. Falk, and D. I. Bolnick. 2011. Effects of founding genetic variation on adaptation to a novel resource. Evolution 65:2481–2491.

Alexander, H. K., G. Martin, O. Y. Martin, and S. Bonhoeffer. 2014. Evolutionary rescue: linking theory for conservation and medicine. Evolutionary Applications 7:1161–1179.

Amarasekare, P. 2004. The role of density-dependent dispersal in source-sink dynamics. Journal of Theoretical Biology 226:159–168.

Anciaux, Y., L.-M. Chevin, O. Ronce, and G. Martin. 2018. Evolutionary rescue over a fitness landscape. Genetics 209:265–279.

Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Bell, G. 2017. Evolutionary rescue. Annual Review of Ecology, Evolution, and Systematics 48:605–627.

Bell, G., and A. Gonzalez. 2009. Evolutionary rescue can prevent extinction following environmental change. Ecology Letters 12:942–948.

———. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. Science 332:1327–1330.

Benkman, C. W. 2017. Matching habitat choice in nomadic crossbills appears most pronounced when food is most limiting. Evolution 71:778–785.

Bestion, E., J. Clobert, and J. Cote. 2015. Dispersal response to climate change: scaling down to intraspecific variation. Ecology Letters 18:1226–1233.

Bolnick, D. I., L. K. Snowberg, C. Patenia, W. E. Stutz, T. Ingram, and O. L. Lau. 2009. Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. Evolution 63:2004–2016.

Boulding, E. G., and T. Hay. 2001. Genetic and demographic parameters determining population persistence after a discrete change in the environment. Heredity 86:313–324.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Bürger, R., and A. Akerman. 2011. The effects of linkage and gene flow on local adaptation: a two-locus continent-island model. Theoretical Population Biology 80:272–288.

Bürger, R., and M. Lynch. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. Evolution 49:151–163.

Carlson, S. M., C. J. Cunningham, and P. A. Westley. 2014. Evolutionary rescue in a changing world. Trends in Ecology and Evolution 29:521–530.

Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Czuppon, P., F. Blanquart, H. Uecker, and F. Débarre. 2021. Data from: The effect of habitat choice on evolutionary rescue in subdivided populations. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.rv15dv47j.

Débarre, F., and S. Gandon. 2011. Evolution in heterogeneous environments: between soft and hard selection. American Naturalist 177:E84–E97.

De Meester, N., and D. Bonte. 2010. Information use and density-dependent emigration in an agrobiont spider. Behavioral Ecology 21:992–998.

Di Giallonardo, F., and E. C. Holmes. 2015. Viral biocontrol: grand experiments in disease emergence and evolution. Trends in Microbiology 23:83–90.

Diniz-Filho, J. A. F., K. S. Souza, L. M. Bini, R. Loyola, R. Dobrovolski, J. F. M. Rodrigues, S. Lima-Ribeiro, et al. 2019. A macroecological approach to evolutionary rescue and adaptation to climate change. Ecography 42:1124–1141.

Dreiss, A. N., S. Antoniazza, R. Burri, L. Fumagalli, C. Sonnay, C. Frey, J. Goudet, and A. Roulin. 2011. Local adaptation and matching habitat choice in female barn owls with respect to melanic coloration. Journal of Evolutionary Biology 25:103–114.

Edelaar, P., and D. I. Bolnick. 2012. Non-random gene flow: an underappreciated force in evolution and ecology. Trends in Ecology and Evolution 27:659–665.

Edelaar, P., A. M. Siepielski, and J. Clobert. 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. Evolution 62:2462–2472.

Endriss, S. B., M. L. Vahsen, E. V. Bitume, J. Grey Monroe, K. G. Turner, A. P. Norton, and R. A. Hufbauer. 2019. The importance of growing up: juvenile environment influences dispersal of individuals and their neighbours. Ecology Letters 22:45–55.

Folt, B., M. A. Donnelly, and C. Guyer. 2018. Spatial patterns of the frog *Oophaga pumilio* in a plantation system are consistent with conspecific attraction. Ecology and Evolution 8:2880–2889.

Gallet, R., R. Froissart, and V. Ravigné. 2018. Experimental demonstration of the impact of hard and soft selection regimes on polymorphism maintenance in spatially heterogeneous environments. Evolution 72:1677–1688.

Gautier, P., K. Olgun, N. Uzum, and C. Miaud. 2006. Gregarious behaviour in a salamander: attraction to conspecific chemical cues in burrow choice. Behavioral Ecology and Sociobiology 59:836–841.

Gignoux-Wolfsohn, S. A., M. Pinsky, K. Kerwin, C. Herzog, M. Hall, A. Bennett, N. Fefferman, and B. Maslo. 2018. Genomic signatures of evolutionary rescue in bats surviving white-nose syndrome. bioRxiv, https://doi.org/10.1101/470294.

Glémin, S., and J. Ronfort. 2013. Adaptation and maladaptation in selfing and outcrossing species: new mutations versus standing variation. Evolution 67:225–240.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural selection prevent extinction? Evolution 49:201–207.

Gomulkiewicz, R., R. D. Holt, and M. Barfield. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. Theoretical Population Biology 55:283–296.

Greene, K. M., S. E. Pittman, and M. E. Dorcas. 2016. The effects of conspecifics on burrow selection in juvenile spotted salamanders (*Ambystoma maculatum*). Journal of Ethology 34:309–314.

Guzella, T. S., S. Dey, I. M. Chelo, A. Pino-Querido, V. F. Pereira, S. R. Proulx, and H. Teotónio. 2018. Slower environmental change hinders adaptation from standing genetic variation. PLoS Genetics 14:1–28.

Haccou, P., P. Jagers, and V. A. Vatutin. 2005. Branching processes: variation, growth, and extinction of populations. Cambridge Studies in Adaptive Dynamics. Cambridge University Press, Cambridge.

Haldane, J. B. S. 1927. A mathematical theory of natural and artificial selection, part V: selection and mutation. Mathematical Proceedings of the Cambridge Philosophical Society 23:838–844.

Hermisson, J., and P. S. Pennings. 2017. Soft sweeps and beyond: understanding the patterns and probabilities of selection footprints under rapid adaptation. Methods in Ecology and Evolution 8:700–716.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28:181–208.

———. 1996. Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. Oikos 75:182–192.

Holt, R. D., and M. Barfield. 2015. The influence of imperfect matching habitat choice on evolution in source-sink environments. Evolutionary Ecology 29:887–904.

Holt, R. D., and R. Gomulkiewicz. 1997. How does immigration influence local adaptation? a reexamination of a familiar paradigm. American Naturalist 149:563–572.

Jacob, S., E. Laurent, B. Haegeman, R. Bertrand, J. G. Prunier, D. Legrand, J. Cote, A. S. Chaine, M. Loreau, J. Clobert, and N. Schtickzelle. 2018. Habitat choice meets thermal specialization: competition with specialists may drive suboptimal habitat

preferences in generalists. Proceedings of the National Academy of Sciences of the USA 115:11988–11993.

Jacob, S., D. Legrand, A. S. Chaine, D. Bonte, N. Schtickzelle, M. Huet, and J. Clobert. 2017. Gene flow favours local adaptation under habitat choice in ciliate microcosms. Nature Ecology and Evolution 1:1407–1410.

Karlin, S., and R. B. Campbell. 1981. The existence of a protected polymorphism under conditions of soft as opposed to hard selection in a multideme population system. American Naturalist 117:262–275.

Kawecki, T. J. 1995. Demography of source-sink populations and the evolution of ecological niches. Evolutionary Ecology 9:38–44.

———. 2000. Adaptation to marginal habitats: contrasting influence of the dispersal rate on the fate of alleles with small and large effects. Proceedings of the Royal Society B 267:1315–1320.

Kawecki, T. J., and R. D. Holt. 2002. Evolutionary consequences of asymmetric dispersal rates. American Naturalist 160:333–347.

Kreiner, J. M., J. R. Stinchcombe, and S. I. Wright. 2018. Population genomics of herbicide resistance: adaptation via evolutionary rescue. Annual Review of Plant Biology 69:611–635.

Lachapelle, J., and G. Bell. 2012. Evolutionary rescue of sexual and asexual populations in a deteriorating environment. Evolution 66:3508–3518.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends in Ecology and Evolution 17:183–189.

Lindsey, H., J. Gallie, S. Taylor, and B. Kerr. 2013. Evolutionary rescue from extinction is contingent on a lower rate of environmental change. Nature 494:463–468.

Martin, G., R. Aguilée, J. Ramsayer, O. Kaltz, and O. Ronce. 2013. The probability of evolutionary rescue: towards a quantitative comparison between theory and evolution experiments. Philosophical Transactions of the Royal Society B 368:20120088.

Massol, F., and F. Débarre. 2015. Evolution of dispersal in spatially and temporally variable environments: the importance of life cycles. Evolution 69:1925–1937.

Mathieu, J., S. Barot, M. Blouin, G. Caro, T. Decaëns, F. Dubs, L. Dupont, P. Jouquet, and P. Nai. 2010. Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, *Aporrectodea icterica* and *Dendrobaena veneta*, in a mesocosm experiment. Soil Biology and Biochemistry 42:203–209.

Matuszewski, S., J. Hermisson, and M. Kopp. 2015. Catch me if you can: adaptation from standing genetic variation to a moving phenotypic optimum. Genetics 200:1255–1274.

Mortier, F., S. Jacob, M. L. Vandegehuchte, and D. Bonte. 2018. Habitat choice stabilizes metapopulation dynamics by enabling ecological specialization. Oikos 128:529–539.

Nagylaki, T. 1978. Clines with asymmetric migration. Genetics 88:813–827.

Orr, H. A., and R. L. Unckless. 2008. Population extinction and the genetics of adaptation. American Naturalist 172:160–169.

Osmond, M. M., and C. de Mazancourt. 2013. How competition affects evolutionary rescue. Philosophical Transactions of the Royal Society B 368:20120085.

Osmond, M. M., S. P. Otto, and C. A. Klausmeier. 2017. When predators help prey adapt and persist in a changing environment. American Naturalist 190:83–98.

Osmond, M. M., S. P. Otto, and G. Martin. 2019. Genetic paths to evolutionary rescue and the distribution of fitness effects along them. Genetics 214:493–510.

Pellerin, F., J. Cote, E. Bestion, and R. Aguilée. 2018. Matching habitat choice promotes species persistence under climate change. Oikos 128:221–234.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Ramsayer, J., O. Kaltz, and M. E. Hochberg. 2013. Evolutionary rescue in populations of *Pseudomonas fluorescens* across an antibiotic gradient. Evolutionary Applications 6:608–616.

Ronce, O. 2007. How does it feel to be like a rolling stone? ten questions about dispersal evolution. Annual Review of Ecology, Evolution, and Systematics 38:231–253.

Schiffers, K., E. C. Bourne, S. Lavergne, W. Thuiller, and J. M. J. Travis. 2013. Limited evolutionary rescue of locally adapted populations facing climate change. Philosophical Transactions of the Royal Society B 368:20120083.

Stelkens, R. B., M. A. Brockhurst, G. D. D. Hurst, and D. Greig. 2014. Hybridization facilitates evolutionary rescue. Evolutionary Applications 7:1209–1217.

Støen, O.-G., A. Zedrosser, S. Sæbø, and J. E. Swenson. 2006. Inversely density-dependent natal dispersal in brown bears *Ursus arctos*. Oecologia 148:356–364.

Storfer, A., and A. Sih. 1998. Gene flow and ineffective antipredator behavior in a stream-breeding salamander. Evolution 52:558–565.

Tazzyman, S. J., and S. Bonhoeffer. 2014. Plasmids and evolutionary rescue by drug resistance. Evolution 68:2066–2078.

Tomasini, M., and S. Peischl. 2018. Establishment of locally adapted mutations under divergent selection. Genetics 209:885–895.

———. 2020. When does gene flow facilitate evolutionary rescue? Evolution 74:1640–1653.

Turgeon, K., and D. L. Kramer. 2012. Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity. Journal of Animal Ecology 81:1161–1170.

Uecker, H. 2017. Evolutionary rescue in randomly mating, selfing, and clonal populations. Evolution 71:845–858.

Uecker, H., and J. Hermisson. 2016. The role of recombination in evolutionary rescue. Genetics 202:721–732.

Uecker, H., S. P. Otto, and J. Hermisson. 2014. Evolutionary rescue in structured populations. American Naturalist 183:E17–E35.

Vander Wal, E., D. Garant, M. Festa-Bianchet, and F. Pelletier. 2012. Evolutionary rescue in vertebrates: evidence, applications and uncertainty. Philosophical Transactions of the Royal Society B 368:20120090.

Vuilleumier, S., J. Goudet, and N. Perrin. 2010. Evolution in heterogeneous populations: from migration models to fixation probabilities. Theoretical Population Biology 78:250–258.

Wilson, B. A., P. S. Pennings, and D. A. Petrov. 2017*a*. Soft selective sweeps in evolutionary rescue. Genetics 205:1573–1586.

Wilson, S., A. E. McKellar, M. W. Reudink, P. P. Marra, and L. M. Ratcliffe. 2017*b*. Density-dependent immigration promotes population stability in a long-distance migratory bird. Population Ecology 59:169–178.

Yamamichi, M., and B. E. Miner. 2015. Indirect evolutionary rescue: prey adapts, predator avoids extinction. Evolutionary Applications 8:787–795.

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