

The effect of habitat choice on evolutionary rescue in subdivided populations

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Abstract

Abstract Evolutionary rescue is the process by which a declining population successfully adapts genetically¹ to avoid extinction. In a structured environment that deteriorates patch by patch, dispersal can substantially alter the chances of evolutionary rescue of a population whose wild type is not viable in deteriorated patches. Here, we investigate the effect of different dispersal schemes and intensities on the probability of successful establishment of a mutant population adapted to the deteriorated environment. We assume that local fitness is determined by a single haploid locus(and that d). ~~Dispersal is genotype-dependent and linked to the adaptive trait, i.e. dispersal does not evolve by itself~~². In this scenario, we find that the probability of evolutionary rescue can undergo up to three phases when increasing the rate of dispersal³: (i) at low dispersal rates, the probability of establishment of a mutant population increases; (ii) at intermediate dispersal rates, the establishment probability decreases; (iii) at large dispersal rates, the population homogenizes, (, which either promotes or suppresses)⁴ the process of evolutionary rescue, depending on the fitness difference between the mutant and the wild type. Our results show that habitat choice⁵, when compared to unbiased dispersal, impedes successful adaptation when the mutant has the same habitat preference as the wild type, but promotes adaptation when the mutant mainly immigrates into patches where it has a growth advantage over the wild type.

¹(remove genetically)(ok to remove)

²([otherwise it sounds like m is changing...] [need to add that it's the bias that is changing, not the probability to emigrate])

³(since you specify “at low disp”, “at intermediate disp” etc., you can remove “when increasing the rate of dispersal” to save words)

⁴(old version: either promoting or suppressing)

⁵(up to now, the reader does not know this is about habitat choice (“schemes” is not precise enough))

Introduction

Facing current anthropogenic environmental changes such as deforestation, soil and water contamination or rising temperatures, the populations of many species are declining and might eventually go extinct [Bellard et al., 2012, Diniz-Filho et al., 2019]. Pests and pathogens experience similarly strong selective pressures as a result of increased consumption of antibiotics and use of pesticides [Kreiner et al., 2018, Ramsayer et al., 2013]. The process of genetic adaptation that saves populations from extinction is termed evolutionary rescue. This process is characterized by an initial population decline (that would result in population extinction) followed by recovery due to the establishment of adapted genotypes, typically 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 by Alexander et al., 2014, Bell, 2017, Carlson et al., 2014]. Evolutionary rescue has been observed directly in laboratory experiments [e.g. Agashe et al., 2011, Bell and Gonzalez, 2009, Lachapelle and Bell, 2012, Lindsey et al., 2013, Stelkens et al., 2014]. In wild populations demographic and genotypic data is rarely monitored at the same time impeding direct observation of evolutionary rescue. Still, it has been suggested as a mechanism that has saved a few wild populations from extinction [e.g. Di Giallonardo and Holmes, 2015, Gignoux-Wolfsohn et al., 2018, Vander Wal et al., 2012].

In mathematical models, 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], reproduction mechanisms [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. Osmond et al., 2017]⁶.

⁶(Does anybody know other references?) (What about Lynch et al. 1991. Adaptive and demographic responses of plankton populations to environmental change. *Limnology and Oceanography* 36:1301–1312., Bürger and Lynch 1995. Evolution and extinction in a changing environment: a quantitative genetic analysis. *Evolution* 49:151–163 and Lande and Shannon 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50:434–437?

In fragmented environments, habitat deterioration is not necessarily synchronized across patches:
there can be a transient spatially heterogeneous environment consisting of old- and new-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 [Tomasini and Peischl, 2019, Uecker et al., 2014]. Experiments that study the effect
of dispersal on evolutionary rescue are rare but indicate that dispersal can increase the likelihood of
successful genetic adaptation [Bell and Gonzalez, 2011].

Evolutionary rescue in a fragmented environment can be interpreted as the intermediate situation
between abrupt change and gradual change: if dispersal is very low, patches are approximately isolate
and thus each patch undergoes an abrupt change independent of the other patches; if the dispersal
rate and the number of patches are very high, the whole environment is gradually changing since
spatial structure and the contribution of a single patch are negligible.

Evolutionary rescue in a situation where one patch after another deteriorates is tightly linked to
the study of adaptation to a heterogeneous environment with source-sink dynamics. These describe a
spatially heterogeneous environment that is constant in time where a population in unfavorable habi-
tats can be maintained by constant immigration of the wild type. Experimental and theoretical studies
have found that increasing dispersal can have a positive or a negative effect on genetic adaptation in a
heterogeneous environment (see e.g. Gomulkiewicz et al. [1999], Holt and Gomulkiewicz [1997] for
positive; Fedorka et al. [2012], García-Ramos and Kirkpatrick [1997], Kirkpatrick and Barton [1997],
Storfer and Sih [1998] for negative; and Gallet et al. [2018], Kawecki [2000], Ronce and Kirkpatrick
[2001] for both effects). (suggestion: focus on discrete traits - thousands of possible papers to cite;
avoid RK2001)

In theoretical studies of local adaptation and evolutionary rescue, dispersal is typically assumed to
be unbiased, i.e. dispersing individuals are distributed uniformly among patches. Only few investiga-
tions in the context of local adaptation in source-sink systems have taken into account non-uniform
dispersal patterns [e.g. Amarasekare, 2004, Holt, 1996, Kawecki, 1995, Kawecki and Holt, 2002]. This
analytical focus on unbiased dispersal is in stark contrast to actually observed dispersal schemes in
nature [Clobert et al., 2009, Edelaar and Bolnick, 2012, Edelaar et al., 2008]. Here, we explore and com-

But please check; it's a long time that I read those...)

pare the effects of several biologically motivated dispersal schemes on adaptation and evolutionary
72 rescue.

One of the best documented modes of non-uniform dispersal is density-dependent dispersal.
74 Density dependence can be positive or negative: either individuals prefer to settle or stay in large
groups (positive density-dependence), or they choose to remain in or move to less populated regions
76 (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.,
78 2019], spiders [De Meester and Bonte, 2010], amphibians [Gautier et al., 2006], birds [Wilson et al.,
2017b], fishes [Turgeon and Kramer, 2012], and mammals [Støen et al., 2006].

80 Another well-established dispersal scheme is habitat choice, whereby individuals tend to immi-
grate into habitats they are best adapted to. This mechanism has for example been reported in lizards
82 [Bestion et al., 2015], birds [Benkman, 2017, Dreiss et al., 2011], fishes [Bolnick et al., 2009], worms
[Mathieu et al., 2010], and ciliates [Jacob et al., 2017, 2018].

84 Although density-dependence or habitat choice can also affect the emigration behavior, i.e. the
likelihood that an individual leaves its current location, or even the vagrant stage when the individual
86 is in the process of dispersal [Bowler and Benton, 2005, Ronce, 2007], we ignore this here. Instead, we
concentrate on non-uniform dispersal effects of the immigration process.

88
In the following, we explicitly account for these biased dispersal schemes in the context of genetic
90 adaptation to a deteriorating and spatially structured environment. We model an environment that
consists of various patches with one of two possible habitats: the ‘old’ habitat, in which both types,
92 wild type and mutant, have a positive growth rate, and the ‘new’ habitat, where in the absence of
immigration the wild-type population will eventually go extinct. In this framework, we study four
94 biologically motivated dispersal patterns and compare them to the unbiased dispersal scheme. We
start by investigating their consequences for the establishment dynamics of an adapted mutant in a
96 time-constant heterogeneous environment. From there, we derive an approximation for adaptation
in a source-sink setting. Using these results, we study the probability of evolutionary rescue, i.e. of
98 adaptation in the scenario where patches, one after another, deteriorate over time until all locations
contain the new habitat. We find that dispersal bias has a direct effect on the local growth rates which

in turn affect the probability of establishment and evolutionary rescue.

Model

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. The transition from the old to the new habitat is assumed to be irreversible. Patches are populated by two types of asexually reproducing, haploid individuals, either wild type or mutant. Generations are measured in discrete time steps and are non-overlapping. Wild-type and mutant individuals both have a positive growth rate in old-habitat patches; the mutant has a lower growth rate there. In new-habitat patches, the wild type population declines locally while the mutant has a positive growth rate – we will therefore call it a ‘rescue mutant’. Both habitat types, old and new, have a (potentially different) carrying capacity. At the end of a life cycle, the local population size is reduced to the carrying capacity if necessary.

We consider a time-varying environment, such that one after another every τ generations, the habitat of a patch deteriorates (from old to new state). Initially ($t < 0$), 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 0, when all patches have undergone the environmental change. This environmental setting corresponds to the one analyzed by Uecker et al. [2014] and more recently in the special case of just two patches by Tomasini and Peischl [2019].

The individuals are assumed to go through the following life-cycle: (i) Dispersal: individuals may move between patches; (ii) Reproduction: individuals reproduce within patches. The number of offspring per parent is modeled by a Poisson number; (iii) Mutation: wild-type individuals mutate to the rescue mutant type with probability θ – back mutations from the mutant to the wild type are neglected; (iv) Regulation: the population size is, if necessary, down-regulated to the carrying capacity K_k where k refers to the habitat type (old or new - the two habitat types can have different carrying capacities). If the population size is below the carrying capacity, the regulation step is ignored.

Old-habitat dynamics

We assume that in old-habitat patches, both types have a positive growth rate such that the population in these patches is typically at carrying capacity K_{old} . We denote the fecundities of the wild-type and the mutant by ω_w and ω_m , respectively. We impose an adaptation trade-off for the rescue mutant, i.e. the mutant is less fit than the wild type in old-habitat patches ($\omega_m < \omega_w$). We assume that mutation from the wild type to the mutant is tied to reproduction. The probability that an offspring of a wild-type individual is a mutant is given by θ . We neglect back-mutation from mutant to wild type. After reproduction, if the population size exceeds the carrying capacity K_{old} we randomly remove individuals from the population until the carrying capacity is reached, i.e. we assume that the wild type and the mutant are competitively equivalent. The mean number of offspring of⁷ one mutant after reproduction and population regulation is then given by

$$K_{\text{old}} \frac{\omega_m}{\omega_w \tilde{N}_w^{\text{old}} + \omega_m} \approx K_{\text{old}} \frac{\omega_m}{\omega_w \tilde{N}_w^{\text{old}}} = 1 + a_{\text{old}}, \quad (1) \quad \{\text{eq:sold}\}$$

where the random variable \tilde{N}_i^k denotes the population sizes of type i (mutant or wild-type) in patches with habitat k (old or new) after the dispersal step. Additionally, we have defined the local growth rate of a single mutant, denoted by $1 + a_{\text{old}}$. The approximation in eq. (1) holds if the number of mutants is much lower than the number of wild types in old-habitat patches – a reasonable assumption since the establishment of the mutant is decided when it is still rare. Compared to the wild type we assume a reduced fecundity of the mutant in the old habitat, i.e. $\omega_m < \omega_w$. Still, the local growth rate can be positive, that is, larger than one ($a_{\text{old}} > 0$). This happens when the wild-type population in a single old-habitat patch after dispersal, \tilde{N}_w^{old} , becomes very small. This strongly depends on the dispersal scheme and rate. The population dynamics of the wild type are analyzed explicitly in Section 1 of the Supplementary Information (SI).

New habitat dynamics

In the new habitat and in the absence of immigration, the wild-type population will go extinct. To account for this, we assume that the number of wild-type offspring per parent in new-habitat patches

⁷(produced by)

is a Poisson distributed value with parameter $(1 - r)$, where r measures how strongly the wild type is affected by the environmental deterioration. For $r = 1$ the wild-type population becomes locally extinct in new-habitat patches after one generation.

The mutant type, in contrast, has a local growth rate larger than one and will (in expectation) grow in numbers. The number of offspring is again Poisson distributed with per-capita rate $(1 + a_{\text{new}})$, the local growth rate of the mutant in new-habitat patches.

In the following analysis we will assume that the mutant dynamics in new-habitat patches are density-independent. This is a valid assumption as long as the carrying capacity in these patches, K_{new} , is not reached. Of course, in the simulations the carrying capacity might sometimes be reached, especially for large frequencies of old-habitat patches. This assumption on density-independence also restricts our choice for the carrying capacity in the new habitat. If the carrying capacity in new-habitat patches is much smaller than in old-habitat patches, the new habitat can reach its carrying capacity merely due to immigration of wild-type individuals (even after reproduction where the wild-type population is reduced).⁸

Dispersal mechanisms

We assume that dispersal is cost-free, i.e. all emigrating individuals will settle in a patch, leaving the global population size before and after dispersal unchanged. Note however, that our methods are in principle also applicable to a scenario where dispersal is associated with a (potentially type-dependent)⁹ cost. We split the dispersal step into emigration and immigration. We focus on habitat choice during immigration. Individuals have a bias to immigrate into patches of a certain habitat type. The bias during immigration for new-habitat patches is set to zero, without loss of generality.¹⁰ The bias for immigration to an old-habitat patch is denoted by π_i , with the index i indicating the wild-type (w) or mutant (m) bias. For $\pi_i < 0$, individuals of type i are more likely to settle in new-habitat patches, for $\pi_i > 0$ the reverse is true. For $\pi_i = 0$, individuals do not have a preference and dispersal is unbiased.

⁸(Rephrase, as this is not clear. What carrying capacity do you choose and whether your approximation holds or not. Maybe: 'Here we examine a carrying capacity in new habitats which is half that in old habitats. If the carrying capacity were much smaller, our analytical approximation would break down.)

⁹(remove bracket)

¹⁰(I did not understand why this is needed)

We consider equal and constant emigration rates for both types and habitats throughout the manuscript. Note again that the method would allow for type- and habitat-dependent emigration rates. We denote the probability that an individual leaves its natal patch by m . Then, the probability that an individual of type i emigrates (from any habitat type) and immigrates into the new habitat is given by

$$m_i^{\text{new}} = m \frac{1 - f_{\text{old}}}{1 - f_{\text{old}} + e^{\pi_i} f_{\text{old}}} = 1 - m_i^{\text{old}}, \quad (2) \quad \text{\texttt{eq:dispersa}}$$

where f_{old} is the frequency of old-habitat patches. We transformed the bias π_i which can take any real value to a positive number, e^{π_i} . This ensures that the fraction in eq. (2) is positive and between zero and one. For the ease of notation we will write $\hat{\pi}_i = e^{\pi_i}$.

From a biological perspective, a number of dispersal schemes are of particular interest. Precisely, we distinguish between the following five scenarios (see also Fig. 1 for an overview):

- **Old-Old:** Individuals prefer to immigrate into the habitat where they have the largest number of offspring before regulation. Since the average number of offspring per parent is higher in the old habitat for both types ($\omega_w > 1 - r$ and $\omega_m > 1 + a_{\text{new}}$), this translates to both π_w and π_m being larger than 0, i.e. a bias towards old-habitat patches. In practice, individuals are thought to use biotic or abiotic cues to preferentially immigrate into habitats where their fecundity is highest when compared to other habitats. This type of dispersal, i.e. matching habitat choice, has for example been observed with common lizards *Zootoca vivipara* [Bestion et al., 2015], three-spine sticklebacks *Gasterosteus aculeatus* [Bolnick et al., 2009], and barn owls *Tyto alba* [Dreiss et al., 2011].

The same range of parameters ($\pi_w, \pi_m > 0$) is obtained when implementing positive density-dependent dispersal on immigration. Individuals are more likely to immigrate into patches with higher population densities, so both, the wild type and the mutant, will prefer the old habitat.¹¹ Highly populated locations can be an indication for a safe shelter, relevant for prey species, and potentially increase the mating success of individuals. This type of positive density-dependent dispersal on immigration (also called conspecific attraction) is for example found in

¹¹(I would turn this around, otherwise this sounds like a fact. ‘Indeed, if both the wt and the mutant prefer the old habitat, individuals are more likely to immigrate into patches with...)

several amphibians, e.g. the salamander species *Mertensiella luschani* [Gautier et al., 2006] and *Ambystoma maculatum* [Greene et al., 2016] or the frogs *Oophaga pumilio* [Folt et al., 2018].

- **Old-New:** Under this dispersal scheme, individuals tend to immigrate into habitats where they are fitter than the other type. This translates into the wild type preferring old patches, i.e. $\pi_w > 0$, while mutant has a bias towards the new habitat, i.e. $\pi_m < 0$. Empirical evidence of this mechanism is scarce. It resembles the recently observed dispersal pattern of the ciliates *Tetrahymena thermophila* with a specialist and generalist type [Jacob et al., 2018]. The specialist disperses to its preferred habitat while the generalist prefers to immigrate to a suboptimal habitat where it outcompetes the specialist.

- **New-New:** This dispersal scheme can be¹² motivated by negative density-dependent dispersal on immigration, whereby individuals are more likely to move to less populated patches. In these locations, resources might be more abundant, intra-specific competition alleviated and the chance of infection transmission decreased, which may compensate for the potentially reduced habitat quality. The corresponding parameter choice in our model is $\pi_w, \pi_m < 0$, i.e. both types have a higher likelihood to immigrate to new-habitat patches. We emphasize that population density in the patches changes over time but the biases are constant. We use the comparison with density-dependent dispersal only to motivate our chosen biases during the relevant phase of rescue, i.e. when the population density in new-habitat patches is low. The mutant being initially rare, it is unlikely that the carrying capacity is reached in new-habitat patches – as assumed throughout the analysis.¹³ Various empirical examples of negative density-dependent dispersal exist. 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., 2017b].

- **New-Old:** For completeness, we also consider the scenario in which both types disperse preferentially into the habitat they are relatively less fit in, i.e. we have $\pi_w < 0$ and $\pi_m > 0$. This dispersal scheme is vaguely related to the concept of an ‘ecological trap’: Individuals tend to

¹²(is)

¹³(Unclear to me. Suggestion: ‘Because the carrying capacity is not typically reached in new patches in the initial phase of rescue, this bias amounts to negative density-dependent dispersal in that phase.)

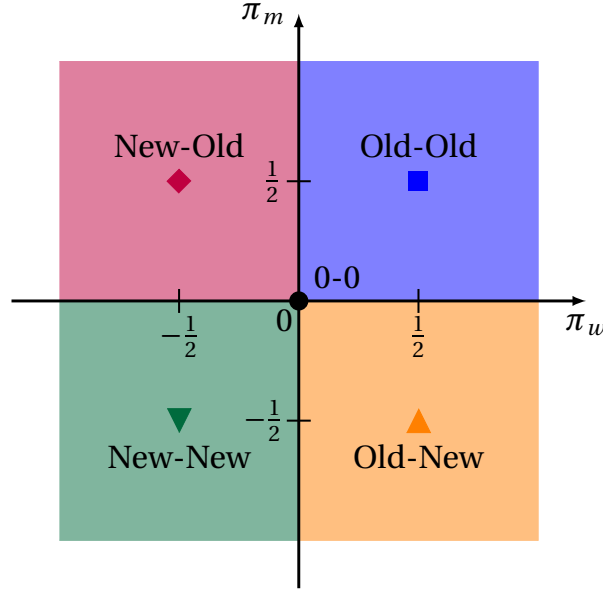


Figure 1: **Parameter sets for the different dispersal schemes.** The colors and markers are the same across all figures. The x and y axes show the dispersal bias of the wild type and mutant, respectively, to immigrate into old-habitat patches (π_w and π_m). The markers are located at the parameter values used for the simulations: $\pi_m = \pi_w = 0$ for unbiased dispersal (0-0; \bullet), $\pi_m = \pi_w = 0.5$ for a type-independent bias towards old-habitat patches (Old-Old; \blacksquare), $\pi_m = -0.5, \pi_w = 0.5$ for a wild-type preference towards the old habitat, and a mutant-bias to the new habitat (Old-New; \blacktriangle), $\pi_m = \pi_w = -0.5$ for a type-independent bias towards the new habitat (New-New; \blacktriangledown), and $\pi_m = 0.5, \pi_w = -0.5$ for the mutant-bias towards the old habitat and a preference of the wild type for the new habitat (New-Old; \blacklozenge). All the results derived below depend continuously on these parameters, so that varying any of the parameters will not result in a sudden change or discontinuity of the corresponding curves. Do we need this last sentence?No.

immigrate into patches that cannot sustain a population, in its most extreme form resulting in the extinction of the species [Battin, 2004]. Note however, that this does not exactly apply to our framework since here the mutant is able to maintain a population in old-habitat patches.¹⁴

- **Unbiased dispersal (0-0):** Individuals do not have a bias towards any of the two habitats, $\pi_w = \pi_m = 0$. Most theoretical results examining the interplay of dispersal and establishment have used this dispersal scheme. Therefore, we use it as a benchmark to which we compare the above defined dispersal patterns.

¹⁴(Consider removing the last part about the ecological trap.)

Parameter	Interpretation	Range	Default value
K_k	Carrying capacity in a patch of type k	–	$K_{\text{old}} = 1000$, $K_{\text{new}} = 500$
ω_j	Expected per-capita number of type j offspring in the old habitat before regulation	$0 \leq \omega_m < \omega_w$	$\omega_w = 1.5$, $\omega_m = 1.45$ (weak sel.), $\omega_m = 1.35$ (strong sel.)
$1 + a_{\text{old}}$	Growth rate of the mutant in the old habitat	$-1 \leq a_{\text{old}}$	–
$1 - r$	Mean number of wild-type offspring in the new habitat	$0 < r \leq 1$	0.75 ($r = 0.25$)
$1 + a_{\text{new}}$	Growth rate of the mutant in the new habitat	$0 < a_{\text{new}}$	1.02 ($a_{\text{new}} = 0.02$)
m	Emigration probability	$0 < m \leq 1$	0.06
π_i	Type i bias towards the old habitat	$\pi_i \in \mathbb{R}$	see Fig.1
$\hat{\pi}_i$	Transformed dispersal bias of type i	$0 < \hat{\pi}_i$	see Fig.1
M	Number of patches	$2 \leq M$	10
f_{old}	Frequency of old-habitat patches	$0 \leq f_{\text{old}} \leq 1$	0.5
θ	Mutation probability	$0 < \theta$	$\frac{1}{25MK_{\text{new}}}$
τ	Time interval between two consecutive deterioration events	$0 < \tau$	100
\hat{N}_i^k	Number of type i individuals in type k habitat patches at stationarity		
\tilde{N}_i^k	Number of type i individuals in type k habitat patches after dispersal		

Table 1: **Model parameters.**

All the model parameters are summarized in Table 1 along with the default parameter values and

234 ranges. If not stated otherwise, the default parameter values are used for the stochastic simulations.

Simulations

236 The algorithm implements the life cycle described above. First, a random number of dispersing individuals from each patch is drawn from a binomial distribution with success probability m and sample size equal to the current patch population size. The dispersing individuals are pooled and distributed according to their type and the dispersal pattern. More precisely, we draw a binomial number of individuals of each type to immigrate into an old-habitat patch with probability $\frac{m_i^{\text{old}}}{m}$ (eq. (2)) and then distribute these individuals uniformly at random over the old-habitat patches. The same is done with the remaining dispersing individuals who are distributed uniformly into the new-habitat patches. In each patch, reproduction is simulated by drawing a Poisson distributed number for each

240

242

type. The mean of this Poisson number is given by the number of individuals of type i in that patch times the mean number of offspring of a single individual of type i which depends on the patch type (old or new). Mutation of the wild-type offspring happens with probability θ , implemented using a binomial distribution. Lastly, if necessary, patches are down-regulated back to carrying capacity by sampling individuals uniformly at random without replacement from the population in a patch until the carrying capacity is reached (hypergeometric sampling).

In Figs. 2-4, we simulate a heterogeneous environment that is constant in time, i.e. no patches deteriorate. Initial population sizes are K_{old} wild-type individuals in old-habitat patches, and the stationary wild-type population size \hat{N}_w^{new} in new-habitat patches (see Section S1 in the SI for details). Simulations for Fig. 2 are started with initially one mutant either in a old- or a new-habitat patch and the corresponding wild-type population size is reduced by one, and the mutation probability is set to zero. In Figs. 3 and 4, mutants solely arise due to mutations over a finite time period. We call the mutant established if the total number of mutants in all new-habitat patches exceeds $0.6 \times K_{\text{new}} \times M(1 - f_{\text{old}})^{16}$ (or in old-habitat patches $0.6 \times K_{\text{old}} \times M f_{\text{old}}$ which is relevant for dispersal schemes where the mutant has a bias towards old-habitat patches, Old-Old and New-Old). In the rescue scenario, where one patch after another deteriorates (Figs. 5 and 6), we initialize all patches with K_{old} wild-type individuals. Simulations are run until either the population has gone extinct or the (global) mutant population size exceeds $0.6 \times K_{\text{new}} \times M$ after the last deterioration event has happened.

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*. The codes and data to generate the figures are deposited on Gitlab¹⁷.

Results

We investigate the effect of the different dispersal schemes on the probability of successful adaptation and evolutionary rescue. We first compute the *establishment probability* of a single mutant individual arising either in an old- or in a new-habitat patch. We then link this probability to the dynamics of

¹⁵(add 'analytical' or 'theoretical')

¹⁶(These thresholds are mysterious at this stage.)

¹⁷https://gitlab.com/pczuppon/evolutionary_rescue_and_dispersal

a source-sink system, i.e. a fixed environment with a certain number of old habitats (sources) and new-habitat patches (sinks). We derive an expression for the probability of a mutation to emerge and establish in a given time interval. We call this second quantity the *probability of adaptation*. Lastly, we study the time-varying scenario where patches, one after another, deteriorate. We consider a third quantity, the *probability of evolutionary rescue*, which corresponds to the probability that a mutant appears by mutation and establishes in the new environment after all patches have deteriorated. The theoretical results are complemented by stochastic simulations that support our predictions and help visualize the differences between the different dispersal schemes.

Establishment probability in a heterogeneous environment

We derive the probability of establishment of a mutant population starting with a single individual initially located either in an old- or a new-habitat patch. In this analysis, we ignore further mutations and are only concerned with the fate of this single mutant lineage. The dynamics of the mutant population can be described by a two-type branching process, i.e. all mutants, the descendants of the initial mutant, reproduce, disperse and die independently of each other. This is a reasonable assumption as long as the overall number of mutants is a lot smaller than the population size of the wild type. The two “types” of the two-type branching process correspond to the two habitat types. The process tracks the total number of mutants in old- and new-habitat patches at the end of the life cycle. The number of offspring of a single mutant can be approximated by Poisson distributed numbers (see eq. (1)). The mean number of offspring of a single mutant, either in an old- or a new-habitat patch, is then given by the following mean reproduction matrix:

$$\begin{array}{cc} & \begin{array}{cc} \text{old patch} & \text{new patch} \end{array} \\ \begin{array}{c} \text{old patch} \\ \text{new patch} \end{array} & \begin{pmatrix} (1 - m_m^{\text{new}})(1 + a_{\text{old}}) & m_m^{\text{new}}(1 + a_{\text{new}}) \\ m_m^{\text{old}}(1 + a_{\text{old}}) & (1 - m_m^{\text{old}})(1 + a_{\text{new}}) \end{pmatrix}, \end{array} \quad (3) \quad \text{\texttt{eq:mean_rep}}$$

where the rows denote the parent locations, and the columns the patch type of the offspring. For example, the top-left entry reads as the probability for the parent to stay in an old-habitat patch $(1 - m_m^{\text{new}})$ times the average number of offspring in these patches, given by the mean of the corresponding Poisson distribution with rate $(1 + a_{\text{old}})$, cf. eq. (1) (see Section S1 in SI for the derivation of a_{old} at the wild-type equilibrium). The other entries are obtained analogously.

294 The survival probability of this multi-type branching process, φ_k with k indicating the initial
 habitat type of the mutant, is then given by the unique positive solution of the following system of
 296 equations [see Haccou et al., 2005, Chapters 5.3 and 5.6]

$$\begin{aligned}
 1 - \varphi_{\text{old}} &= \sum_{j=0}^{\infty} \left(\mathbf{P}(j \text{ offspring in old habitat}) (1 - \varphi_{\text{old}})^j \right. \\
 &\quad \left. + \mathbf{P}(j \text{ offspring in new habitat}) (1 - \varphi_{\text{new}})^j \right) \\
 &= \exp \left[- \left(1 - m_m^{\text{old} \rightarrow \text{new}} \right) (1 + a_{\text{old}}) \varphi_{\text{old}} - m_m^{\text{old} \rightarrow \text{new}} (1 + a_{\text{new}}) \varphi_{\text{new}} \right], \\
 1 - \varphi_{\text{new}} &= \exp \left[- m_m^{\text{new} \rightarrow \text{old}} (1 + a_{\text{old}}) \varphi_{\text{old}} - \left(1 - m_m^{\text{new} \rightarrow \text{old}} \right) (1 + a_{\text{new}}) \varphi_{\text{new}} \right].
 \end{aligned} \tag{4} \quad \text{\texttt{eq:ext_prob}}$$

Intuitively the left hand side, the extinction probability, equals the sum over all possible scenarios of
 298 the trajectories towards extinction, e.g. the initial individual having j offspring in a patch of type k ,
 old or new, and all of these j offspring becoming extinct $((1 - \varphi_k)^j)$. Unfortunately, a general analytical
 300 solution to these equations is not accessible, but they can be solved numerically. For weak selection
 and (potentially) weak dispersal – i.e. $a_{\text{old}}, a_{\text{new}}, m \ll 1$ needs to hold for at least two of the three
 302 parameters – an approximation is available: see for example Haccou et al. [2005, Theorem 5.6] for the
 general theory and Tomasini and Peischl [2018] for an application in a similar setting. The detailed
 304 derivation is presented in the SI, Section S2. We find

$$\begin{aligned}
 \varphi_{\text{old}} &\approx a_{\text{old}} + a_{\text{old}} \frac{(1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}})}{\sqrt{C}} (a_{\text{old}} - a_{\text{new}}) \\
 &\quad + \frac{m}{\sqrt{C}} (a_{\text{new}} (1 - f_{\text{old}}) + a_{\text{old}} \hat{\pi}_m f_{\text{old}} - (a_{\text{old}} - a_{\text{new}}) (1 - f_{\text{old}})), \\
 \varphi_{\text{new}} &\approx \underbrace{a_{\text{new}}}_{(1) \text{ local growth parameter}} + \underbrace{a_{\text{new}} \frac{(1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}})}{\sqrt{C}} (a_{\text{new}} - a_{\text{old}})}_{(2) \text{ effect of the heterogeneous environment}} \\
 &\quad + \underbrace{\frac{m}{\sqrt{C}} (a_{\text{new}} (1 - f_{\text{old}}) + a_{\text{old}} \hat{\pi}_m f_{\text{old}} - (a_{\text{new}} - a_{\text{old}}) \hat{\pi}_m f_{\text{old}})}_{(3) \text{ effect of dispersal: new patches + old patches - loss to the other patch type}},
 \end{aligned} \tag{5} \quad \text{\texttt{eq:estab_ap}}$$

where C is a scaling constant that depends on $m, f_{\text{old}}, \hat{\pi}_m, a_{\text{old}}$ and a_{new} through

$$C = (1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}}) \left((1 - f_{\text{old}}) (a_{\text{new}} - a_{\text{old}} + m)^2 + \hat{\pi}_m f_{\text{old}} (a_{\text{new}} - a_{\text{old}} - m)^2 \right). \tag{6} \quad \text{\texttt{eq:normaliz}}$$

306 The first term in the approximation of the establishment probabilities (φ_{old} and φ_{new}) in eq. (5)
 describes the local growth depending on the habitat type under study. The second term captures the
 308 growth rate differences between the two habitat types. The factor $(1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}})$ accounts for the

biased dispersal patterns (when $\pi_m \neq 0$ so that $\hat{\pi}_m \neq 1$). The third term in the equations corresponds to the direct effect of dispersal on the establishment probability. The first two summands in the bracket are the same for both establishment probabilities. They represent the general effect of dispersal due to the dynamics from new-habitat patches (first summand) and old-habitat patches (second summand). The dispersal bias induced by π_m changes the relative impact of old- vs. new-habitat patches. Finally, the last summand in the bracket measures the growth rate loss (or gain) due to dispersal to the other patch type. It therefore differs between the two approximations.

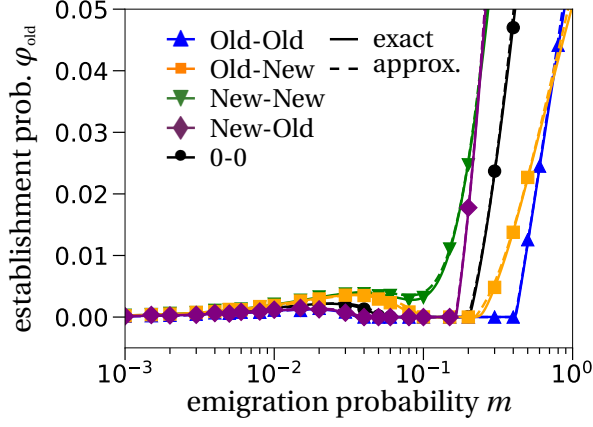
Note that in these equations, the competition of the mutant with the wild type in old-habitat patches appears in the local growth rate a_{old} , defined in eq. (1). This quantity is not constant, but instead depends on the wild type population size in old-habitat patches, which itself depends on the wild type's dispersal and growth rate in both habitats (see SI, Section S1).

If the emigration probability is zero ($m = 0$), the subpopulations in each habitat evolve in isolation from each other and we recover Haldane's classical result for the establishment probability of a slightly advantageous mutant in new habitats: $\varphi_{\text{new}} = 2a_{\text{new}}$ [Haldane, 1927]. In old-habitat patches, where the mutation is deleterious, we see that term (1) and (2) cancel each other so that the establishment probability is simply $\varphi_{\text{old}} = 0$. Furthermore, (when the emigration probability is strictly positive ($m > 0$)) in the case of unbiased dispersal ($\pi_w = \pi_m = 0$) and for equal number of old- and new-habitat patches ($f_{\text{old}} = 1/2$), we obtain the approximation found in Tomasini and Peischl [2018] (compare system (5) to their eqs. (4) and (5)). Note that the approximation is independent of the actual number of patches, but only depends on the environmental configuration determined by the frequency of old-habitat patches f_{old} .

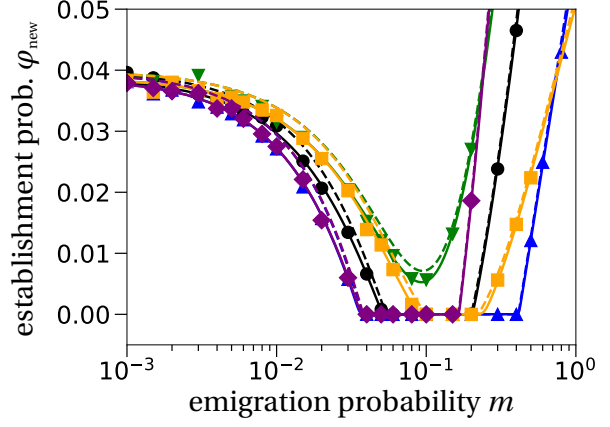
Comparison to simulations and qualitative behavior

We compare in Fig. 2 our predictions from eqs. (4) and (5) to simulation results for different values of the emigration rate m . We find good agreement with the numerical solution of eq. (4) (solid lines). The approximation given in eq. (5) (dashed lines) deviates slightly from the simulation results in regions where m , a_{new} and a_{old} are not small, i.e. when the assumptions made in the analytical derivation do not hold anymore.

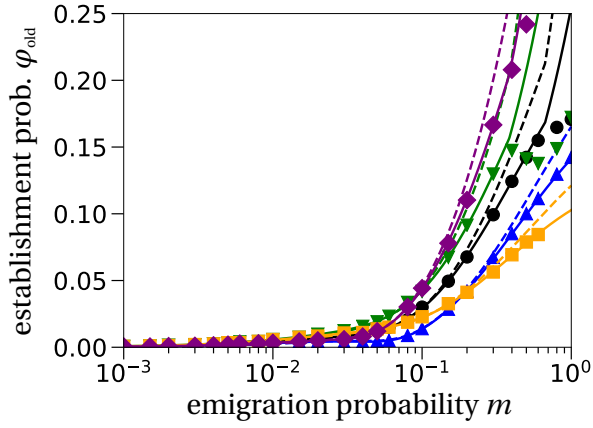
The qualitative dependence of the establishment probabilities φ_{old} and φ_{new} on the dispersal



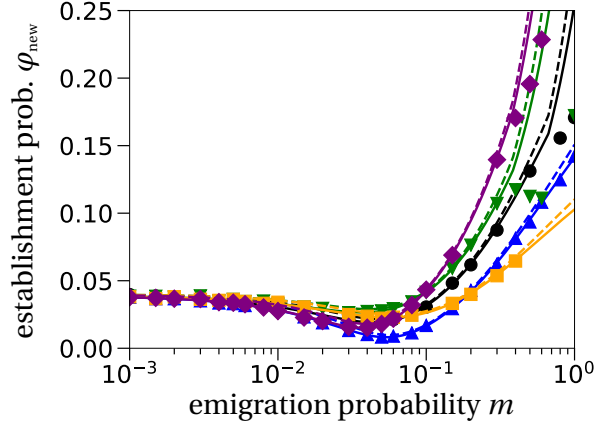
(a) ϕ_{old} with $\omega_m = 1.35$ (large fecundity difference)



(b) ϕ_{new} with $\omega_m = 1.35$



(c) ϕ_{old} with $\omega_m = 1.45$ (small fecundity difference)



(d) ϕ_{new} with $\omega_m = 1.45$

Figure 2: Establishment probability when varying the emigration rate. We plot the theoretical results for ϕ_{old} in (a) and (c), and for ϕ_{new} in (b) and (d) for $\omega_m = 1.35$ in (a), (b) and $\omega_m = 1.45$ in (c), (d). Comparison with the results from stochastic simulations (symbols) show very good agreement with our approximation found in eq. (5) (dashed lines). The solid lines are the numerical solution of eq. (4). The lines in (a) show a clear separation of the three regions of the establishment probability as discussed in the main text: (i) an initial increase due to higher probabilities of dispersal from old- to new-habitat patches; (ii) a local maximum due to increasing number of mutants emigrating from new-habitat patches; (iii) an increase due to relaxed competition in old-habitat patches, a result of wild-type emigration.

probability m is similar for all dispersal schemes. The shape of the curve however strongly depends on the fecundity ω_m of mutants in the old habitat. Before discussing the differences between the dispersal schemes, we first provide a qualitative understanding of this general behavior.

For the probability of establishment of a single mutant in an old-habitat patch (φ_{old}), we observe up to three different regions, cf. 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) an initial increase of the establishment probability at low dispersal rates m ; (ii) a local maximum with a subsequent decrease of the establishment probability; (iii) an increase of the establishment probability for high dispersal rates.

A detailed assessment and explanation of the regions is provided in the SI, Section S2.1. Briefly, in region (i), the prevalent effect is the dispersal of mutants from old- to new-habitat patches where they are fitter than the wild type, thus increasing the establishment probability. This effect is mediated through the third term of the establishment probability in eq. (5). Region (ii), beginning with the local maximum, is a result of two counteracting processes: If we increase the emigration probability m , a mutant is more likely to emigrate out of old-habitat patches and thus has a higher chance to establish. However, higher dispersal rates also have a negative effect on mutant establishment through increasing the probability that a mutant migrates from a new- to an old-habitat patch. More precisely, the number of offspring in the new habitat on average is given by the product of the terms $(1 - m_m^{\text{old}})$ and $(1 + a_{\text{new}})$. 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. Finally, in region (iii), dispersal is so large that the population is close to being well-mixed. Most importantly, many wild-type individuals leave old-habitat patches which results in less competitive pressure in old-habitat patches. In this case the local growth rate of the mutant in these patches, a_{old} (first term in eq. (5)), becomes positive. This effect called ‘relaxed competition’ [Uecker et al., 2014]. The onset of this effect, in terms of the emigration probability m , is strongly dependent on the fecundity values of the mutant in the old habitat. The larger it is, the ‘earlier’ (i.e. for smaller emigration rates m) relaxed competition becomes relevant.

In line with this reasoning we find that the width of region (ii) strongly depends on the fecundity of the mutant in the old habitat, ω_m . If ω_m is high, the local growth rate of the mutant a_{old} starts to increase at a lower dispersal rate and region (ii) disappears, as visible in Fig. 2(c). In contrast, for low mutant fecundity values ω_m , region (iii) might vanish (see Fig. S2 in SI). There, the mutant is strongly disadvantageous in old-habitat patches when compared to the wild type, and the wild-type

population will always outcompete the mutant due to the much higher offspring numbers.

We analyze the qualitative behavior of the establishment probability of a mutant emerging in the new habitat, φ_{new} in a similar way (Figs. 2(b,d)). The establishment probability φ_{new} decreases at low dispersal rates: Since we let the mutant start in a new-habitat patch, where it fares better than the wild type, there is no initial benefit due to dispersal (the third term in eq. (5) is negative for φ_{new}). The interpretation of region (ii), describing the trajectory for intermediate emigration rates m , is the same as for φ_{old} above. For large emigration rates m , region (iii), the resulting establishment probability is a combination of the local growth rate and the dispersal effect, the first and third terms in eq. (5). This is because the mutant can migrate to old-habitat patches, where it will enjoy relaxed competition.

Lastly, for large emigration probabilities m in Fig. 2(c,d) we observe a decrease in the establishment probability of the simulation results of the New-New dispersal scheme (and to a lesser extent in the unbiased scheme). This is explained by ‘gene swamping’ whereby a too large number of immigrants of a less-well adapted type (wild type) inhibits the establishment of a locally better adapted type (mutant) [Lenormand, 2002, Nagylaki, 1978]. Here, gene swamping occurs because of the different carrying capacities of the two patch types, $K_{\text{new}} < K_{\text{old}}$. A proper analysis of the gene swamping regime, where density-dependence in new-habitat patches is important, is beyond the scope of this manuscript, but see for instance Tomasini and Peischl [2018] and Section S5 in the SI where such a situation is studied.¹⁸

Comparison of dispersal schemes

We now compare the establishment probabilities for the different dispersal schemes. We consistently observe that a bias towards the new habitat (New-New in Fig. 2) enhances establishment when compared to the unbiased dispersal scheme (0-0). This can be attributed to two reasons: (1) the mutant is more likely to disperse to the new habitat where it outcompetes the wild type (stronger weighting of new-habitat patches in the third term in eq. (5)); and (2) since the wild type prefers to settle in new-habitat patches ($\pi_w < 0$), individuals in old-habitat patches experience relaxed competition for lower dispersal rates m , thus increasing the local growth rate a_{old} , i.e. region (iii) is shifted to the

¹⁸(If I do not mention gene swamping here, I think people will wonder what this effect is and misinterpret it as a late relaxed competition effect.)

left. An analogous (but reversed) argument explains why a bias towards the old habitat (Old-Old) is

always lower than the unbiased dispersal scheme.

The effect of the asymmetric dispersal scheme Old-New, where each type has a bias to move to the habitat where it is relatively fitter than the other type, is more involved. We disentangle the effects separately for each region. In region (i) at low emigration probabilities, the curve is almost identical to that of the New-New pattern. The mutant preference (new habitats) of these two dispersal modes is the same. The movement of the rare mutant is the prevailing process in this parameter regime, which explains the alignment of the corresponding curves. For intermediate dispersal rates, region (ii), the effect of the heterogeneous environment (second term in eq. (5)) becomes stronger, i.e. the local growth rate a_{old} increases because of relaxed competition in old-habitat patches. For the Old-New scheme, the wild type is more likely to immigrate into old-habitat patches and to increase the population size in these locations when compared to the New-New dispersal scheme. This reduces the effect of relaxed competition. Therefore, the Old-New line drops below the New-New curve and even starts to decrease (Fig. 2(a)). For high emigration probabilities m , region (iii), the competitive pressure in old-habitat patches relaxes. Again, this region is dominated by the movement of wild-type individuals. In the unbiased dispersal scheme, the wild type has a lower likelihood to be in old-habitat patches than with the Old-New scheme, explaining the order of these curves. For very large dispersal rates, also (moreover?) the Old-Old scheme can lead to higher values of φ_{old} than the type-dependent preference Old-New, cf. Fig. 2(c). For these parameters, the mutant has a larger growth rate in old- than in the new-habitat patches ($a_{old} > a_{new}$). It is therefore beneficial for the mutant to be in old-habitat patches.

Finally, for the asymmetric dispersal scheme New-Old, where the types have a bias to the habitat they are less well adapted to, we see that for low dispersal rates m the results match those obtained under the Old-Old scheme. The mutant preferences being the same, this again shows that this region is dominated by the mutant's dispersal behavior. For intermediate to large dispersal rates though, the New-Old scheme results in the largest establishment probabilities. This is explained by the effect of strongly relaxed competition (wild-type individuals preferentially move into the new habitat) and the bias of mutants to disperse into old-habitat patches where their number of offspring individuals is now very large.

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} . Later, in the analysis of the probability for evolutionary rescue, this time will be replaced by the time between two consecutive patch deterioration events, τ .¹⁹

The probability of adaptation in this setting, P_{adapt} , is given by

$$P_{\text{adapt}} = 1 - \exp \left(-\theta t_{\text{fin}} M \left(\underbrace{\varphi_{\text{old}} f_{\text{old}} K_{\text{old}}}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}} (1 - f_{\text{old}}) \hat{N}_w^{\text{new}}}_{\text{new habitat contribution}} \right) \right). \quad (7) \quad \text{\texttt{eq:source_s}}$$

In words, the right-hand side is one minus the probability of no mutant establishing within the $[0, t_{\text{fin}}]$ time interval. More precisely, the exponential is the probability of zero successes of a Poisson distribution. The rate of this Poisson distribution is given by the expected number of successfully emerging mutant lineages until time t_{fin} . Assuming a Poisson distribution for the number of successful mutant lineages is an approximation of a Binomial distribution with large sample size (the wild-type populations $t_{\text{fin}} M f_{\text{old}} K_{\text{old}}$ in the old and approximately $t_{\text{fin}} M (1 - f_{\text{old}}) \hat{N}_w^{\text{new}}$ in the new habitats, see SI eq. (S5)) with small success probability (the establishment probabilities φ_k). The sample size denotes the number of mutations in the system until time t_{fin} and each of these mutants has, independently of each other (another approximation), has a survival probability of φ_k , dependent on the habitat it is born in. Note also, that for t_{fin} tending to infinity, there will almost surely be a successful mutant so that $P_{\text{adapt}} = 1$.

In Fig. 3 we compare our predictions to simulation results. The shape of the probability of adaptation as function of the emigration probability m depends on the fecundity of the mutant in

¹⁹(I think we can get rid of this last sentence. Thoughts?)(Yes.)

old-habitat patches, ω_m (Figs. 3(a,c)). This is similar to the behavior of the establishment probability φ_{old} in Fig. 2. Likewise, the qualitative effects of the different dispersal schemes are comparable to the ones observed for the establishment probability. This holds because the probability of adaptation, P_{adapt} , is given by $1 - \exp(-C_1\varphi_{\text{old}} - C_2\varphi_{\text{new}})$ where two constants C_1 and C_2 depend on the dispersal scheme (see eq. (7)). The small differences in the ranking of the dispersal schemes between subfigures Figs. 2(c) and Figs. 3(c) can be explained by the mutational input, i.e. larger stationary populations sizes of the wild type in new habitats, \hat{N}_w^{new} result in more mutations during the observed time frame. This population size is altered by the different dispersal schemes, most importantly it is largest for the wild type having a bias towards old habitats, i.e. the Old-Old and the Old-New dispersal schemes.

In subfigures (b) and (d), we plot the probability of adaptation as a function of the frequency of old-habitat patches f_{old} . We observe a maximum which is the result of two effects: (1) the likelihood for a mutation to appear 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. A general bias towards the new habitat (New-New), when compared to unbiased dispersal (0-0), always shifts the maximum to higher frequencies of old habitats while also increasing its quantitative value. Since for the New-New dispersal scheme, both types prefer settling in new-habitat patches ($\pi_w, \pi_m < 0$), the local population before reproduction in these patches is increased. Thus, the overall population size is higher compared to the other dispersal schemes and therefore a higher number of mutants is generated under this scheme. Additionally, the probability of establishment is also increased for the New-New dispersal scheme, further increasing the probability of adaptation (see also the discussion around Fig. 2). Again, a reversed argument explains why the general preference for old-habitat patches (Old-Old) always yields lower probabilities of adaptation than unbiased dispersal.

Habitat of origin of the adaptive mutation

We now identify the habitat type where the successful mutation arises. The established mutant population often arises from a single mutant that is born in an old- or in a new-habitat patch. However, the rescued population can sometimes be traced back to two (or more) mutant individuals, at least one

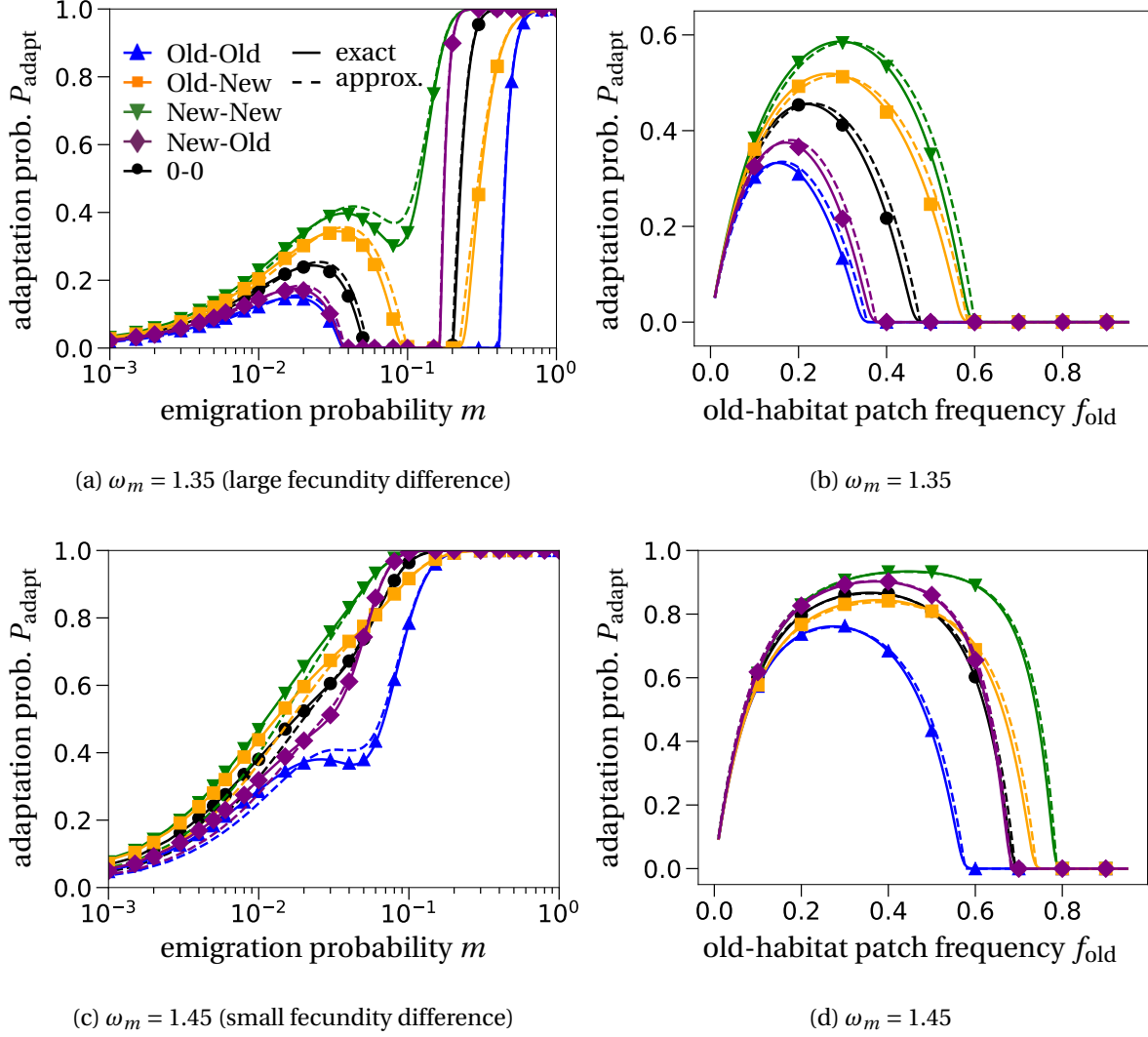


Figure 3: Probability of adaptation in a heterogeneous environment. In (a) and (c), we vary the emigration rate m and observe a similar qualitative behavior as for the establishment probability φ_k in Fig. 2. In (b) and (d), we vary the frequency of old-habitat patches. The maximum is the result of two 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 less old-patch habitats there are in the environment (the lower f_{old}), the higher the probability of successful establishment of a mutant population. The curves labeled ‘approx.’ are given by eq. (7), the exact solution refers to solving the establishment probabilities φ_k from eq. (4) numerically and plugging these solutions into eq. (7). In all panels, the mutation probability is $u = 1/(MK)$ and the final time for a mutant to appear is $t_{\text{fin}} = 100$.

from either patch type. This is a special type of a soft selective sweep [see Hermisson and Pennings, 2017, for a review]. The approximate probability to observe a soft sweep from mutants from both

habitat types is

$$\begin{aligned} & \mathbf{P}(\text{successful adaptation from old habitat}) \mathbf{P}(\text{successful adaptation from new habitat}) \\ & \approx (1 - \exp(-\theta t_{\text{fin}} M \varphi_{\text{old}} f_{\text{old}} K)) (1 - \exp(-\theta t_{\text{fin}} M \varphi_{\text{new}} (1 - f_{\text{old}}) \hat{N}_w^{\text{new}})) . \end{aligned} \quad (8) \quad \{\text{eq:origin}\}$$

The approximation uses our basic assumption that different mutant individuals and consequently also the offspring of different mutants do not affect each others dynamics (branching process). In the simulations, we label a run as a soft sweep from mutants arising in different locations if these lineages are still alive after 1000 generations. This ensures that we do not count any false-positives where a mutant in one of the habitats has just arisen right before the mutant population exceeds the establishment threshold.

In Fig. 4 we compare simulation results with our predictions for the origin of a successful mutant when varying the old habitat frequency f_{old} . We see that for both mutant fecundity values most successful mutations arise in old-habitat patches. The difference in the input from the two different patches is the factor $\varphi_k \hat{N}_w^k f_k$. In Fig. SX we plot the establishment probability φ_k and the stationary population sizes \hat{N}_w^k when varying the frequency of old-habitat patches f_{old} . We see that the establishment probability for mutants arising in new-habitat patches, φ_{new} , is always larger than the corresponding probability for mutants from old-habitat patches, φ_{old} . Conversely, the stationary population size of the wild type in the old habitat measured over the whole environment is always larger than that of the wild type in new habitats. Combining these two observations we find that for this choice of parameters the mutational input, i.e. the absolute number of rescue mutants, has a larger influence on the origin of the rescue mutant than the corresponding establishment probability.

Evolutionary rescue

Finally, we consider a time-inhomogeneous environment where patches deteriorate one after another at regular time intervals τ , until all patches have switched to the new habitat. If the wild-type population fails to generate a successful mutant, the population will inevitably go extinct. The probability of evolutionary rescue is therefore tightly linked to the probabilities of adaptation and establishment that we have computed in eqs. (5) and (7). Typically, in formulas expressing the probability of evolutionary rescue, one splits the contributions into mutations arising *de novo* and evolutionary rescue due to standing genetic variation, i.e. mutations that are present in the population before the environmental

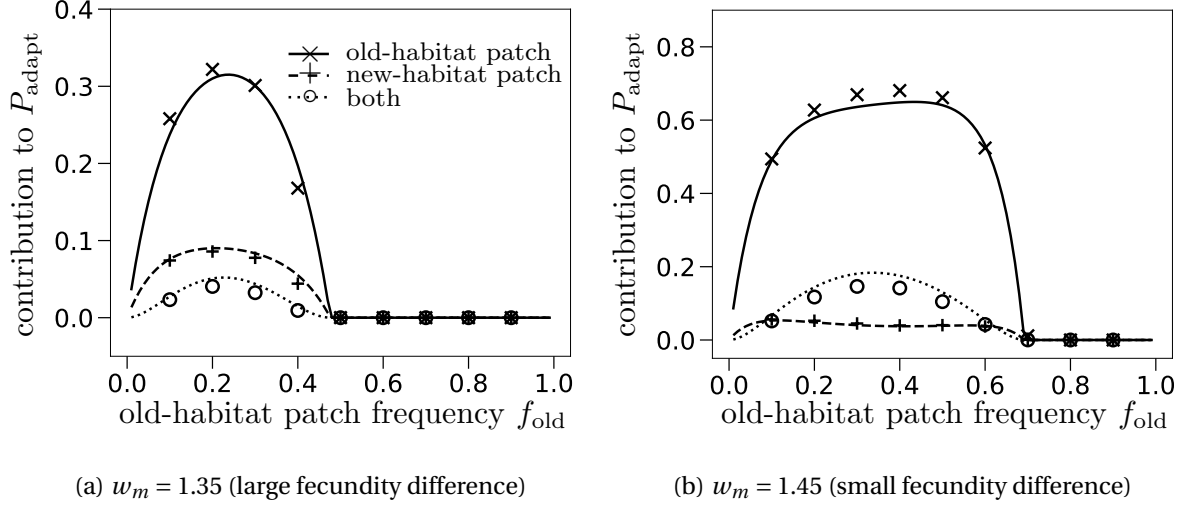


Figure 4: Origin of the adaptive mutant. The origin of the adaptive mutant is strongly affected by the fecundity differences in the old habitat. If the difference is large as illustrated in panel (a), mutants appear more often in old-habitat patches than in new-habitat patches. Still, mutants arising in new-habitat patches contribute to the overall probability of adaptation. If fecundity differences are small like in panel (b), the successful mutant largely arises in old-habitat patches. In this case, the contribution from new-habitat patches is negligible. Circles correspond to simulations identified as soft selective sweeps with (at least) one lineage (successful mutation) arising in an old- and one in a new-habitat patch. The curves are given by eq. (8) (or the adjusted versions of it) under the unbiased dispersal scheme ($\pi_w = \pi_m = 0$). Note the different scaling on the y-axes.

change [Alexander et al., 2014]. We will discuss the effect of standing genetic variation in our system in the following section. For now, we focus on evolutionary rescue due to de novo mutations. We approximate the probability of evolutionary rescue, denoted by P_{rescue} , as

$$P_{\text{rescue}} \approx 1 - \exp \left(-\theta \sum_{i=0}^{M-2} \left(\underbrace{\varphi_{\text{old}}(f_{\text{old}}(i)) \sum_{j=i\tau}^{(i+1)\tau-1} N_w^{\text{old}}(j)}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}}(f_{\text{old}}(i)) \sum_{j=i\tau}^{(i+1)\tau-1} N_w^{\text{new}}(j)}_{\text{new habitat contribution}} \right) \right. \\ \left. - \underbrace{\theta \varphi_{\text{new}}(0) \sum_{j=\tau(M-1)}^{\infty} N_w^{\text{new}}(j)}_{\text{contribution after the last patch deteriorated}} \right), \quad (9) \quad \text{\texttt{eq:evol_res}}$$

where $f_{\text{old}}(i) = (M - i - 1)/M$ is the frequency of old-habitat patches after the $(i + 1)$ -th deterioration event, the establishment probability is given as a function of the patch frequency, $\varphi_k(f_{\text{old}}(i))$, and

510 $N_w^k(j)$ denotes the overall number of wild-type individuals living in habitat k (old or new) in genera-
 tion j (see SI, Section S1 for an approximation). The interpretation of this equation is the same as for
 512 eq. (7). The only difference is that we now need to account for a changing environment, which alters
 the population sizes, N_w^k , and the establishment probabilities φ_k over time. In the formula, these
 514 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
 516 wild-type population size deterministically over time, instead of assuming it to be already in its steady
 state as in eq. (7) (see also Section S1 in the SI).

518 As visible in Fig. 5, the approximation explains the order of dispersal schemes. Yet, it does not ac-
 curately predict the simulated data. This discrepancy can be explained: in the formula we assume that
 520 for a mutant born in a certain patch configuration, say with j old-habitat patches, the environment
 does not change anymore. That is, a mutant born in patch-type k (old or new) in this environment
 522 contributes $\varphi_k(j)$ to the probability of evolutionary rescue despite further patches deteriorating. Thus,
 this mutants probability of establishment is underestimated. This is especially true for mutants that
 524 emerge just before a deterioration event. These mutants are more likely to establish during the subse-
 quent environmental configuration giving them a higher probability of survival than approximated by
 526 our formula. Additionally, $\varphi_k(j)$ assumes stationary wild-type population sizes and therefore does not
 reflect the decreasing wild-type population size right after the deterioration of a patch. This explains
 528 why the simulation results are higher than our approximation. A time-dependent establishment
 probability could account for these effects but unfortunately is not amenable to approximations in our
 530 framework. In Uecker et al. [2014], scenarios with an accessible time-dependent solution were studied,
 more precisely situations with either full mixing of the global population ($m = 1$) or a non-viable
 532 mutant in old-habitat patches ($\omega_m = 0$).

The different dispersal schemes exhibit substantial differences. The dispersal schemes affect the
 534 dispersal pattern of both types and as such alter their respective population dynamics. Both small
 and large fecundity differences in the old habitat, $\omega_m = 1.45$ and $\omega_m = 1.35$, conserve the ranking of
 536 dispersal schemes obtained for the probabilities of establishment and adaptation²⁰: New-New (green)
 is higher than unbiased dispersal (black) which is higher than Old-Old (blue), with Old-New decreasing

²⁰ (difficult to follow) (We could also get rid of the explicit description of the figure and remove the following sentence)

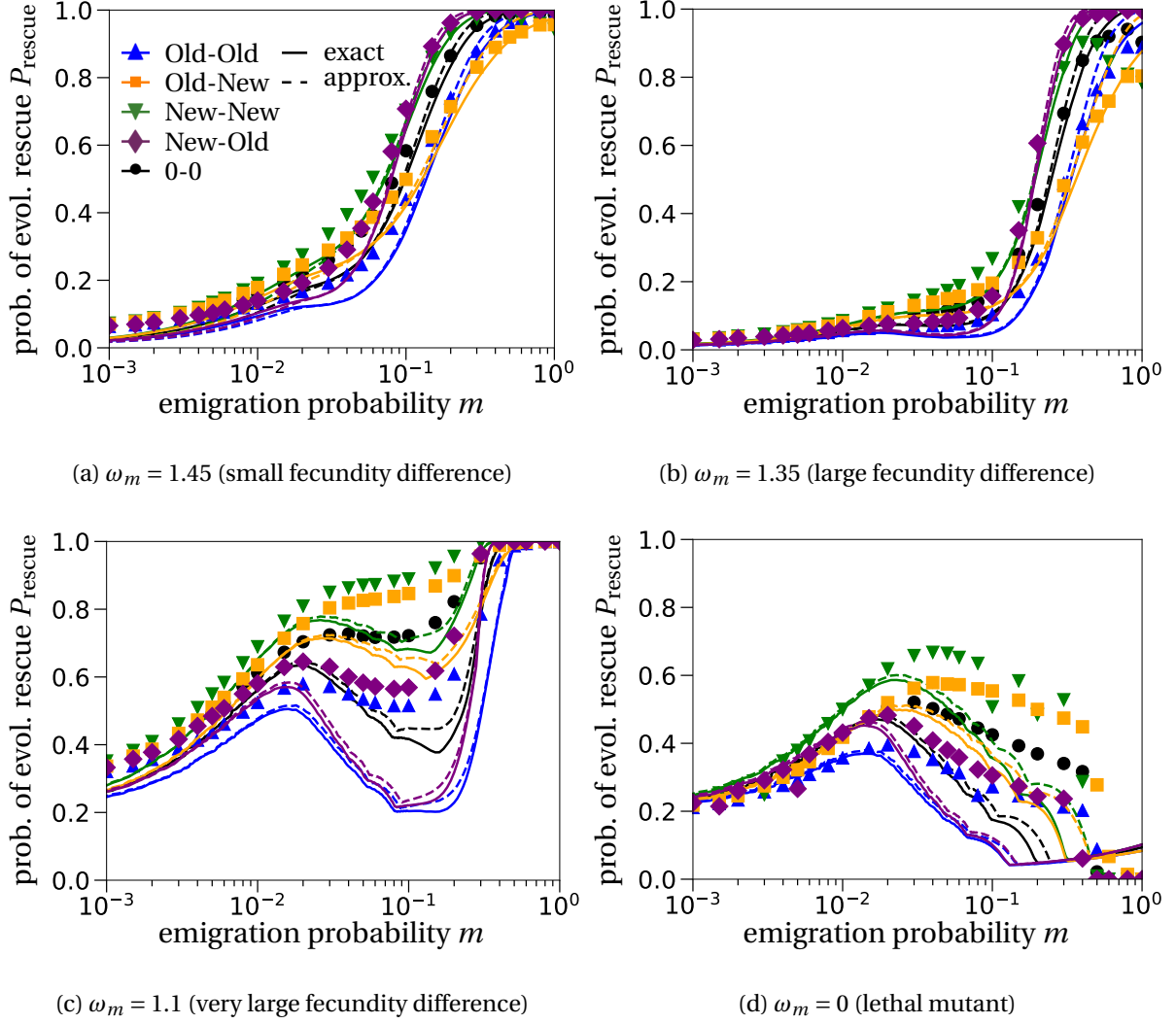


Figure 5: The probability of evolutionary rescue compared to simulation results. Our predictions, computed with eq. (9), match the qualitative behavior of the simulated data for the probability of evolutionary rescue. All rankings of the dispersal schemes align well. Quantitatively though, we find that our predictions tend to underestimate the simulated data. In (a,b) the mutation probability is set to $u = 1/(25MK_{\text{new}})$ while in (c,d) it is $u = 1/(MK_{\text{new}})$. The label ‘exact’ refers to the exact solution of eq. (4) which is then plugged into the approximation of the probability of evolutionary rescue in eq. (9).

and New-Old increasing their positions with increasing emigration probability m , cf. Fig. 5(a,b). Based on our discussion of the same behavior in Fig. 2(a,c), i.e. the change in hierarchy of the dispersal schemes Old-New and New-Old, The most influential factor in these parameter sets is the growth rate of the mutant in old-habitat patches, a_{old} , as discussed around Fig. 2. The ranking of the symmetric dispersal schemes is mostly determined by the mutant dispersal bias.

For very large fecundity differences in the old habitat ($\omega_m = 1.1$ and $\omega_m = 0$), the ranking of dispersal schemes is the same for all emigration probabilities; from highest to lowest, we find **New-New, Old-New, unbiased dispersal, New-Old, and Old-Old** (cf. Fig. 5(c,d)). In this parameter setting, the probability of evolutionary rescue is dominated by the dispersal behavior of the mutant. Since the mutant is barely viable in old-habitat patches, it is always preferential for it to disperse towards new-habitat patches. Two schemes follow this rule, **the New-New and Old-New dispersal scheme**, but differ in the preference of the wild type. Since wild-type individuals also preferentially disperse to new-habitat patches under **the New-New scheme**, more individuals are present in those patches. Therefore, the total amount of mutations over the deterioration time is increased which generates more mutants on average. This explains the New-New dispersal scheme being consistently higher than the Old-New dispersal scheme.

Lastly, the probability of evolutionary rescue often reaches a local (or global) maximum for intermediate emigration probabilities (Figs. 5(c,d)). This extends previous results [Tomasini and Peischl, 2019, Uecker et al., 2014] to arbitrary dispersal schemes affecting the immigration process. The maximum can be attributed to the interaction of the three regions we identified when analyzing the establishment probability φ_k (see also Fig. 2). As such it is a result of the largely positive effect of dispersal (initial increase of the probability of evolutionary rescue) and the negative effect of population mixing (**dispersal to old patches**).²¹

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. Mutations are more likely to appear in the more populated patches (old-habitat). However, a low mutant fecundity ω_m decreases the chance of establishment of these mutants that appear in old-habitat patches (compare black and yellow symbols in Fig. 6(a)). Lower fecundity values ω_m therefore comparatively increase the probability for the rescue mutation to have appeared in the already deteriorated habitat, i.e. in new-habitat patches. **The probability of a soft selective sweep for evolutionary rescue from mutants of the different habitat types is very low (circles in Fig. 6(a)). Our choice of a small mutation rate implies a hard selective sweep regime ($\theta K_{\text{old}} M = 0.08 < 1$)** [Hermisson

²¹(This discussion is still difficult.)

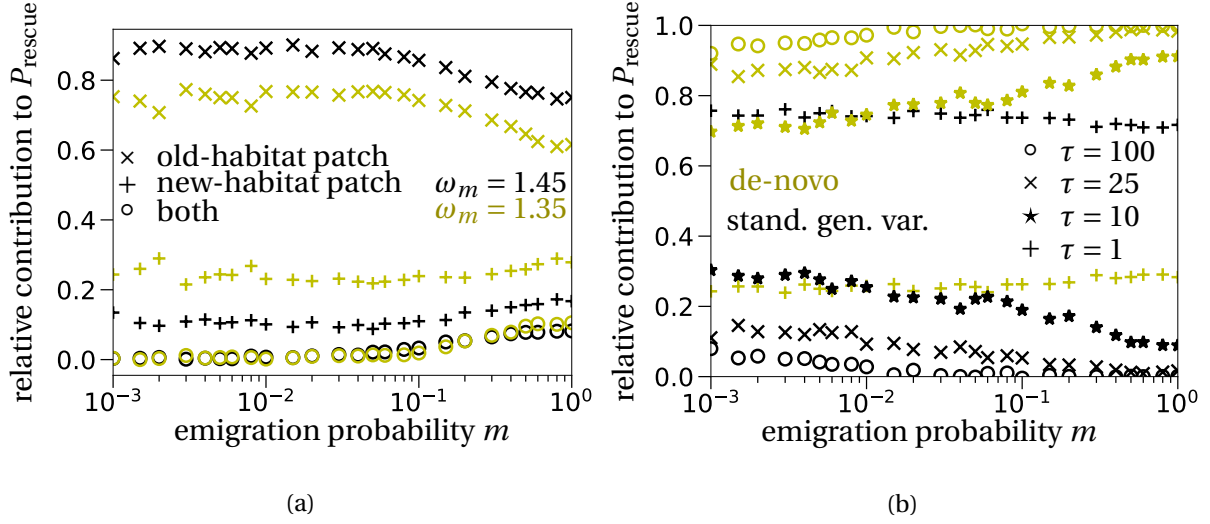


Figure 6: Habitat of origin of the rescue mutation and the impact of standing genetic variation. (a) We compare the source of successful mutations under small (black) and large (yellow) fecundity differences in the old habitat. Decreasing the fecundity of the mutant results in more successful mutations emerging in new-habitat patches (+) when compared to the contribution from old-habitat patches (x). We have chosen $\pi_m = \pi_w = 0$. (b) For slower environmental degradation, i.e. $\tau = 200$, the influence of standing genetic variation (sgv) on the probability of evolutionary rescue decreases. 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 all scenarios and $\omega_m = 1.45$. The relative contribution is then determined by $(P_{\text{rescue with sgv}} - P_{\text{rescue only de novo}}) / P_{\text{rescue with sgv}}$.

and Pennings, 2017, Wilson et al., 2017a].

So far, we have considered settings where evolutionary rescue is exclusively due to de novo mutations. To explore the role of standing genetic variation²², we ran simulations where we let the system evolve for 1,000 generations before the first degradation event happened. Fig. 6(b) shows the relative contribution of de novo mutations and of standing genetic variation, i.e. mutations that appeared before the first degradation event happened. For a successful rescue event due to standing genetic variation, mutants that were initially present (at time $t = 0$) need to survive at least until sufficiently many patches have deteriorated that the probability of adaptation, P_{adapt} , becomes positive, compare to Fig. 3(b,d) and Fig. SX in the SI. Decreasing the value of τ reduces the time between two consecutive degradation events and the overall time-span of the entire environmental change. Therefore, the impact of standing genetic variation on the probability of evolutionary rescue

²²(or variance? is there a difference? why use one over the other?)

increases for smaller values of τ .

582 Additionally, the relative contribution of standing genetic variation declines as the emigration rate
584 m increases. This holds because the mutant is almost exclusively found in old-habitat patches if the
586 frequency of these patches, f_{old} , and emigration rates m are high (see Fig. SX in SI). Thus, mutants that
existed prior to the first deterioration event are very unlikely to survive even for a rapidly changing
environment.

Discussion

588 We have studied the probabilities of establishment, adaptation and evolutionary rescue under four
non-uniform dispersal schemes and compared them to unbiased dispersal. Our analysis builds on
590 the probability of establishment of a single mutant lineage in a heterogeneous environment with a
fixed patch configuration. In line with previous results, we find that the probabilities of establishment,
592 adaptation and evolutionary rescue can display up to three different phases when varying the dispersal
rate m . The different dispersal schemes, by changing the population dynamics, alter the parameter
594 range of these regions.²³

Dispersal and adaptation

596 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. One type of models, classically
598 analyzed in a population genetic context (framework), assumes constant population sizes in all patches,
independent of their local habitat type and of dispersal strength. Results obtained in this framework
600 show that larger dispersal rates tend to decrease the probability of successful establishment of a rare
mutant favored in some part of the environment [e.g. García-Ramos and Kirkpatrick, 1997]. This
602 inhibiting effect of dispersal on adaptation, also (effect) termed “gene swamping”, is a result of an
increase in absolute numbers of non-adapted individuals in the habitat where the rare mutant is
604 beneficial before reproduction and density regulation. This results in a lower mutant frequency
[Lenormand, 2002, Tomasini and Peischl, 2018] and thus in lower reproductive success. Additionally,

²³(Unclear. Suggestion (not great but a bit better maybe): "The dispersal scheme determines the population dynamics
and consequently the parameter regions corresponding to the three phases.")

for very high dispersal rates, the population homogenizes and individuals encounter an averaged environment. Therefore, the type with the largest overall growth rate, averaged over the environment, is favored. (In our model, gene swamping was rarely observed; the dominant effects were explained by the impact of dispersal on demography.)²⁴.

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]. In accordance with this result (these results), we find that dispersal (monotonically) increases the probability of adaptation if the mutant is just slightly less fit than the wild type in the old habitat (Fig. 2(c)). When the mutant's fecundity in old habitats, ω_m , is smaller (than what?), establishment probabilities are non-monotonic with a local maximum at intermediate dispersal rates (and increases at large dispersal rates thanks to relaxed competition) (Fig. 2(a)). However, if the mutant's disadvantage in old habitat patches is even greater, i.e. ω_m (When the fecundity of the mutant is even smaller, the local maximum remains but relaxed competition no longer occurs) adaptation is also hindered for large dispersal rates. The establishment probability becomes hump-shaped (cf. Fig. S2 in SI).²⁵.

Hence, models with and without demographic change differ most at higher emigration rates. This corresponds to region (iii) in our analysis; we illustrate this point in (Compared to models with implicit demography, explicitly modelling the population dynamics causes relaxed competition that increases the probability of establishment at high dispersal rates) Fig. S5 in SI, the non-demographic version of Fig. 2.

(In figure S5, there does seem to have relaxed competition for curves orange purple. So it's a bit confusing. Maybe remove those? Also I think a more balanced discussion of the three phases: initial rise thanks to exportation of mut in new habitats; decline due to back-migration; final increase due to relaxed competition, and which effect appears or not in the pop gen model, would be nice. Right now we focus a lot on relaxed competition.)

²⁴(Would consider shortening this paragraph which is not directly relevant. e.g. remove the sentence "this results in a lower mutant frequency...", but keep the references)

²⁵(I was confused by this paragraph so rephrased to make it more uniform and better describe the figures and the key differences)

Standing genetic variation and evolutionary rescue

Besides the general structure of the probability of evolutionary rescue when varying the emigration probability m , we also studied the effect (contribution) of standing genetic variation on this quantity (to evolutionary rescue). We find that the contribution of standing genetic variation on the overall probability of evolutionary rescue increases with the speed of the environmental change, determined by τ (Fig. 6(b)). 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* indicate that under slow environmental change the impact of standing genetic variation is small [Guzella et al., 2018]. This is because the evolution of the trait is driven by *de novo* mutations with small effects. For a sudden or fast environmental change (small τ), standing genetic variation becomes increasingly important for the probability of evolutionary rescue. These observations are in line with our findings in Fig. 6(b).

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 [Clobert et al., 2009, Edelaar and Bolnick, 2012, Edelaar et al., 2008]. This has led to a number of simulation studies exploring the effect of various dispersal schemes onto (local) adaptation [e.g. Holt and Barfield, 2015, Mortier et al., 2018, Pellerin et al., 2018, Vuilleumier et al., 2010].

Two of these simulation studies examined the effects of matching habitat choice on adaptation in a heterogeneous environment [Holt and Barfield, 2015, Vuilleumier et al., 2010]. Both investigations indicate that matching habitat choice increases the probability of adaptation when compared to unbiased dispersal. This is in line with our findings: we predict that type-dependent habitat choice where each type favors patches they are relatively more fit in (Old-New), generates higher probabilities of establishment (and evolutionary rescue) than unbiased dispersal (0-0) (Figs. 2, 3, 5).

The dispersal schemes also slightly affect the origin of the successful mutant lineage, cf. SI, Fig. S6. Population densities, especially in new-habitat patches, are altered when compared to the unbiased dispersal scheme.²⁶

²⁶(This paragraph could be dropped in line with a comment of a reviewer.) (agree to drop it)

To conclude, the effects of dispersal schemes are two-fold. By changing population densities in both habitat types, the dispersal schemes **alter** the growth rate of the mutant in old-habitat patches. This is the primary reason for the ranking of the dispersal schemes. In addition, they also affect the number of mutations arising in either habitat type. This has a minor effect on the probability of evolutionary rescue for the explored parameter range but is relevant when studying the origin of the successful mutant(**mutation**) lineage (see also SI, Fig. S6). (As the genetic background may vary across patches, the origin of a successful mutation will also affect which neutral and deleterious mutations will hitchhike with it). The origin of a successful mutant is of special interest once multiple loci are considered(. Rescue by a single mutant implies) **which might promote** neutral (or even deleterious) hitchhiking effects. Similarly, in the case of polygenic rescue or under recombination [e.g. Uecker and Hermisson, 2016], **the origin of a mutant is likely to affect its success.([mention genetic background])**

Generality of our theoretical analysis and future directions

Our mathematical results apply in the case where the mutant offspring numbers can be written in the form “migration times reproduction (and potential regulation)” with rates that are constant in time (**or as in case of evolutionary rescue, constant between two deterioration events**; see the mean reproduction matrix in eq. (3)). Biologically, this means that the resident population is stationary and the mutant is either at low numbers or unaffected by its own density. Furthermore, for our approximation in eq. (5) to generate accurate predictions, it is essential that growth rate differences between the wild type and the mutant are weak and dispersal is low. Formally, just two of these parameters need to be small – see also the corresponding discussion in Tomasini and Peischl [2018].

Since we summarize the population dynamics in our parameters of the reproduction matrix, the approach taken here is quite general and can account for various dispersal schemes and local **type-dependent** population dynamics, **i.e. different reproduction and competitive parameters**. However, it cannot account for **type-dependent carrying capacities, explicit spatial structure or ~~time-inhomogeneous~~ (rapidly changing) environments**. The **latter** is the reason for our **poor**²⁷ approximation in the context of evolutionary rescue (Fig. 5)²⁸. Additionally, in order to obtain analytical solutions, it

²⁷ (any better word here?)

²⁸ (I would remove this sentence)

is important that the stationary population sizes of the wild type have an accessible solution. This is not the case if we consider non-linear emigration rates that depend on habitat choice like those incorporated in some simulation studies [e.g Holt and Barfield, 2015, Mortier et al., 2018].

In contrast, it is possible to implement a cost of dispersal or a different life cycle. In particular, the variation of the life cycle could yield distinct results regarding adaptation [Holt and Barfield, 2015] and, more generally, in the context of the evolution of dispersal [Massol and Débarre, 2015].

In conclusion, we studied the effect of dispersal and different dispersal schemes on the probability of establishment, adaptation and evolutionary rescue of a mutant under divergent selection in a subdivided population. Our quantitative approach disentangles the interaction of dispersal and adaptation. We recover previous results on adaptation and provide a general framework for studying 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, respectively. We find that including population demography significantly alters the results for high dispersal rates. For constant population sizes, 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. Our results indicate that habitat choice does not necessarily result in an increased adaptive potential and might even hinder successful establishment of a mutant population that would avoid population extinction. These results show that non-uniform dispersal patterns can have a strong influence on population survival and adaptation in a heterogeneous environment.

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References

Deepa Agashe, Jay J. Falk, and Daniel I. Bolnick. Effects of founding genetic variation on adaptation to a novel resource. *Evolution*, 65(9):2481–2491, 2011. doi: 10.1111/j.1558-5646.2011.01307.x.

Helen K. Alexander, Guillaume Martin, Oliver Y. Martin, and Sebastian Bonhoeffer. Evolutionary rescue: linking theory for conservation and medicine. *Evolutionary Applications*, 7(10):1161–1179, 2014. doi: 10.1111/eva.12221.

Priyanga Amarasekare. The role of density-dependent dispersal in source–sink dynamics. *Journal of Theoretical Biology*, 226(2):159 – 168, 2004. doi: <https://doi.org/10.1016/j.jtbi.2003.08.007>.

Yoann Anciaux, Luis-Miguel Chevin, Ophélie Ronce, and Guillaume Martin. Evolutionary rescue over a fitness landscape. *Genetics*, 209(1):265–279, 2018. doi: 10.1534/genetics.118.300908.

James Battin. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conservation Biology*, 18(6):1482–1491, 2004.

Graham Bell. Evolutionary rescue. *Annual Review of Ecology, Evolution, and Systematics*, 48(1): 605–627, 2017. doi: 10.1146/annurev-ecolsys-110316-023011.

Graham Bell and Andrew Gonzalez. Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters*, 12(9):942–948, 2009. doi: 10.1111/j.1461-0248.2009.01350.x.

Graham Bell and Andrew Gonzalez. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science*, 332(6035):1327–1330, 2011. doi: 10.1126/science.1203105.

Céline Bellard, Cleo Bertelsmeier, Paul Leadley, Wilfried Thuiller, and Franck Courchamp. Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4):365–377, 2012. doi: 10.1111/j.1461-0248.2011.01736.x.

Craig W. Benkman. Matching habitat choice in nomadic crossbills appears most pronounced when food is most limiting. *Evolution*, 71(3):778–785, 2017. doi: 10.1111/evo.13146.

- Elvire Bestion, Jean Clobert, and Julien Cote. Dispersal response to climate change: scaling down to
 738 intraspecific variation. *Ecology Letters*, 18(11):1226–1233, 2015. doi: 10.1111/ele.12502.
- Daniel I. Bolnick, Lisa K. Snowberg, Claire Patenia, William E. Stutz, Travis Ingram, and On Lee Lau.
 740 Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and
 stream stickleback. *Evolution*, 63(8):2004–2016, 2009. doi: 10.1111/j.1558-5646.2009.00699.x.
- 742 Diana E. Bowler and Tim G. Benton. Causes and consequences of animal dispersal strategies: relating
 individual behaviour to spatial dynamics. *Biological Reviews*, 80(2):205–225, 2005. doi: 10.1017/
 744 S1464793104006645.
- Stephanie M. Carlson, Curry J. Cunningham, and Peter A.H. Westley. Evolutionary rescue in a changing
 746 world. *Trends in Ecology & Evolution*, 29(9):521–530, 2014. doi: 10.1016/j.tree.2014.06.005.
- Jean Clobert, Jean-François Le Galliard, Julien Cote, Sandrine Meylan, and Manuel Massot. Informed
 748 dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured
 populations. *Ecology Letters*, 12(3):197–209, 2009. doi: 10.1111/j.1461-0248.2008.01267.x.
- 750 Nele De Meester and Dries Bonte. Information use and density-dependent emigration in an agrobiont
 spider. *Behavioral Ecology*, 21(5):992–998, 2010. doi: 10.1093/beheco/arq088.
- 752 Francesca Di Giallonardo and Edward C. Holmes. Viral biocontrol: grand experiments in disease
 emergence and evolution. *Trends in Microbiology*, 23(2):83–90, 2015. doi: 10.1016/j.tim.2014.10.004.
- 754 José Alexandre F. Diniz-Filho, Kelly S. Souza, Luis M. Bini, Rafael Loyola, Ricardo Dobrovolski, João
 Fabricio M. Rodrigues, S. Lima-Ribeiro, Levi C. Terribile, Thiago F. Rangel, Igor Bione, Roniel Freitas,
 756 Iberê F. Machado, Tainá Rocha, Maria L. Lorini, Mariana M. Vale, Carlos A. Navas, Natan M. Maciel,
 Fabricio Villalobos, Miguel A. Olalla-Tarraga, and Sidney Gouveia. A macroecological approach to
 758 evolutionary rescue and adaptation to climate change. *Ecography*, 2019. doi: 10.1111/ecog.04264.
- A. N. Dreiss, S. Antoniazza, R. Burri, L. Fumagalli, C. Sonnay, C. Frey, J. Goudet, and A. Roulin. Local
 760 adaptation and matching habitat choice in female barn owls with respect to melanic coloration.
Journal of Evolutionary Biology, 25(1):103–114, 2011. doi: 10.1111/j.1420-9101.2011.02407.x.

762 Pim Edelaar and Daniel I. Bolnick. Non-random gene flow: an underappreciated force in evolution
and ecology. *Trends in Ecology & Evolution*, 27(12):659–665, 2012. doi: 10.1016/j.tree.2012.07.009.

764 Pim Edelaar, Adam M. Siepielski, and Jean Clobert. Matching habitat choice causes directed gene
flow: A neglected dimension in evolution and ecology. *Evolution*, 62(10):2462–2472, 2008. doi:
766 10.1111/j.1558-5646.2008.00459.x.

Stacy B. Endriss, Megan L. Vahsen, Ellyn V. Bitume, J. Grey Monroe, Kathryn G. Turner, Andrew P.
768 Norton, and Ruth A. Hufbauer. The importance of growing up: juvenile environment influences
dispersal of individuals and their neighbours. *Ecology Letters*, 22(1):45–55, 2019. doi: 10.1111/ele.
770 13166.

K. M. Fedorka, W. E. Winterhalter, K. L. Shaw, W. R. Brogan, and T. A. Mousseau. The role of gene flow
772 asymmetry along an environmental gradient in constraining local adaptation and range expansion.
Journal of Evolutionary Biology, 25(8):1676–1685, 2012. doi: 10.1111/j.1420-9101.2012.02552.x.

774 Brian Folt, Maureen A. Donnelly, and Craig Guyer. Spatial patterns of the frog *Oophaga pumilio* in a
plantation system are consistent with conspecific attraction. *Ecology and Evolution*, 8(5):2880–2889,
776 2018. doi: 10.1002/ece3.3748.

Romain Gallet, Rémy Froissart, and Virginie Ravigné. Experimental demonstration of the impact
778 of hard and soft selection regimes on polymorphism maintenance in spatially heterogeneous
environments†. *Evolution*, 72(8):1677–1688, 2018. doi: 10.1111/evo.13513.

780 Gisela García-Ramos and Mark Kirkpatrick. Genetic models of adaptation and gene flow in peripheral
populations. *Evolution*, 51(1):21, 1997. doi: 10.2307/2410956.

782 Patrick Gautier, Kurtulus Olgun, Nazan Uzum, and Claude Miaud. Gregarious behaviour in a salaman-
der: attraction to conspecific chemical cues in burrow choice. *Behavioral Ecology and Sociobiology*,
784 59(6):836–841, 2006. doi: 10.1007/s00265-005-0130-8.

Sarah A Gignoux-Wolfsohn, Malin Pinsky, Kathleen Kerwin, Carl Herzog, Mackenzie Hall, Alyssa
786 Bennett, Nina Fefferman, and Brooke Maslo. Genomic signatures of evolutionary rescue in bats
surviving white-nose syndrome. *bioRxiv*, 2018. doi: 10.1101/470294.

788 Sylvain Glémin and Joëlle Ronfort. Adaptation and maladaptation in selfing and outcrossing species:
New mutations versus standing variation. *Evolution*, 67(1):225–240, 2013. doi: 10.1111/j.1558-5646.
790 2012.01778.x.

Richard Gomulkiewicz and Robert D. Holt. When does evolution by natural selection prevent extinc-
792 tion? *Evolution*, 49(1):201, 1995. doi: 10.2307/2410305.

Richard Gomulkiewicz, Robert D. Holt, and Michael Barfield. The effects of density dependence and
794 immigration on local adaptation and niche evolution in a black-hole sink environment. *Theoretical
Population Biology*, 55(3):283 – 296, 1999. doi: 10.1006/tpbi.1998.1405.

796 Kathryn M. Greene, Shannon E. Pittman, and Michael E. Dorcas. The effects of conspecifics on burrow
selection in juvenile spotted salamanders (*ambystoma maculatum*). *Journal of Ethology*, 34(3):
798 309–314, 2016. doi: 10.1007/s10164-016-0476-6.

Thiago S. Guzella, Snigdhadip Dey, Ivo M. Chelo, Ania Pino-Querido, Veronica F Pereira, Stephen R.
800 Proulx, and Henrique Teotónio. Slower environmental change hinders adaptation from standing
genetic variation. *PLOS Genetics*, 14(11):1–28, 11 2018. doi: 10.1371/journal.pgen.1007731.

802 Patsy Haccou, Peter Jagers, and Vladimir A. Vatutin. *Branching Processes: Variation, Growth, and
Extinction of Populations*. Cambridge Studies in Adaptive Dynamics. Cambridge University Press,
804 2005. doi: 10.1017/CBO9780511629136.

J. B. S. Haldane. A mathematical theory of natural and artificial selection, part v: Selection and
806 mutation. *Mathematical Proceedings of the Cambridge Philosophical Society*, 23(7):838–844, 1927.
doi: 10.1017/S0305004100015644.

808 Joachim Hermisson and Pleuni S. Pennings. Soft sweeps and beyond: understanding the patterns and
probabilities of selection footprints under rapid adaptation. *Methods in Ecology and Evolution*, 8(6):
810 700–716, 2017. doi: 10.1111/2041-210X.12808.

Robert D. Holt. Population dynamics in two-patch environments: Some anomalous consequences
812 of an optimal habitat distribution. *Theoretical Population Biology*, 28(2):181 – 208, 1985. doi:
[https://doi.org/10.1016/0040-5809\(85\)90027-9](https://doi.org/10.1016/0040-5809(85)90027-9).

- 814 Robert D. Holt. Adaptive evolution in source-sink environments: Direct and indirect effects of density-
dependence on niche evolution. *Oikos*, 75(2):182–192, 1996.
- 816 Robert D. Holt and Michael Barfield. The influence of imperfect matching habitat choice on evo-
lution in source–sink environments. *Evolutionary Ecology*, 29(6):887–904, 2015. doi: 10.1007/
818 s10682-015-9789-0.
- Robert D. Holt and Richard Gomulkiewicz. How does immigration influence local adaptation? a
820 reexamination of a familiar paradigm. *The American Naturalist*, 149(3):563–572, 1997. doi: 10.1086/
286005.
- 822 Staffan Jacob, Delphine Legrand, Alexis S. Chaine, Dries Bonte, Nicolas Schtickzelle, Michèle Huet,
and Jean Clobert. Gene flow favours local adaptation under habitat choice in ciliate microcosms.
824 *Nature Ecology & Evolution*, 1(9):1407–1410, 2017. doi: 10.1038/s41559-017-0269-5.
- Staffan Jacob, Estelle Laurent, Bart Haegeman, Romain Bertrand, Jérôme G. Prunier, Delphine Legrand,
826 Julien Cote, Alexis S. Chaine, Michel Loreau, Jean Clobert, and Nicolas Schtickzelle. Habitat choice
meets thermal specialization: Competition with specialists may drive suboptimal habitat prefer-
828 ences in generalists. *Proceedings of the National Academy of Sciences*, 115(47):11988–11993, 2018.
doi: 10.1073/pnas.1805574115.
- 830 Tadeusz J. Kawecki. Demography of source—sink populations and the evolution of ecological niches.
Evolutionary Ecology, 9(1):38–44, 1995. doi: 10.1007/BF01237695.
- 832 Tadeusz J. Kawecki. 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 of London. Series B:*
834 *Biological Sciences*, 267(1450):1315–1320, 2000. doi: 10.1098/rspb.2000.1144.
- Tadeusz J. Kawecki and Robert D. Holt. Evolutionary consequences of asymmetric dispersal rates. *The*
836 *American Naturalist*, 160(3):333–347, 2002. doi: 10.1086/341519.
- Mark Kirkpatrick and N. H. Barton. Evolution of a species’ range. *The American Naturalist*, 150(1):
838 1–23, 1997. doi: 10.1086/286054.

Julia M. Kreiner, John R. Stinchcombe, and Stephen I. Wright. Population genomics of herbicide resistance: Adaptation via evolutionary rescue. *Annual Review of Plant Biology*, 69(1):611–635, 2018. doi: 10.1146/annurev-arplant-042817-040038.

Josianne Lachapelle and Graham Bell. Evolutionary rescue of sexual and asexual populations in a deteriorating environment. *Evolution*, 66(11):3508–3518, 2012. doi: 10.1111/j.1558-5646.2012.01697.x.

Thomas Lenormand. Gene flow and the limits to natural selection. *Trends in Ecology & Evolution*, 17(4):183–189, 2002. doi: 10.1016/s0169-5347(02)02497-7.

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

Guillaume Martin, Robin Aguilée, Johan Ramsayer, Oliver Kaltz, and Ophélie Ronce. The probability of evolutionary rescue: towards a quantitative comparison between theory and evolution experiments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1610):20120088, 2013. doi: 10.1098/rstb.2012.0088.

François Massol and Florence Débarre. Evolution of dispersal in spatially and temporally variable environments: The importance of life cycles. *Evolution*, 69(7):1925–1937, 2015. doi: 10.1111/evo.12699.

Jérôme Mathieu, Sébastien Barot, Manuel Blouin, Gaël Caro, Thibaud Decaëns, Florence Dubs, Lise Dupont, Pascal Jouquet, and Philippe Nai. 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(2):203 – 209, 2010. doi: <https://doi.org/10.1016/j.soilbio.2009.10.018>.

Sebastian Matuszewski, Joachim Hermisson, and Michael Kopp. Catch me if you can: Adaptation from standing genetic variation to a moving phenotypic optimum. *Genetics*, 200(4):1255–1274, 2015. doi: 10.1534/genetics.115.178574.

Frederik Mortier, Staffan Jacob, Martijn L. Vandegehuchte, and Dries Bonte. Habitat choice stabilizes

metapopulation dynamics by enabling ecological specialization. *Oikos*, 128(4):529–539, December
2018. doi: 10.1111/oik.05885.

Thomas Nagylaki. Clines with asymmetric migration. *Genetics*, 88(4):813–827, 1978.

Matthew M. Osmond, Sarah P. Otto, and Christopher A. Klausmeier. When predators help prey
adapt and persist in a changing environment. *The American Naturalist*, 190(1):83–98, 2017. doi:
10.1086/691778.

Matthew M. Osmond, Sarah P. Otto, and Guillaume Martin. Genetic paths to evolutionary rescue and
the distribution of fitness effects along them. *Genetics*, 2019. doi: 10.1534/genetics.119.302890.

Matthew Miles Osmond and Claire de Mazancourt. How competition affects evolutionary rescue.
Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1610):20120085, 2013. doi:
10.1098/rstb.2012.0085.

Félix Pellerin, Julien Cote, Elvire Bestion, and Robin Aguilée. Matching habitat choice promotes species
persistence under climate change. *Oikos*, 128(2):221–234, September 2018. doi: 10.1111/oik.05309.

H. Ronald Pulliam. Sources, sinks, and population regulation. *The American Naturalist*, 132(5):
652–661, 1988.

Johan Ramsayer, Oliver Kaltz, and Michael E. Hochberg. Evolutionary rescue in populations of
pseudomonas fluorescens across an antibiotic gradient. *Evolutionary Applications*, 6(4):608–616,
2013. doi: 10.1111/eva.12046.

Ophélie Ronce. How does it feel to be like a rolling stone? ten questions about dispersal evolution.
Annual Review of Ecology, Evolution, and Systematics, 38(1):231–253, 2007. doi: 10.1146/annurev.
ecolsys.38.091206.095611.

Ophélie Ronce and Mark Kirkpatrick. When sources become sinks: migrational meltdown in heteroge-
neous habitats. *Evolution*, 55(8):1520–1531, 2001. doi: 10.1111/j.0014-3820.2001.tb00672.x.

Rike B. Stelkens, Michael A. Brockhurst, Gregory D. D. Hurst, and Duncan Greig. Hybridization
facilitates evolutionary rescue. *Evolutionary Applications*, 7(10):1209–1217, 2014. doi: 10.1111/eva.
12214.

Ole-Gunnar Støen, Andreas Zedrosser, Solve Sæbø, and Jon E. Swenson. Inversely density-
dependent natal dispersal in brown bears *Ursus arctos*. *Oecologia*, 148(2):356, 2006. doi:
10.1007/s00442-006-0384-5.

Andrew Storfer and Andrew Sih. Gene flow and ineffective antipredator behavior in a stream-breeding
salamander. *Evolution*, 52(2):558–565, 1998. doi: 10.1111/j.1558-5646.1998.tb01654.x.

Samuel J. Tazzyman and Sebastian Bonhoeffer. Plasmids and evolutionary rescue by drug resistance.
Evolution, 68(7):2066–2078, 2014. doi: 10.1111/evo.12423.

Matteo Tomasini and Stephan Peischl. Establishment of locally adapted mutations under divergent
selection. *Genetics*, 209(3):885–895, 2018. doi: 10.1534/genetics.118.301104.

Matteo Tomasini and Stephan Peischl. When does gene flow facilitate evolutionary rescue? *bioRxiv*,
2019. doi: 10.1101/622142.

Katrine Turgeon and Donald L. Kramer. Compensatory immigration depends on adjacent population
size and habitat quality but not on landscape connectivity. *Journal of Animal Ecology*, 81(6):1161–
1170, 2012. doi: 10.1111/j.1365-2656.2012.01990.x.

Hildegard Uecker. Evolutionary rescue in randomly mating, selfing, and clonal populations. *Evolution*,
71(4):845–858, 2017. doi: 10.1111/evo.13191.

Hildegard Uecker and Joachim Hermisson. The role of recombination in evolutionary rescue. *Genetics*,
202(2):721–732, 2016. doi: 10.1534/genetics.115.180299.

Hildegard Uecker, Sarah P. Otto, and Joachim Hermisson. Evolutionary rescue in structured popula-
tions. *The American Naturalist*, 183(1):E17–E35, 2014. doi: 10.1086/673914.

E. Vander Wal, D. Garant, M. Festa-Bianchet, and F. Pelletier. Evolutionary rescue in vertebrates:
evidence, applications and uncertainty. *Philosophical Transactions of the Royal Society B: Biological
Sciences*, 368(1610):20120090–20120090, 2012. doi: 10.1098/rstb.2012.0090.

S. Vuilleumier, J. Goudet, and N. Perrin. Evolution in heterogeneous populations: From migration
models to fixation probabilities. *Theoretical Population Biology*, 78(4):250 – 258, 2010. doi: <https://doi.org/10.1016/j.tpb.2010.08.004>.

Benjamin A. Wilson, Pleuni S. Pennings, and Dmitri A. Petrov. Soft selective sweeps in evolutionary

918 rescue. *Genetics*, 205(4):1573–1586, 2017a. doi: 10.1534/genetics.116.191478.

Scott Wilson, Ann E. McKellar, Matthew W. Reudink, Peter P. Marra, and Laurene M. Ratcliffe. Density-

920 dependent immigration promotes population stability in a long-distance migratory bird. *Population Ecology*, 59(2):169–178, 2017b. doi: 10.1007/s10144-017-0582-5.

922 Masato Yamamichi and Brooks E. Miner. Indirect evolutionary rescue: prey adapts, predator avoids extinction. *Evolutionary Applications*, 8(8):787–795, 2015. doi: 10.1111/eva.12295.