

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

Current anthropogenic environmental changes such as deforestation, soil and water contamination or rising temperatures, contribute to the decline of the populations of many species, that 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 genetic⁶ 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, (classically) resulting in a U-shaped demographic trajectory over time [Gomulkiewicz and Holt, 1995]. In recent years, empirical examples of evolutionary rescue have accumulated [as reviewed by Alexander et al., 2014, Bell, 2017, Carlson et al., 2014]. Laboratory experiments have provided direct evidence of evolutionary rescue [e.g. Agashe et al., 2011, Bell and Gonzalez, 2009, Lachapelle and Bell, 2012, Lindsey et al., 2013, Stelkens et al., 2014]. In the wild, however, demographic and genotypic data are rarely monitored together at the same time, which impedes direct observation of evolutionary rescue. Still, evolutionary rescue has been suggested as a mechanism that has saved a few wild populations from extinction [e.g. Di Giallonardo and Holmes, 2015, Gignoux-Wolfsohn et al., 2018, Vander Wal et al., 2012].

([Need a paragraph on the genetic makeup. We are not explaining this at all at the moment and this is lacking] Rescue can occur through plasticity (refs Chevin? ⁷) or genetic adaptation (refs). The traits involves can be continuous (ref) or discrete (ref). In this work, we consider genetic adaptation mediated by discrete traits. Specifically, we consider that a single mutation can prevent extinction, and...)

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], repro-

⁶(rescue by plasticity as well)

⁷<https://royalsocietypublishing.org/doi/full/10.1098/rspb.2016.1690> , <https://royalsocietypublishing.org/doi/abs/10.1098/rstb.2012.0089> and/or <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1558-5646.2009.00875.x>

duction 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]⁸. Such gradual changes can in particular occur in fragmented environments.

In fragmented environments, habitat deterioration is not necessarily synchronized across patches: there can be a transient spatially heterogeneous environment consisting of a mosaic of old and of degraded habitat patches, until eventually the whole environment has deteriorated. If individuals that populate different patches are able to move between those, the effect of dispersal on evolutionary rescue needs to be taken into account [Tomasini and Peischl, 2019, Uecker et al., 2014]. The intensity of dispersal among patches tunes how abruptly environmental change is experienced. With very low dispersal, patches are essentially isolated from each other, and each patch undergoes an abrupt change independently of the other patches. With higher dispersal, asynchronous deterioration among patches is experienced as a more gradual change overall. Experiments that study the effect of dispersal on evolutionary rescue are rare, but, for instance, Bell and Gonzalez [2011] found that dispersal can increase the likelihood of successful genetic adaptation.

The transient mosaic of degraded and non-degraded patches that results from asynchronous degradation in a fragmented habitat is similar to the setting of models of source-sink dynamics. These models represent a spatially heterogeneous environment, constant in time, in which wild-type populations in unfavorable habitats can only be maintained thanks to recurrent immigration from favorable habitats. 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., for studies on discrete traits, ([refocus the citations with papers on discrete traits; otherwise there are too many possible citations – it's fine to do so given that we now explicitly say the paper is focused on

⁸(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? But please check; it's a long time that I read those...)

discrete traits)) Gomulkiewicz et al. [1999], Holt and Gomulkiewicz [1997] for positive; Fedorka et al.
70 [2012], García-Ramos and Kirkpatrick [1997], Kirkpatrick and Barton [1997], Storfer and Sih [1998] for
negative; and Gallet et al. [2018], Kawecki [2000] for both effects).

72 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-
74 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
76 analytical focus on unbiased dispersal is in stark contrast to dispersal schemes observed in nature
[Clobert et al., 2009, Edelaar and Bolnick, 2012, Edelaar et al., 2008].

78 One of the best documented modes of non-uniform dispersal is density-dependent dispersal.
Density dependence can be positive or negative: either individuals prefer to settle or stay in large
80 groups (positive density-dependence), or they choose to remain in or move to less populated regions
(negative density-dependence). Density-dependent dispersal, of either form, is ubiquitously found in
82 nature and has been reported in many species across the tree of life, including insects [Endriss et al.,
2019], spiders [De Meester and Bonte, 2010], amphibians [Gautier et al., 2006], birds [Wilson et al.,
84 2017b], fishes [Turgeon and Kramer, 2012], and mammals [Støen et al., 2006].

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

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

92 We model an environment that consists of various patches with one of two possible habitats: the
'old' habitat, in which both types, wild type and mutant, have a positive growth rate, and the 'new'
94 habitat, where in the absence of immigration the wild-type population will eventually go extinct. We
study four biologically motivated dispersal schemes, which correspond to the four combinations of
96 biases towards old vs. new patches for wild type and mutants, and we compare these dispersal schemes
to unbiased dispersal. Our analysis is carried out step-wise. We first consider a temporally constant

98 but spatially heterogeneous environment with two ('old' and 'new') patch types. In this setting, we first
study the probability of establishment of a single mutant, assuming there are no further mutations
100 between types. We then relax the assumption of no further mutations, and compute a probability of
adaptation, i.e. of establishment of the mutant lineage⁹. Finally, we let habitat degradation proceed,
102 assuming that patches, one after another, deteriorate over time until all locations contain the new
habitat. Using the previous results, we approximate a probability of evolutionary rescue, i.e. that a
104 mutation appears, establishes, thereby allowing the population to persist in spite of environmental
degradation. We find that dispersal biases affect the probabilities of establishment and of evolutionary
106 rescue, because it directly affects the local growth rates.

Model and methods

108 *Main assumptions and life-cycle*

We consider a spatially structured environment consisting of M patches all connected to each other.
110 The habitat of a patch is either in the *old* or in the *new* state, corresponding to habitat quality before and
after environmental deterioration, respectively. One after another every τ generations, the habitat of a
112 patch deteriorates, from old to new state, the transition being irreversible. 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
114 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
116 each environmental deterioration event, until it eventually hits 0, when all patches have undergone
the environmental change. This setting corresponds to the one analyzed by Uecker et al. [2014], and
118 more recently by Tomasini and Peischl [2019] in the special case of just two patches¹⁰. The maximum
numbers of individuals that can live in a patch of a given habitat type, i.e. the carrying capacities, are
120 denoted K_{old} and K_{new} for old- and new-habitat patches respectively; K_{old} and K_{new} may differ.

The population living in this environment consists of asexually reproducing, haploid individuals;
122 generations are discrete and non-overlapping. There are two possible types of individuals, wild types

⁹(not sure about this defn, please check)

¹⁰(what about carrying capacities in these papers?)

and mutants. The individuals go through the following life-cycle:

- 124 (i) Dispersal: individuals may move between patches. Further details about this step are given
below.
- 126 (ii) Reproduction: individuals reproduce within patches. The number of offspring produced by an
individual of type i in habitat k (before density regulation, if any), i.e. its fecundity, is drawn in
128 a Poisson distribution of expectation ω_i^k . Having fewer than 1 offspring in expectation means
that the local subpopulation will get extinct in the absence of immigration, because the deaths
130 of the parents at each generation are not compensated by enough births on average. On the
contrary, the local population is viable if the expected fecundity is greater than 1. We assume
132 that wild-type and mutant populations are viable in old-habitat patches, and that the mutant's
expected fecundity there is lower than the wild type's: $1 \leq \omega_m^{\text{old}} < \omega_w^{\text{old}}$ ¹¹. In new-habitat patches,
134 a wild-type population will eventually go extinct, while a mutant one would persist, hence the
term “rescue mutant”: $\omega_w^{\text{new}} < 1 < \omega_m^{\text{new}}$. All parents die at the end of this step.
- 136 (iii) Mutation: wild-type offspring mutate to the rescue mutant type with probability θ (back muta-
tions from the mutant to the wild type are neglected).
- 138 (iv) Regulation: if the number of offspring produced locally exceeds the local carrying capacity K_k
(where k refers to the habitat type, old or new), the population size is down-regulated to the K_k :
140 individuals are randomly removed until the local population size is equal to K_k . One mutant
offspring has the same chance of being removed as one wild-type offspring: we assume that
142 wild-type and mutant individuals are competitively equivalent. If the number of offspring is
below the carrying capacity, the regulation step is ignored. At the end of this step, all offspring
144 become adults, and a new cycle then begins.

Dispersal mechanisms

146 We split the dispersal step into emigration and immigration. Emigration is unbiased: all individuals
have the same probability m of leaving the patch they were born in. We assumed that dispersal biases

¹¹ (In the table, it is $0 \leq$, yet the populations are supposed to be viable)

148 affect the immigration step. We denote by π_i the bias for immigration to an old-habitat patch, where
the index i refers to the type of the dispersing individual (w for wild type, m for mutant). When $\pi_i < 0$,
150 individuals of type i are relatively more likely to settle in new-habitat patches than in old-habitat
patches; conversely, their bias is towards old-habitat patches when $\pi_i > 0$. The case $\pi_i = 0$ corresponds
152 to unbiased dispersal. For simplicity, we assume that dispersal is cost-free. While local population
sizes may be affected by dispersal, the global size of the metapopulation remains the same before
154 and after dispersal. Note that our methods can readily be applied to costly dispersal (including to
costs that differ among wild-type and mutant individuals), and also to type- and habitat-dependent
156 emigration probabilities.

The probability that an individual of type i migrates from a patch of any habitat type into a patch
158 of the new-habitat type is

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

where, as defined above, f_{old} is the frequency of old-habitat patches and π_i the dispersal bias into
160 old-habitat patches. The use of an exponential e^{π_i} ensures that the fraction in eq. (1) is positive and
between zero and one. For the ease of notation we will write $\hat{\pi}_i = e^{\pi_i}$.¹²

162 Qualitatively, there are four possible combinations of dispersal biases. We name them according to
the preferences of wild type and then of the mutant (e.g., “Old-New”, wild-type individuals have a bias
164 toward old-habitat patches, and mutant individuals toward new-habitat patches). We add to these
four dispersal schemes the case of unbiased dispersal. Fig. 1 provides an overview of the different
166 schemes, together with the parameter values used in the numerical simulations¹³

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

168 **Old-Old** ($\pi_w > 0, \pi_m > 0$) Both types of individuals have a bias towards old-habitat patches. If we
assume that mutant individuals have a higher fecundity in old-habitat patches than in new-
170 habitat patches (i.e., $\omega_m^{\text{old}} > \omega_m^{\text{new}}$, which is the case in our numerical examples), then this
dispersal scheme correspond to biases towards the habitat where individuals have the highest

¹²(TODO remove hat notation)

¹³(note that all our results depend continuously on the dispersal parameters, so that varying any of the parameters will
not result in a sudden change or discontinuity of the corresponding curves; in other words.).(I am not sure whether this
should be said somewhere, and where – maybe discussion?)

fecundity. This type of dispersal, which can be described as matching habitat choice, has for example been observed with common lizards *Zootoca vivipara* [Bestion et al., 2015], three-spine sticklebacks *Gasterosteus aculeatus* [Bolnick et al., 2009], and barn owls *Tyto alba* [Dreiss et al., 2011].

Population densities being high in the old-habitat patches, this dispersal scheme can also be interpreted as positive density-dependent immigration. For prey species, highly populated locations can be an indication for a safe shelter, or of a place with numerous mating opportunities. This type of positive density-dependent immigration (also called conspecific attraction) is for example found in several amphibians, 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 ($\pi_w > 0, \pi_m < 0$) Wild-type individuals preferentially immigrate into old-habitat patches, while mutants prefer new-habitat patches. This corresponds to immigration to patches where the focal type is fitter than the other type (since $\omega_w^{\text{old}} > \omega_m^{\text{old}}$ and $\omega_m^{\text{new}} > \omega_w^{\text{new}}$). A similar dispersal scheme was recently observed for the ciliates *Tetrahymena thermophila* with a specialist and generalist type [Jacob et al., 2018], and where the specialist disperses to its preferred habitat while the generalist prefers to immigrate to a suboptimal habitat where it outcompetes the specialist.

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

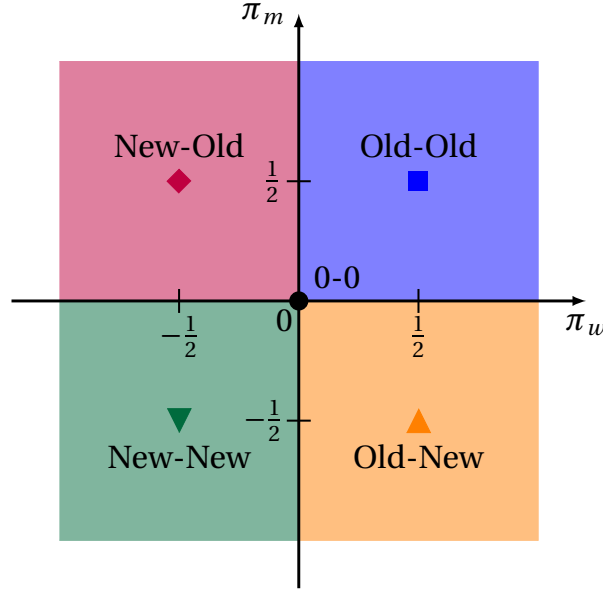


Figure 1: **Parameter sets and legends for the different dispersal schemes.** The colors and markers are the same across all figures. The horizontal axis is the dispersal bias of the wild type, π_w (positive values corresponding to preferential immigration into old-habitat patches), and the vertical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

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

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

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

Analysis steps

We decompose our analysis into several steps of increasing complexity.

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	$0 \leq \omega_m^{\text{old}} < \omega_w^{\text{old}}$	$\omega_w^{\text{old}} = 1.5$, $\omega_m^{\text{old}} = 1.45$ (weak sel.), $\omega_m^{\text{old}} = 1.35$ (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.**

1. We first consider an environment that is constant over time, and heterogeneous over space, with a fraction f_{old} of old-habitat patches and $1 - f_{\text{old}}$ of new-habitat patches. The population is initiated with wild-type individuals at carrying capacity in old-habitat patches, and at the migration-selection equilibrium \hat{N}_w^{new} in new-habitat patches (see Section S1 in the SI for details), and with a single mutant individual, either in an old- or in a new-habitat patch. There are no further mutations ($\theta = 0$), and we compute the probability of establishment of a mutant lineage.
2. We then consider the same environmental setting, but initialize the population with only wild-type individuals. Mutants can appear by mutation during the simulation ($\theta > 0$). We compute the probability of adaptation, i.e. that, during a fixed time interval, a mutant appears by mutation and then establishes.

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

Additional assumptions for the analytical part

We make a few additional assumptions in the analytical part of our work; these assumptions are relaxed in the stochastic simulations.

Our calculations assume that the subpopulations in old-habitat patches are always at carrying capacity, i.e. that there are always enough offspring that are produced to at least replace all the parents. We also consider that mutants are rare compared to wild-type individuals in old-habitat patches. Temporarily ignoring mutations, and denoting by \tilde{N}_i^k the population sizes of type i (mutant or wild-type) in patches with habitat k (old or new) after the dispersal step, the expected number of mutants in an old-habitat patch at the beginning of the next generation is

$$K_{\text{old}} \frac{\omega_m^{\text{old}} \tilde{N}_m^{\text{old}}}{\omega_w^{\text{old}} \tilde{N}_w^{\text{old}} + \omega_m^{\text{old}} \tilde{N}_m^{\text{old}}} \approx K_{\text{old}} \frac{\omega_m^{\text{old}} \tilde{N}_m^{\text{old}}}{\omega_w^{\text{old}} \tilde{N}_w^{\text{old}}} = (1 + a_{\text{old}}) \tilde{N}_m^{\text{old}}. \quad (2) \quad \{\text{eq:sold}\}$$

The approximation comes from the assumption that mutants are rare compared to wild-type individuals in old-habitat patches. Eq. (2) defines the per-capita expected growth rate of mutants in old-habitat patches, a_{old} . The sign of this local growth rate depends on the value of \tilde{N}_w^{old} , the size of the local wild-type population right after dispersal. Mutants are less fecund than wild-type individuals in old-habitat patches ($\omega_m^{\text{old}} < \omega_w^{\text{old}}$), yet the number of mutants can increase in old-habitat patches if \tilde{N}_w^{old} is low enough. In this case indeed, the population is far from carrying capacity, and the offspring of all types of individuals can make it to the next generation. Competition is fiercer as carrying capacity is nearer.¹⁴ The population dynamics of the wild type are analyzed explicitly in Section 1 of the Supplementary Information (SI).

In new-habitat patches, on the contrary, we assume that population size remains much lower than carrying capacity, so that all offspring make it to the next generation (no regulation is necessary after

¹⁴ (I think this is more Results than Model)

reproduction).¹⁵ The expected number of mutants in a new-habitat patch at the beginning of the next generation, given that there are \tilde{N}_m^{new} mutants in the patch right after dispersal, is

$$\omega_m^{\text{new}} \tilde{N}_m^{\text{new}} = (1 + a_{\text{new}}) \tilde{N}_m^{\text{new}}, \quad (3) \quad \{\text{eq: defanew}\}$$

which defines a_{new} , the per-capita growth rate of mutants in new-habitat patches. This assumption constrains the differences in carrying capacities among old- and new-habitat patches under which our analysis remains valid. In particular, K_{new} cannot be too much lower than K_{old} , because in this case, the flow of migrants from old- to new-habitat patches would substantially increase local population sizes in new-habitat patches.

These assumptions are relaxed in our stochastic simulations; population sizes can be lower than carrying capacity in old-habitat patches, and high enough in new-habitat patches for the local dynamics to become density-dependent.

Simulations

The algorithm implements the life cycle described above. We specify here the sampling distributions¹⁶

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

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

¹⁵(I am getting rid of notation r)

¹⁶(please check the wording of this sentence) that we use.

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

(iv) Density regulation: if the number of offspring in a patch is higher than the local carrying capacity (K_k for a patch of habitat-type k (old or new)), patches, we sample K_k individuals uniformly at random without replacement from the offspring population of the patch (hypergeometric sampling). Otherwise, the local population is left unchanged.

We consider that the mutant population has established if its total population size in patches of a given habitat type (old or new) is greater than 60% the total carrying capacity of patches of that type ($(0.6 \times K_{\text{new}} \times M(1 - f_{\text{old}}))$ for new-habitat patches, $(0.6 \times K_{\text{old}} \times M f_{\text{old}})$ for old-habitat patches).¹⁷

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 Gitlab¹⁸.

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 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.

¹⁷(simulation duration in non-rescue scenarios?)

¹⁸https://gitlab.com/pczuppon/evolutionary_rescue_and_dispersal

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. (2)). 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:

$$\begin{array}{cc} & \begin{array}{cc} \text{old patch} & \text{new patch} \end{array} \\ \begin{array}{c} \text{old patch} \\ \text{new patch} \end{array} & \begin{pmatrix} (1 - m_m^{\text{new}})(1 + a_{\text{old}}) & m_m^{\text{new}}(1 + a_{\text{new}}) \\ m_m^{\text{old}}(1 + a_{\text{old}}) & (1 - m_m^{\text{old}})(1 + a_{\text{new}}) \end{pmatrix}, \end{array} \quad (4) \quad \text{\texttt{eq:mean_rep}}$$

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. (2) (see Section S1 in SI for the derivation of a_{old} at the wild-type equilibrium). The other entries are obtained analogously.

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 equations [see Haccou et al., 2005, Chapters 5.3 and 5.6]

$$\begin{aligned} 1 - \varphi_{\text{old}} &= \sum_{j=0}^{\infty} \left(\mathbf{P}(j \text{ offspring in old habitat}) (1 - \varphi_{\text{old}})^j \right. \\ &\quad \left. + \mathbf{P}(j \text{ offspring in new habitat}) (1 - \varphi_{\text{new}})^j \right) \\ &= \exp \left[- \left(1 - m_m^{\text{old} \rightarrow \text{new}} \right) (1 + a_{\text{old}}) \varphi_{\text{old}} - m_m^{\text{old} \rightarrow \text{new}} (1 + a_{\text{new}}) \varphi_{\text{new}} \right], \\ 1 - \varphi_{\text{new}} &= \exp \left[- m_m^{\text{new} \rightarrow \text{old}} (1 + a_{\text{old}}) \varphi_{\text{old}} - \left(1 - m_m^{\text{new} \rightarrow \text{old}} \right) (1 + a_{\text{new}}) \varphi_{\text{new}} \right]. \end{aligned} \quad (5) \quad \text{\texttt{eq:ext_prob}}$$

Intuitively the left hand side, the extinction probability, equals the sum over all possible scenarios of 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 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 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 derivation is presented in the SI, Section S2. We find

$$\begin{aligned}
\varphi_{\text{old}} \approx & \underbrace{a_{\text{old}}}_{(1) \text{ local growth parameter}} + \underbrace{a_{\text{old}} \frac{(1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}})}{\sqrt{C}} (a_{\text{old}} - a_{\text{new}})}_{(2) \text{ effect of the heterogeneous environment}} \\
& + \underbrace{\frac{m}{\sqrt{C}} (a_{\text{new}}(1 - f_{\text{old}}) + a_{\text{old}} \hat{\pi}_m f_{\text{old}} - (a_{\text{old}} - a_{\text{new}})(1 - f_{\text{old}}))}_{(3) \text{ effect of dispersal: new patches + old patches - loss to the other patch type}}, \\
\varphi_{\text{new}} \approx & \underbrace{a_{\text{new}}}_{(1) \text{ local growth parameter}} + \underbrace{a_{\text{new}} \frac{(1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}})}{\sqrt{C}} (a_{\text{new}} - a_{\text{old}})}_{(2) \text{ effect of the heterogeneous environment}} \\
& + \underbrace{\frac{m}{\sqrt{C}} (a_{\text{new}}(1 - f_{\text{old}}) + a_{\text{old}} \hat{\pi}_m f_{\text{old}} - (a_{\text{new}} - a_{\text{old}}) \hat{\pi}_m f_{\text{old}})}_{(3) \text{ effect of dispersal: new patches + old patches - loss to the other patch type}},
\end{aligned} \tag{6}$$

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

$$C = (1 - f_{\text{old}} + \hat{\pi}_m f_{\text{old}}) \left((1 - f_{\text{old}})(a_{\text{new}} - a_{\text{old}} + m)^2 + \hat{\pi}_m f_{\text{old}}(a_{\text{new}} - a_{\text{old}} - m)^2 \right). \tag{7}$$

The first term in the approximation of the establishment probabilities (φ_{old} and φ_{new}) in eq. (6) describes the local growth depending on the habitat type under study. The second term captures the 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. (2). 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).

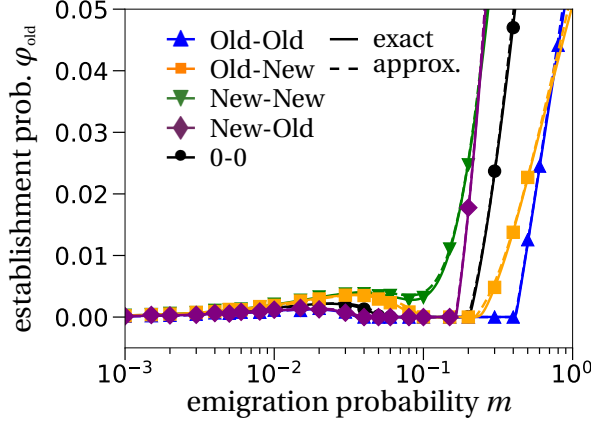
If the emigration probability is zero ($m = 0$), the subpopulations in each habitat evolve in isolation from each other and we recover Haldane's classical result for the establishment probability of a slightly advantageous mutant in new habitats: $\varphi_{\text{new}} = 2a_{\text{new}}$ [Haldane, 1927]. 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 (6) 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

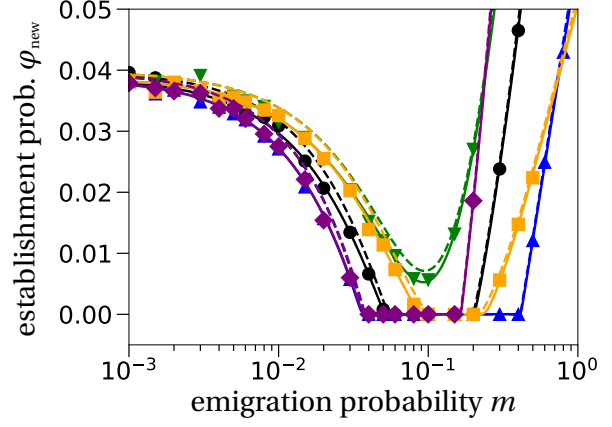
We compare in Fig. 2 our predictions from eqs. (5) and (6) to simulation results for different values of the emigration rate m . We find good agreement with the numerical solution of eq. (5) (solid lines). The approximation given in eq. (6) (dashed lines) deviates slightly from the simulation results 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 probability m is similar for all dispersal schemes. The shape of the curve however strongly depends on the fecundity ω_m^{old} of mutants in the old habitat. Before discussing the differences between the dispersal schemes, we first provide a qualitative understanding of this general behavior.

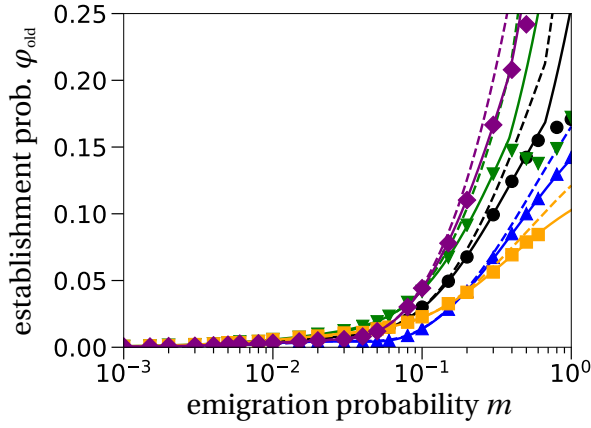
For the probability of establishment of a single mutant in an old-habitat patch (φ_{old}), we observe up to three different regions, cf. Fig. 2(a). This is in line with previous observations in the context of local adaptation [e.g. Kawecki, 1995, Tomasini and Peischl, 2018] and evolutionary rescue [Uecker 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.



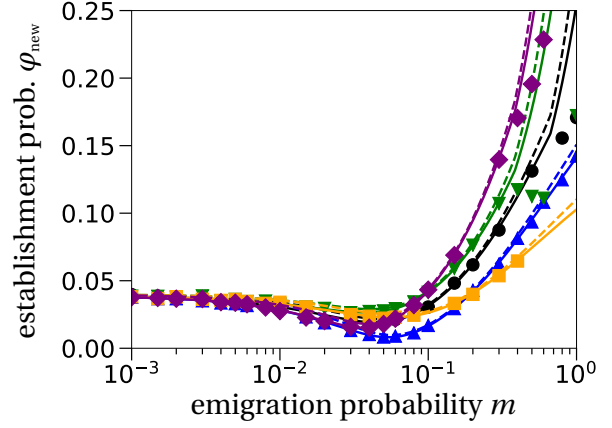
(a) ϕ_{old} with $\omega_m^{\text{old}} = 1.35$ (large fecundity difference)



(b) ϕ_{new} with $\omega_m^{\text{old}} = 1.35$



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



(d) ϕ_{new} with $\omega_m^{\text{old}} = 1.45$

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 $\omega_m^{\text{old}} = 1.35$ in (a), (b) and $\omega_m^{\text{old}} = 1.45$ in (c), (d). Comparison with the results from stochastic simulations (symbols) show very good agreement with our approximation found in eq. (6) (dashed lines). The solid lines are the numerical solution of eq. (5). 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.

366 A detailed assessment and explanation of the regions is provided in the SI, Section S2.1. Briefly,
 367 in region (i), the prevalent effect is the dispersal of mutants from old- to new-habitat patches where
 368 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. (6). 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. (6)), 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^{old} . If ω_m^{old} 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^{old} , 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. (6) 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. (6). This is because the mutant can migrate to old-habitat patches, where it will enjoy relaxed competition.

398 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
 400 unbiased scheme). This is explained by ‘gene swamping’ whereby a to large number of immigrants of
 a less-well adapted type (wild type) inhibits the establishment of a locally better adapted type (mutant)
 402 [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
 404 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
 406 studied.¹⁹

Comparison of dispersal schemes

408 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
 410 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
 412 weighting of new-habitat patches in the third term in eq. (6)); and (2) since the wild type prefers to settle
 in new-habitat patches ($\pi_w < 0$), individuals in old-habitat patches experience relaxed competition
 414 for lower dispersal rates m , thus increasing the local growth rate a_{old} , i.e. region (iii) is shifted to the
 left. An analogous (but reversed) argument explains why a bias towards the old habitat (Old-Old) is
 416 always lower than the unbiased dispersal scheme.

The effect of the asymmetric dispersal scheme Old-New, where each type has a bias to move
 418 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
 420 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
 422 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. (6)) becomes stronger, i.e.

¹⁹(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.)

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 ($a_{\text{old}} > a_{\text{new}}$). 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 .²⁰

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

$$P_{\text{adapt}} = 1 - \exp \left(-\theta t_{\text{fin}} M \left(\underbrace{\varphi_{\text{old}} f_{\text{old}} K_{\text{old}}}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}} (1 - f_{\text{old}}) \hat{N}_w^{\text{new}}}_{\text{new habitat contribution}} \right) \right). \quad (8) \quad \text{\texttt{eq:source_s}}$$

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 old-habitat patches, ω_m^{old} (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. (8)). 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.

²⁰(I think we can get rid of this last sentence. Thoughts?)(Yes.)

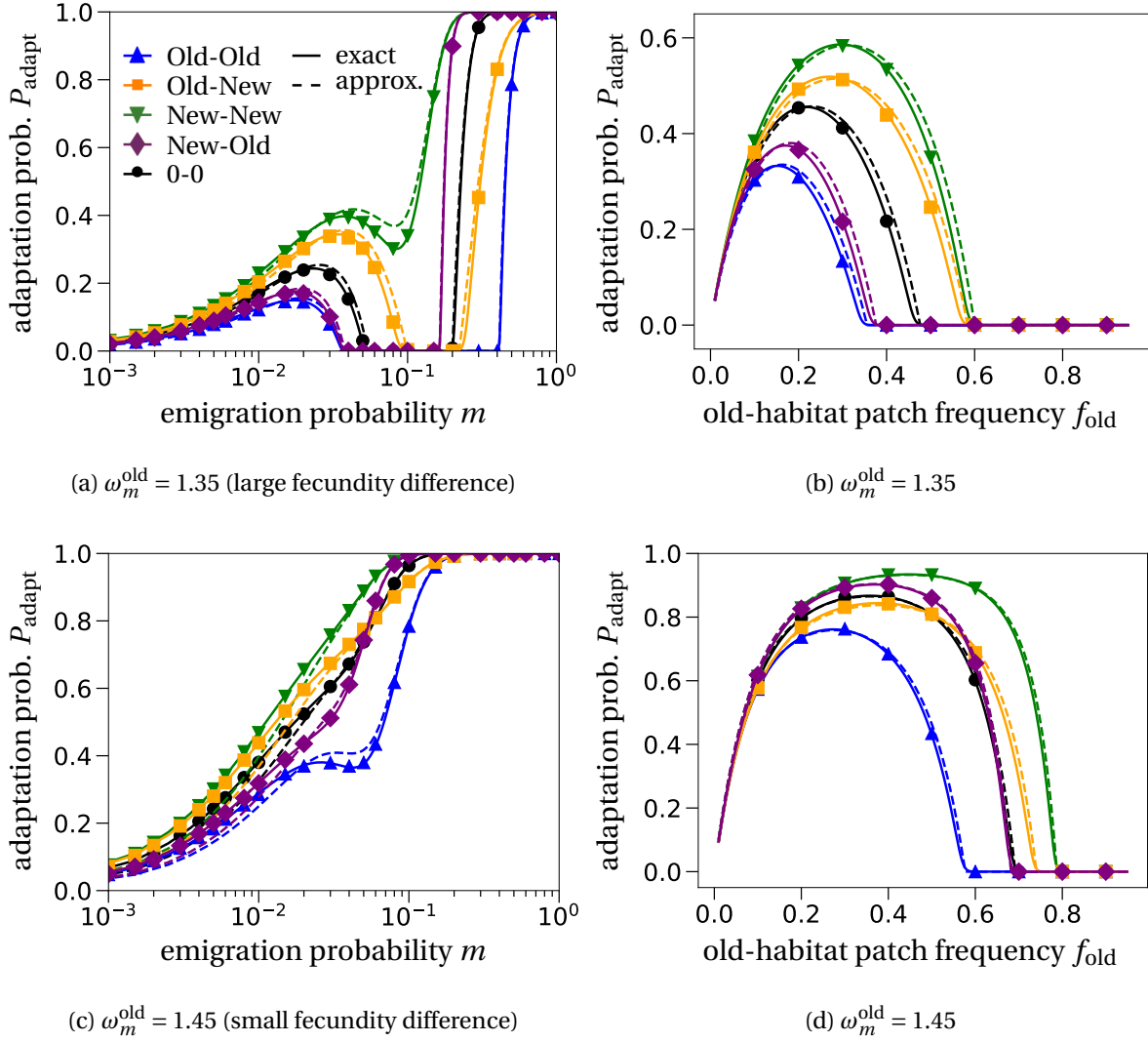


Figure 3: Probability of adaptation in a heterogeneous environment. In (a) and (c), we vary the emigration rate m and observe a similar qualitative behavior as for the establishment probability φ_k in Fig. 2. In (b) and (d), we vary the frequency of old-habitat patches. The maximum is the result of two 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. (8), the exact solution refers to solving the establishment probabilities φ_k from eq. (5) numerically and plugging these solutions into eq. (8). In all panels, the mutation probability is $u = 1/(MK)$ and the final time for a mutant to appear is $t_{\text{fin}} = 100$.

478

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 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

$$\begin{aligned} & \mathbf{P}(\text{successful adaptation from old habitat}) \mathbf{P}(\text{successful adaptation from new habitat}) \\ & \approx (1 - \exp(-\theta t_{\text{fin}} M \varphi_{\text{old}} f_{\text{old}} K)) (1 - \exp(-\theta t_{\text{fin}} M \varphi_{\text{new}} (1 - f_{\text{old}}) \hat{N}_w^{\text{new}})) . \end{aligned} \quad (9) \quad \{\text{eq:origin}\}$$

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.

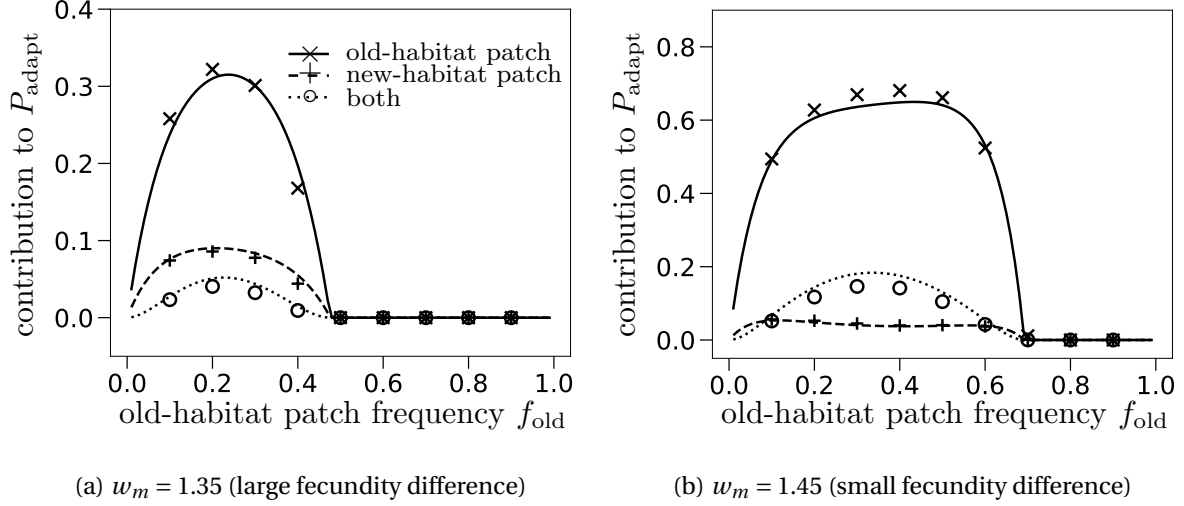


Figure 4: Origin of the adaptive mutant. The origin of the adaptive mutant is strongly affected by the fecundity differences in the old habitat. If the difference is large as illustrated in panel (a), mutants appear more often in old-habitat patches than in new-habitat patches. Still, mutants arising 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. (9) (or the adjusted versions of it) under the unbiased dispersal scheme ($\pi_w = \pi_m = 0$). Note the different scaling on the y-axes.

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. (6) and (8). 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 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

$$P_{\text{rescue}} \approx 1 - \exp \left(-\theta \sum_{i=0}^{M-2} \left(\underbrace{\varphi_{\text{old}}(f_{\text{old}}(i)) \sum_{j=i\tau}^{(i+1)\tau-1} N_w^{\text{old}}(j)}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}}(f_{\text{old}}(i)) \sum_{j=i\tau}^{(i+1)\tau-1} N_w^{\text{new}}(j)}_{\text{new habitat contribution}} \right) \right. \\ \left. - \underbrace{\theta \varphi_{\text{new}}(0) \sum_{j=\tau(M-1)}^{\infty} N_w^{\text{new}}(j)}_{\text{contribution after the last patch deteriorated}} \right), \quad (10) \quad \text{\texttt{eq:evol_res}}$$

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 $N_w^k(j)$ denotes the overall number of wild-type individuals living in habitat k (old or new) in generation j (see SI, Section S1 for an approximation). The interpretation of this equation is the same as for eq. (8). 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 changes are accounted for by the sums that iterate through the (discrete) time steps and by the time dependence of the corresponding quantities. We further note that we follow the expected value of the wild-type population size deterministically over time, instead of assuming it to be already in its steady state as in eq. (8) (see also Section S1 in the SI).

As visible in Fig. 5, the approximation explains the order of dispersal schemes. Yet, it does not accurately predict the simulated data. This discrepancy can be explained: in the formula we assume that

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 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 emerge just before a deterioration event. These mutants are more likely to establish during the subsequent environmental configuration giving them a higher probability of survival than approximated by 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 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 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 mutant in old-habitat patches ($\omega_m^{\text{old}} = 0$).

The different dispersal schemes exhibit substantial differences. The dispersal schemes affect the dispersal pattern of both types and as such alter their respective population dynamics. Both small and large fecundity differences in the old habitat, $\omega_m^{\text{old}} = 1.45$ and $\omega_m^{\text{old}} = 1.35$, conserve the ranking of dispersal schemes obtained for the probabilities of establishment and adaptation²¹: New-New (green) is higher than unbiased dispersal (black) which is higher than Old-Old (blue), with Old-New decreasing 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 ($\omega_m^{\text{old}} = 1.1$ and $\omega_m^{\text{old}} = 0$), 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

²¹(difficult to follow) (We could also get rid of the explicit description of the figure and remove the following sentence)

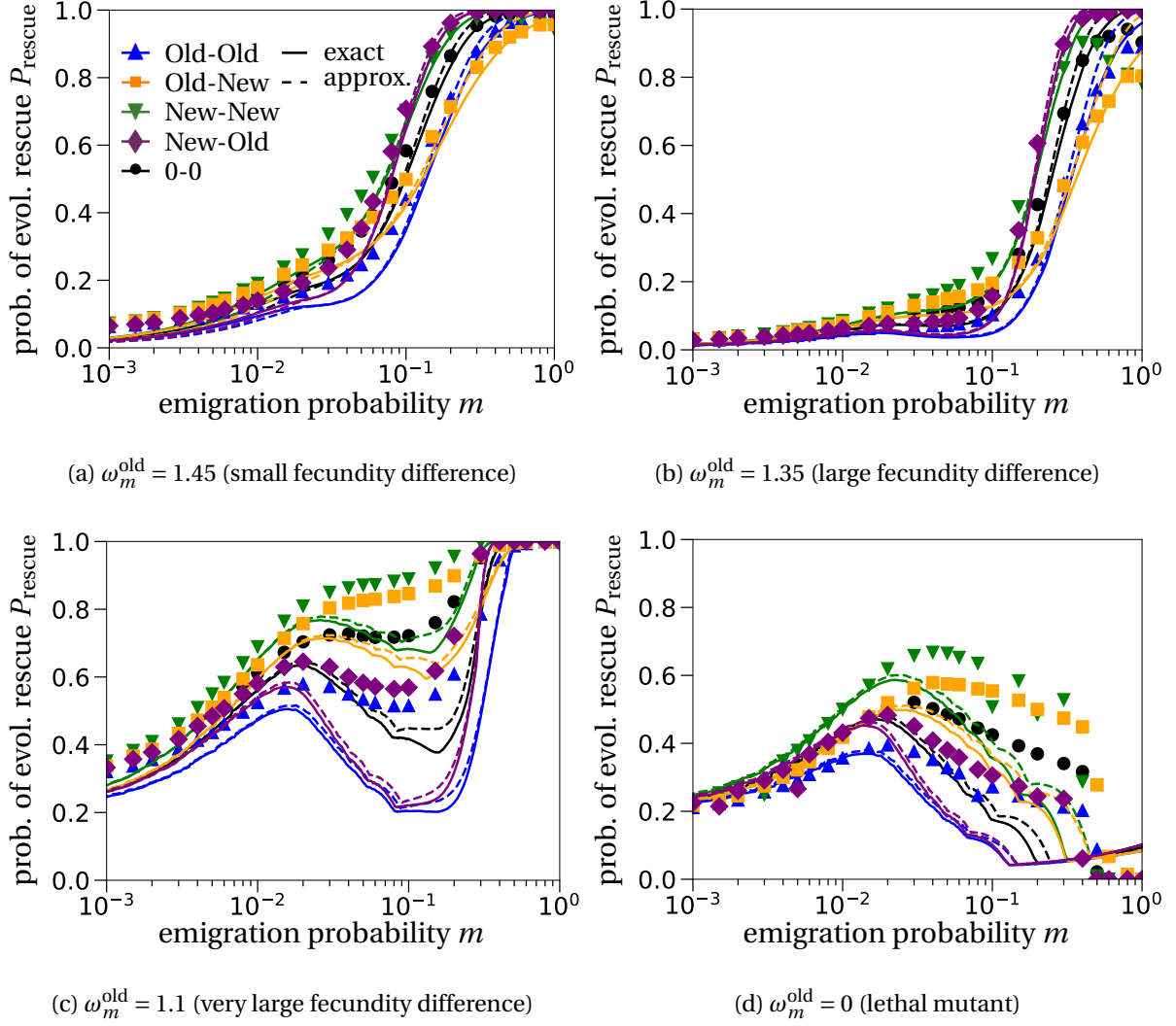


Figure 5: The probability of evolutionary rescue compared to simulation results. Our predictions, computed with eq. (10), match the qualitative behavior of the simulated data for the probability of evolutionary rescue. All rankings of the dispersal schemes align well. Quantitatively though, we find that 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. (5) which is then plugged into the approximation of the probability of evolutionary rescue in eq. (10).

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.

574 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, 576 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 578 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 580 mixing (dispersal to old patches).²²

Habitat of origin of the rescue mutant and standing genetic variation

582 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). 584 However, a low mutant fecundity ω_m^{old} 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 586 ω_m^{old} 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 588 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 590 and Pennings, 2017, Wilson et al., 2017a].

So far, we have considered settings where evolutionary rescue is exclusively due to de novo 592 mutations. To explore the role of standing genetic variation²³, we ran simulations where we let the system evolve for 1,000 generations before the first degradation event happened. Fig. 6(b) shows 594 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 596 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 598 positive, compare to Fig. 3(b,d) and Fig. SX in the SI. Decreasing the value of τ reduces the time

²²(This discussion is still difficult.)

²³(or variance? is there a difference? why use one over the other?)

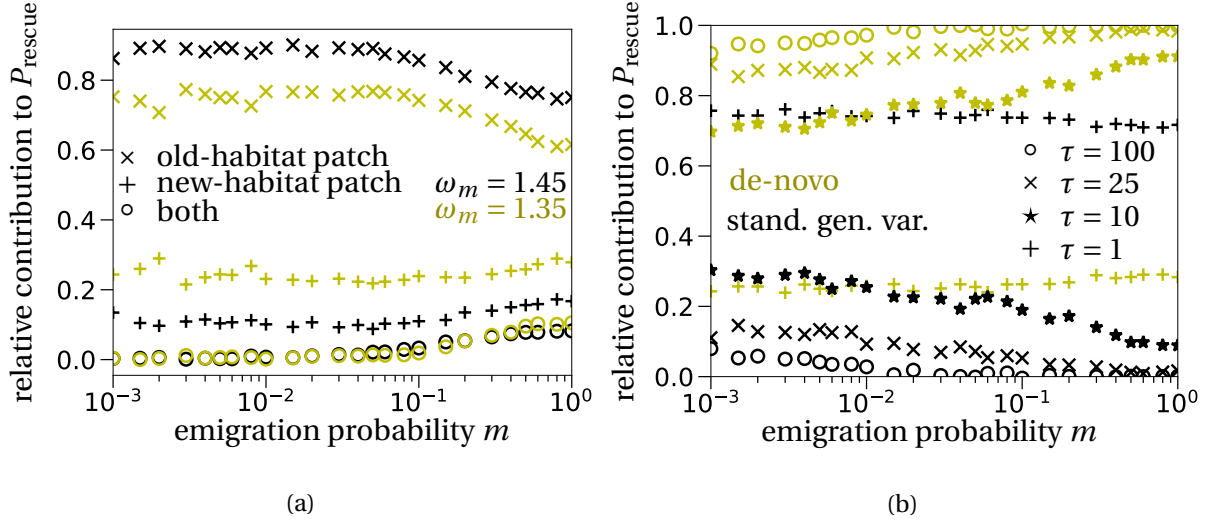


Figure 6: Habitat of origin of the rescue mutation and the impact of standing genetic variation. (a) We compare the source of successful mutations under small (black) and large (yellow) fecundity differences in the old habitat. Decreasing the fecundity of the mutant results in more successful mutations 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 $\omega_m^{\text{old}} = 1.45$. The relative contribution is then determined by $(P_{\text{rescue with sgv}} - P_{\text{rescue only de novo}}) / P_{\text{rescue with sgv}}$.

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 increases for smaller values of τ .

Additionally, the relative contribution of standing genetic variation declines as the emigration rate m increases. This holds because the mutant is almost exclusively found in old-habitat patches if the 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

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 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, 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 range of these regions.²⁴

Dispersal and adaptation

Theoretical studies that investigated the effects of spatial subdivision on the adaptation of a population in a heterogeneous environment can be classified into two types. One type of models, classically 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 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 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 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, 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.)²⁵.

The second type of models explicitly takes into account demographic effects due to dispersal,

²⁴(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.")

²⁵(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)

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^{old} , 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^{old} (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).²⁶

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 and 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.)

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

²⁶(I was confused by this paragraph so rephrased to make it more uniform and better describe the figures and the key differences)

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.²⁷

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**

²⁷ (This paragraph could be dropped in line with a comment of a reviewer.) (agree to drop it)

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. (4)). 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. (6) 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 poor²⁸ approximation in the context of evolutionary rescue (Fig. 5)²⁹. Additionally, in order to obtain analytical solutions, it 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].

²⁸(any better word here?)

²⁹(I would remove this sentence)

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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