The effect of habitat choice on evolutionary rescue in subdivided populations

Peter Czuppon[1,2,*], François Blanquart[1,3], Hildegard Uecker[4,†],

Florence Débarre[2,†]

[1] Center for Interdisciplinary Research in Biology, CNRS, Collège de France, PSL Research University, Paris, France.

[2] Institute of Ecology and Environmental Sciences of Paris, Sorbonne Université, UPEC, CNRS, IRD, INRA, Paris, France.

[3] IAME, UMR 1137, INSERM, Université Paris Diderot, Paris, France.

[4] Research Group "Stochastic evolutionary dynamics", Department of Evolutionary Theory, Max-Planck Institute for Evolutionary Biology, Plön, Germany.

[*] Corresponding author; e-mail: peter.czuppon@college-de-france.fr.

[†] Equal contribution.

The authors wish to be identified to the reviewers (the manuscript is already on bioRxiv so the identities of all authors can be easily found).

Manuscript elements: Figures 1-6, Table 1, Supplementary Information including figures S1-S6. All figures are to print in color.

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

Manuscript type: Article.

Abstract

(will do this in the very end) **Abstract** Evolutionary rescue is the process by which a declining population successfully adapts genetically[1] 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 dispersal[3]: (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 choice[5], 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

20 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

22 go extinct (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.,

24 2013). The process of 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)

26 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

28 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.,

30 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

32 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;

34 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

36 is lacking] Rescue can occur through plasticity (refs Chevin? [6]) or genetic adaptation (refs). The traits involves can be continuous (ref) or discrete (ref). In this work, we consider genetic adaptation mediated

38 by a discrete trait.)

In mathematical models, evolutionary rescue is often studied in a spatially homogeneous situation

40 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

42 and Hermisson, 2016) and horizontal gene transfer (Tazzyman and Bonhoeffer, 2014), reproduction

---

[6]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

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)[7]. 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,

---

[7](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...)

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) for both effects).

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 investigations 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 dispersal schemes observed in nature (Clobert et al., 2009; Edelaar and Bolnick, 2012; Edelaar et al., 2008).

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 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 nature and has been reported in many species across the tree of life, including insects (Endriss et al., 2019), spiders (De Meester and Bonte, 2010), amphibians (Gautier et al., 2006), birds (Wilson et al., 2017*b*), fishes (Turgeon and Kramer, 2012), and mammals (Støen et al., 2006).

Another well-established dispersal scheme is a type of habitat choice whereby individuals tend to immigrate into habitats 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), worms (Mathieu et al., 2010), and ciliates (Jacob et al., 2018, 2017).

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

We model an environment that consists of various patches with one of two possible habitats: the 'old' habitat, in which both types, wild type and mutant, have a positive growth rate, and the 'new' habitat,

5

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 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 but spatially heterogeneous environment with two ('old' and 'new') patch types. In this setting, we first study the probability of establishment of a single mutant, assuming there are no further mutations between types. We then relax the assumption of no further mutations, and compute a probability of adaptation, i.e. of establishment of the mutant lineage[8]. Finally, we let habitat degradation proceed, assuming that patches, one after another, deteriorate over time until all locations contain the new habitat. Using the previous results, we approximate a probability of evolutionary rescue, i.e. that a 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 rescue.

Model and methods

Main assumptions and life-cycle

We consider a spatially structured environment consisting of M patches all connected to each other. The habitat of a patch is either in the *old* or in the *new* state, corresponding to habitat quality before and after environmental deterioration, respectively. One after another every τ generations, the habitat of a patch deteriorates, from 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 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 setting corresponds to the one analyzed by Uecker et al. (2014), and more recently by Tomasini and

---

[8](not sure about this defn, please check)

Peischl (2019) in the special case of just two patches[9]. The maximum numbers of individuals that can live in a patch of a given habitat type, i.e. the carrying capacities, are denoted K_{old} and K_{new} for old- and new-habitat patches respectively; K_{old} and K_{new} may differ.

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

(i) Dispersal: individuals may move between patches. Further details about this step are given below.

(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 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 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 that wild-type and mutant populations are viable in old-habitat patches[10], 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, 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.

(iii) Mutation: wild-type offspring mutate to the rescue mutant type with probability θ (back mutations from the mutant to the wild type are neglected).

(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: 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 wild-type and mutant individuals are competitively equivalent. If the number of offspring is below the

---

[9] (what about carrying capacities in these papers?)

[10] (this won't be the case in fig 5d)

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

7

¹⁴⁰ carrying capacity, the regulation step is ignored. We call "successful offspring" offspring that survive the density regulation step, and become adults at the next generation. At the end of this step, all ¹⁴² offspring become adults, and a new cycle then begins.

Dispersal mechanisms

¹⁴⁴ 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 affect ¹⁴⁶ 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 $\pi_i < 0$, individuals of ¹⁴⁸ 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 to unbiased dispersal. ¹⁵⁰ For simplicity, we assume that dispersal is cost-free. While local population sizes may be affected by dispersal, the global size of the metapopulation remains the same before and after dispersal. Note that ¹⁵² 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 emigration probabilities.

¹⁵⁴ The probability that a dispersing individual of type i settles in a patch of the new-habitat type is

$$\mu_i^{\text{new}} = \frac{1 - f_{\text{old}}}{1 - f_{\text{old}} + e^{\pi_i} f_{\text{old}}} = 1 - \mu_i^{\text{old}}, \tag{1} \quad \texttt{\{eq:dispersa}}$$

where, as defined above, f_{old} is the frequency of old-habitat patches and π_i the dispersal bias into old-¹⁵⁶ habitat patches. The use of an exponential e^{π_i} ensures that the fraction in eq. (1) is positive and between zero and one.

¹⁵⁸ 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 ¹⁶⁰ 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 schemes, ¹⁶² together with the parameter values used in the numerical simulations [12]

---

[12](note that all our results depend continuously on the dispersal parameters, so that varying any of the parameters will not

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

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-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 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

---

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?)

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., 2017*b*).

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.

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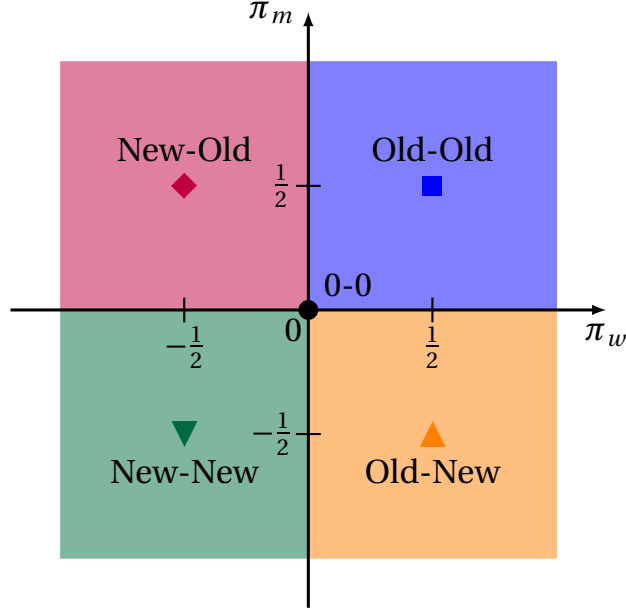
Figure 1: **Parameter sets and legends for the different dispersal schemes.** The colors and markers are the same across all figures. The horizontal axis is the dispersal bias of the wild type, π_w (positive values corresponding to preferential immigration into old-habitat patches), and the vertical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

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 evolutionary rescue*, i.e. that a mutant appears by mutation and establishes before the population goes extinct.

11

Notation	Interpretation	Range	Default value
K_k	Carrying capacity in a patch of type k	–	$K_{\text{old}} = 1000$, $K_{\text{new}} = 500$
ω_w^{old}	Fecundity of wild-type individuals in old-habitat patches	$1 < \omega_w^{\text{old}}$	1.5
ω_m^{old}	Fecundity of mutant individuals in old-habitat patches	$0 \leq \omega_m^{\text{old}} < \omega_w^{\text{old}}$	1.45 or 1.35
ω_w^{new}	Fecundity of wild-type individuals in new-habitat patches	$0 \leq \omega_w^{\text{new}} < 1$	0.75
ω_m^{new}	Fecundity of mutant individuals in new-habitat patches	$1 < \omega_m^{\text{new}}$	1.02
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
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
a_{old}	Growth rate of the mutant in the old habitat	$-1 \leq a_{\text{old}}$	eq. (2)
$\widehat{N}_i^k$	Number of type i individuals in type k habitat patches at stationarity	$0 \leq \widehat{N}_i^k \leq K_i$	eq. (A3)
$\widetilde{N}_i^k$	Number of type i individuals in type k habitat patches after dispersal	$0 \leq \widetilde{N}_i^k$	eq. (A4)

Table 1: **Model parameters and variables.**

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.

A key assumption to our mathematical analysis is that the mutant individuals are rare enough that their dynamics do not affect the wild-type population, at least during the establishment phase of the mutant lineage. Because of their rarity, we can also consider that all mutants reproduce, disperse and die independently of each other. The wild-type population sets a demographic context that affects mutants dynamics. The mathematical analysis therefore focuses on the population dynamics of the mutant

²²⁸ population, considering the wild-type population as constant over time.[13]

We 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. Denoting by $\widetilde{N}_i^k$ the number of type-i individuals in a k-habitat patch right after dispersal, then the expected number of successful offspring of mutant individuals in this old-habitat patch (i.e., of offspring that survive density regulation and become adults in the next generation) is

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

The approximation results 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}. It depends on $\widetilde{N}_w^{\text{old}}$, the size of the local wild-type population right after dispersal, which is calculated in Section A of the Supplementary Information (SI) (Eq. (A4a)). (I suggest adding plots of a_{old} in the SI, with the same parameters and axes as in the other figures of the main text)

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 reproduction).[14] The expected number of successful offspring of mutant individuals in a new-habitat patch, given that there are $\widetilde{N}_m^{\text{new}}$ mutants in the patch right after dispersal, is

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

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.

We finally combine the different steps of the life cycle. The expected per capita numbers of successful offspring (i.e., offspring that become adults at the next generation) in habitat k' of an individual in a

---

[13](please check this is correct)

[14](I am getting rid of notation r)

k-habitat patch at the beginning of the generation, $\lambda_{k,k'}$, are the following:

$$\lambda_{\text{old,old}} = \left(1 - m\mu_m^{\text{new}}\right)(1 + a_{\text{old}}), \quad \lambda_{\text{old,new}} = m\mu_m^{\text{new}}(1 + a_{\text{new}}),$$
$$\lambda_{\text{new,old}} = m\mu_m^{\text{old}}(1 + a_{\text{old}}), \qquad \lambda_{\text{new,new}} = \left(1 - m\mu_m^{\text{old}}\right)(1 + a_{\text{new}}). \tag{4} \quad \texttt{\{eq:lambda\}}$$

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

All of these assumptions, made for the sake of mathematical analysis, are relaxed in our stochastic simulations.

Simulations

The simulation algorithm implements the life cycle described above. We specify here the sampling distributions[15] that we use.

(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.

---

[15](please check the wording of this sentence)

14

(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.

(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). [16]

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 Gitlab[17].

Results

We proceed step-wise towards the computation of a probability of evolutionary rescue. For each step, we first present a mathematical analysis, for then compare our results to the output of simulations that relax the assumptions made for mathematical purposes.

---

[16] (simulation duration in non-rescue scenarios?)

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

Establishment probability in a heterogeneous environment

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

Mathematical analysis

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

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

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

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

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

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

$$1 - \varphi_{\text{old}} = \exp\left[-\left(1 - m\mu_m^{\text{new}}\right)(1 + a_{\text{old}})\varphi_{\text{old}} - m\mu_m^{\text{new}}(1 + a_{\text{new}})\varphi_{\text{new}} \right]. \tag{7a}$$

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

The establishment probabilities φ_{old} and φ_{new} are then given by the unique positive solution of system (7) (see Haccou et al., 2005, Chapters 5.3 and 5.6). This system of equations can be solved numerically. An

16

analytical approximate solution is available in the case of 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); 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 B. We find

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

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

with

$$
C = (1 - f_{\text{old}} + e^{\pi_m} f_{\text{old}}) \left((1 - f_{\text{old}})(a_{\text{new}} - a_{\text{old}} + m)^2 + e^{\pi_m} f_{\text{old}}(a_{\text{new}} - a_{\text{old}} - m)^2 \right).
\tag{8c}
$$
{eq:normaliz

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

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

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

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

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

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 recover the approximation found in Tomasini and Peischl (2018) (compare system (8) to their eqs. (4) and (5)). Note that the approximation is independent of the actual number of patches (two patches in total in Tomasini and

17

326 Peischl (2018) [18]), but only depends on the environmental configuration determined by the frequency of old-habitat patches f_{old}.

Comparison to simulations and qualitative behavior

328 Our mathematical analysis provided two kinds of results for the establishment probability: an implicit 330 solution in eq.(7), which we solve numerically, and an explicit but approximate solution in eq.(8). In Fig. 2, we compare these solutions to simulation results for different values of the emigration rate m. We find 332 good agreement with the numerical solution of eq. (7) (solid lines). The approximation given in eq. (8) (dashed lines) deviates slightly from the simulation results in regions where m, a_{new} and a_{old} are not small, 334 i.e. when the assumptions made in the analytical derivation do not hold anymore.

We identify up to three different regions that define how the probability of establishment of a single 336 mutant initially in an old-habitat patch (φ_{old}) changes with the emigration probability m (Fig. 2a). This is in line with previous observations in the context of local adaptation (e.g. Kawecki, 1995; Tomasini and 338 Peischl, 2018) and evolutionary rescue (Uecker et al., 2014). We define the regions as follows: (i) at low dispersal rates m, an initial increase of the establishment probability with m ; (ii) a local maximum with a 340 subsequent decrease of the establishment probability; (iii) at high dispersal rates m, an increase of the establishment probability with m.

342 A detailed assessment and explanation of the regions is provided in the Appendix, Section B.3[19]. In region (i), the beneficial effect of dispersal on the establishment probability φ_{old} is due to mutants 344 dispersing from old- to new-habitat patches where they are fitter than the wild type. While this effect is still present in region (ii), the establishment probability φ_{old} now decreases with dispersal because 346 back-dispersal into the old-habitat patches becomes more prevalent. More precisely, the expected per capita number of successful offspring in the new habitat of an adult in a new-habitat patch is $\lambda_{\text{new, new}} =$ 348 $(1 - m\mu_m^{\text{old}})(1 + a_{\text{new}})$. This product can, for large emigration probabilities m, be smaller than 1, i.e. a mutant in a new-habitat patch has on average less than one offspring. This is detrimental to the mutant

---

[18](please check if this is correct)

[19](reconsider whether to include)

18
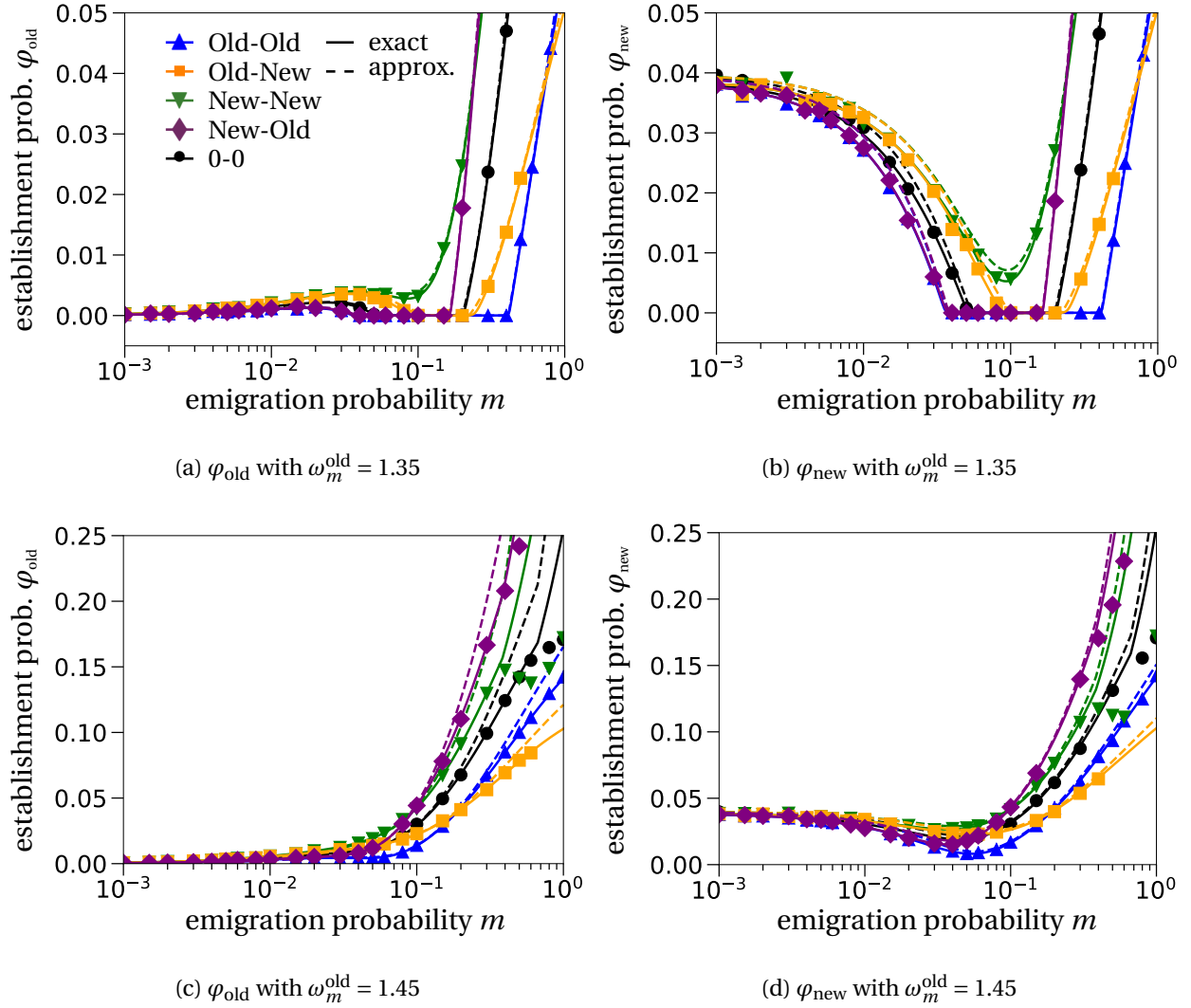
Figure 2: **Establishment probability as a function of the emigration rate.** Panels (a) and (c) show the establishment probabilities when the first mutant arises in an old-habitat patch (φ_{old}), and panels (b) and (d) the establishment probabilities when the mutant arises in a new-habitat patch (φ_{new}), for mutant fecundity in old-habitat patches $\omega_m^{\mathrm{old}} = 1.35$ in (a), (b) and $\omega_m^{\mathrm{old}} = 1.45$ in (c), (d). Markers: simulations; full lines: numerical solution of eq. (7); dashed lines, approximate solution shown eq. (8). The colors and marker shapes correspond to the different dispersal schemes, with the same parameters as in Fig.1.

350 because it means mutants do not efficiently reproduce in the habitat where they are fitter. Finally, in region (iii) at high dispersal, some many wild-type individuals leave old-habitat patches that competitive pressure

19

in old-habitat patches is substantially decreases. The post-dispersal size of the wild-type population $\widetilde{N}_w^{\text{old}}$ is then low enough that the local growth rate of the mutant in these patches, a_{old} (first term in eq. (8)), becomes positive[20]. 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 of the mutant in the old habitat, ω_m^{old}. The larger it is, the 'earlier' (i.e. for smaller emigration rates m) relaxed competition becomes relevant (compare panels 2a to 2c), to a point that region (ii) vanishes (panel 2c) and there is no decrease of φ_{old} with m any longer. In contrast, for lower mutant fecundity values ω_m^{old}, region (iii) might vanish (see Fig. S2 in SI), because the mutant's fecundity in old-habitat patches is too low compared to the wild type's.

The qualitative behavior of the establishment probability of a mutant emerging in the new habitat, φ_{new}, can be interpreted in a similar way (panels 2b, 2d). The establishment probability φ_{new} decreases with the emigration probability m at low m, because the mutant appeared in a new-habitat patch, where it fares better than the wild type, so there is no initial benefit due to dispersal. When the emigration probability is higher, however, mutants can back emigrate to new-habitat patches, while those that land in old-habitat patches can enjoy relaxed competition when m is high. This is why φ_{new} increases with m at higher m.

An additional effect can take place at high dispersal and reduce mutant establishment probabilities, in particular when the wild type is biased toward new-habitat patches (see for instance the New-New scheme in Figs. 2c, 2d). The high dispersal of wild types individuals into new-habitat patches can lead to 'gene swamping', inhibiting the establishment of a locally better adapted type (mutant) (Lenormand, 2002; Nagylaki, 1978). Note that the lower carrying capacity in new-habitat patches than in old-habitat patches ($K_{\text{new}} < K_{\text{old}}$) creates a favorable setting to gene swamping. A proper analysis of the gene swamping regime is beyond the scope of this manuscript, but see for instance Tomasini and Peischl (2018) and Section S5(I don't understand why S5 is about swamping) in the SI where such a situation is studied.[21]

---

[20](add ref to figures of aold as function of m)

[21](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.)

Comparison of dispersal schemes

We now compare the establishment probabilities across the different dispersal schemes. We consistently observe that a bias towards the new habitat (New-New in Fig. 2) enhances mutant establishment compared to the unbiased dispersal scheme (0-0). This can be attributed to two reasons. First, the mutant is more likely to disperse to the new habitat where it outcompetes the wild type. Secondly, competition in old-habitat patches is relaxed starting at low emigration probabilities m because the wild type preferentially disperses to new-habitat patches. Conversely, a bias towards the old habitat (Old-Old) lowers mutant establishment probabilities compared to the unbiased dispersal scheme.

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

Probability of adaptation in a heterogeneous environment

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

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

$$P_{\text{adapt}} = 1 - \exp\left(-\theta\, t_{\text{fin}} M \left(\underbrace{\varphi_{\text{old}} f_{\text{old}} K_{\text{old}}}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}}(1 - f_{\text{old}}) \widehat{N}_w^{\text{new}}}_{\text{new habitat contribution}} \right)\right). \qquad (10) \quad \texttt{\{eq:source\_s}}$$

This is one minus the probability that zero mutant establishes within the $[0, t_{\text{fin}}]$ time interval, given by the probability of zero successes of a Poisson distribution. The rate of this Poisson distribution is the expected number of successfully emerging mutant lineages until time t_{fin}. Mutants arise with probability θ; $M f_{\text{old}} K_{\text{old}}$ is the total number of wild-type individuals in old-habitat patches, $M(1 - f_{\text{old}}) \widehat{N}_w^{\text{new}}$ the total number of wild-type individuals in new-habitat patches. A mutant arising in a k-habitat patch has a probability φ_k of establishing in the population; we assume that mutants establish independently of one another. Assuming a Poisson distribution for the number of successful mutant lineages is an approximation of a Binomial distribution with large sample size (the wild-type population size) and small success probability (the establishment probabilities φ_k). Note also that for t_{fin} tending to infinity, there will almost surely be a successful mutant, so that $P_{\text{adapt}} = 1$.

The probability of adaptation P_{adapt} calculated with eq. 10 is compared to simulation results in Fig. 3. In spite of our approximations, the fit to simulation results is still very good. As P_{adapt} includes the probabilities of establishment φ_k, here again, the shapes of the curves as function of the emigration probability m depend on the fecundity of the mutant in old-habitat patches, ω_m^{old} (Figs. 3a, 3c). Likewise, the rankings of the different dispersal schemes are comparable to the ones observed for the establishment probability. The small differences in the ranking of the dispersal schemes between panels 2c and 3c can be explained by the mutational input. Larger stationary populations sizes of the wild type in new habitats, $\widehat{N}_w^{\text{new}}$ 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 (It does not make intuitive sense why $\widehat{N}_w^{\text{new}}$ is higher with WT biased towards old... maybe then figures with $\widehat{N}_w^{\text{old}}$ and $\widehat{N}_w^{\text{new}}$ would help).

Panels 3b and 3d show the probability of adaptation as a function of the frequency of old-habitat patches f_{old}. The maximum of P_{adapt} at intermediate f_{old} is the result of two antagonistic effects: (1) the likelihood for a mutation to appear increases with the number of wild-type individuals present in

22

the system, which is highest for high frequencies of old-habitat patches f_{old}, and (2) the probability of establishment of a mutant decreases with the number of old-habitat patches.

The different dispersal schemes alter both effects. The probability of adaptation is highest when there is a general bias towards the new habitat (New-New), due to a combination of high establishment probabilities (Fig. 2) and high local population sizes thanks to the bias (ref to figure of Nhatnew?). Conversely, a general preference for old-habitat patches (Old-Old) yields lower probabilities of adaptation.
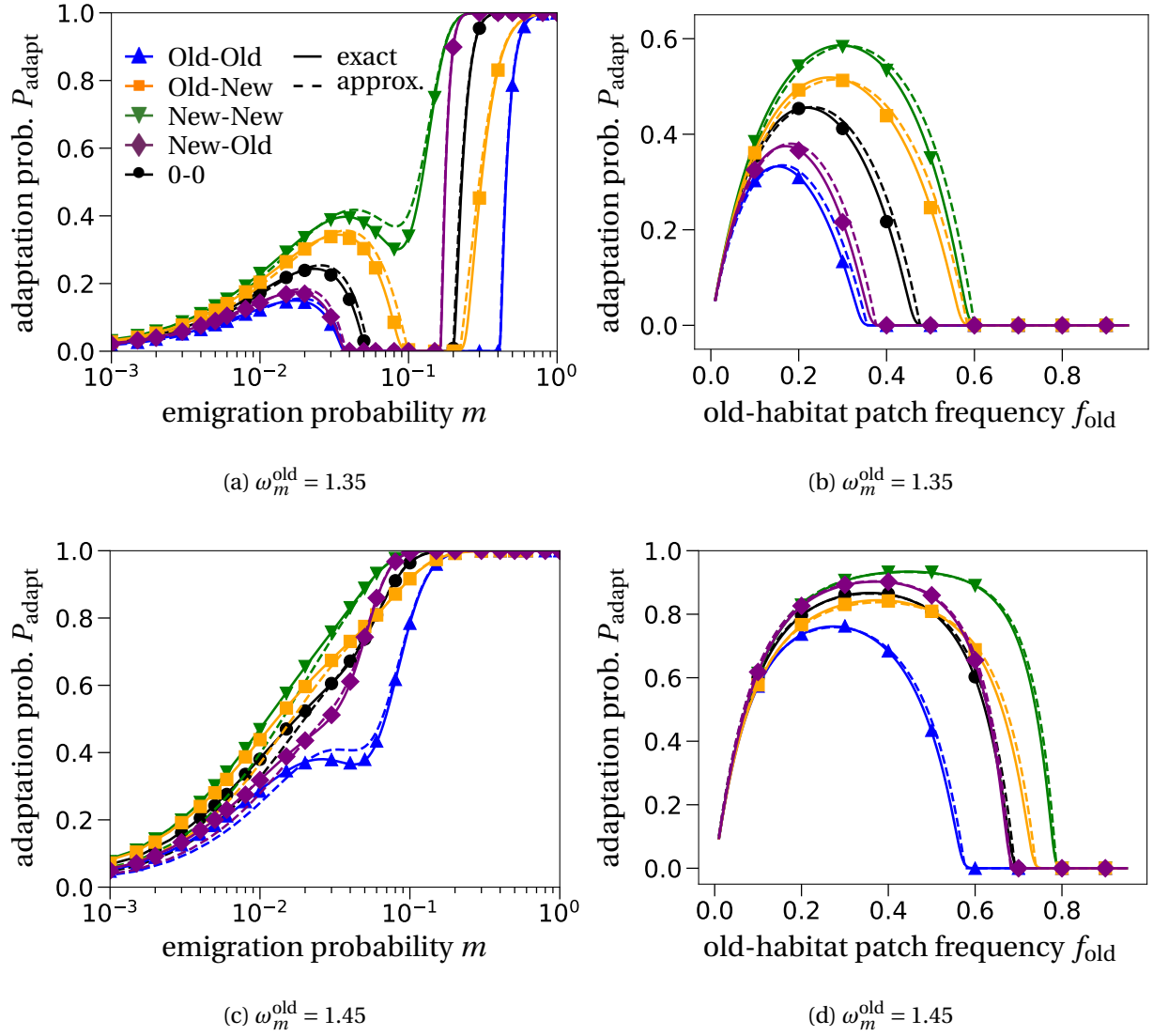
Figure 3: **Probability of adaptation in a heterogeneous environment.** In (a) and (c), we vary the emigration rate m and observe a similar qualitative behavior as for the establishment probability φ_k in Fig. 2. In (b) and (d), we vary the frequency of old-habitat patches. The maximum is the result 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. (10), the exact solution refers to solving the establishment probabilities φ_k from eq. (7) numerically and plugging these solutions into eq. (10). In all panels, the mutation probability is $u = 1/(MK)$ and the final time for a mutant to appear is $t_{\text{fin}} = 100$.

Habitat of origin of the adaptive mutation

432 We now ask in which habitat mutations leading to successful establishment appear. To do so, we distinguish in the simulations between mutants that appear in old-habitat patches and mutants that appear in

434 new-habitat patches, and identify the habitat of origin of the mutation by considering the composition of the mutant population after establishment. We however do not distinguish between separate mutations

436 that appear in the same type of habitat, meaning that we cannot rule out the presence of multiple lineages if they all appeared in the same type of patch: there may be soft selective sweeps (see Hermisson and

438 Pennings, 2017, for a review). Only if the established mutant population contains mutants appeared in both old- and new-habitat patches can we be sure that multiple lineages contributed.

440 Analytically, we approximate the probability to observe a mutant population that can be traced back to a mutant from an old-habitat patch by

$$\mathbb{P}\big(\text{successful adaptation from old habitat}\big)\ \big(1 - \mathbb{P}\big(\text{successful adaptation from new habitat}\big)\big)$$
$$\approx \big(1 - \exp\big(-\theta\, t_{\text{fin}} M \varphi_{\text{old}} f_{\text{old}} K\big)\big) \big(\exp\big(-\theta\, t_{\text{fin}} M \varphi_{\text{new}} (1 - f_{\text{old}}) \widehat{N}_w^{\text{new}}\big)\big).$$

(11) {eq:origin}

442 The corresponding probabilities for the other two scenarios can be computed analogously. The approximation uses our key assumption that different mutant individuals and their offspring do not

444 affect each others dynamics (branching process). In the simulations, we label a run as having established lineages originated from different habitat types ("both" in Fig. 4) if these lineages are still alive after 1000

446 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.

448 We compare our calculations to simulation results in Fig. 4, varying the frequency of old-habitat patches f_{old}. Most successful mutations arise in old-habitat patches. The contributions of old- vs. new-

450 habitat patches depend on the product $\varphi_k \widehat{N}_w^k f_k$, which we decompose in Fig. S3. Even though the establishment probability from old-habitat patches is lower ($\varphi_{\text{old}} < \varphi_{\text{new}}$), the total population size of

452 the wild type in the old-habitat patches is larger than that in new-habitat patches, so that more mutants appear in old-habitat patches than in new-habitat patches, which compensate their lower establishment
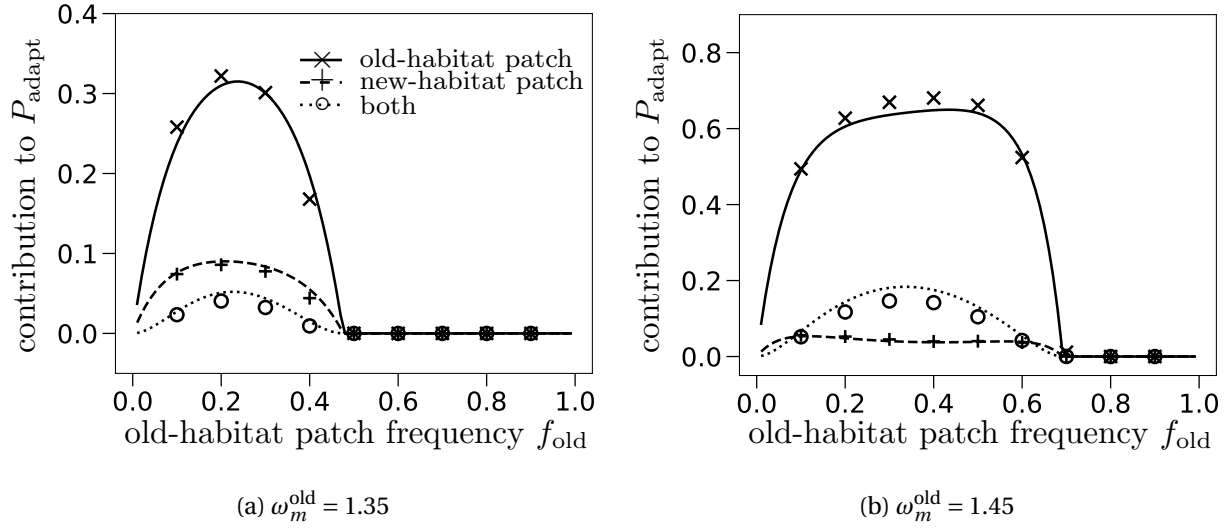
454 probability.

25

Figure 4: **Origin of the adaptive mutant,** depending on mutant fecundity in old-habitat patches ω_m^{old} (recall that $\omega_w^{\mathrm{old}} = 1.5$). The points correspond to simulations, were mutants arising in old- vs. new-habitat patches are differently labeled, and were we consider the composition of the mutation population at the end of the simulation. The curves are given by eq. (11) (or the adjusted versions of it) under the unbiased dispersal scheme ($\pi_w = \pi_m = 0$). Note the different scaling on the y-axes.

Evolutionary rescue

456 Finally, we assume that 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

458 population will inevitably go extinct, because the entire environment will consist of new-habitat patches, and because a wild-type population is assumed not to be viable there. We first focus on evolutionary

460 rescue due to *de novo* mutations. We approximate the probability of evolutionary rescue, denoted by

P_{rescue}, as

$$P_{\text{rescue}} \approx 1 - \exp\left(-\theta \sum_{i=0}^{M-2} \left(\underbrace{\varphi_{\text{old}}\left(f_{\text{old}}(i)\right) \sum_{j=i\tau}^{(i+1)\tau-1} N_w^{\text{old}}(j)}_{\text{old habitat contribution}} + \underbrace{\varphi_{\text{new}}(f_{\text{old}}(i)) \sum_{j=i\tau}^{(i+1)\tau-1} N_w^{\text{new}}(j)}_{\text{new habitat contribution}} \right) \right.$$

$$\left. - \underbrace{\theta \varphi_{\text{new}}(0) \sum_{j=\tau(M-1)}^{\infty} N_w^{\text{new}}(j)}_{\text{contribution after the last patch deteriorated}} \right),$$

(12) `{eq:evol_res`

where $f_{\text{old}}(i) = (M - i - 1)/M$ is the frequency of old-habitat patches after the $(i+1)^{\text{th}}$ 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 Appendix, Section A.3 for an approximation). The interpretation of this equation is the same as for the probability of adaptation in eq. (10). 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. (10) (see also Section A in the SI) (but this is still the stationary population size in phiold ? – I'd remove this sentence as it is confusing (but would like to learn why not the stationary pop size)).

Comparison to simulated data indicates that the approximation in eq. (12) correctly predicts the ranking of dispersal schemes; the actual fit to data is however less good that for the previous steps of our analysis. This discrepancy can be explained: our analysis assumes 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 a k-habitat patch in this environment contributes $\varphi_k(j)$ to the probability of evolutionary rescue despite further patches deteriorating – while more new-habitat patches increases the probability of establishment[22]. Thus, the probability of establishment is underestimated. This is especially true for mutants that emerge just before a deterioration event. Additionally, $\varphi_k(j)$ assumes stationary wild-type

---

[22](this calls for plots of phinew and phiold as functions of fold)

population sizes and therefore does not reflect the decreasing wild-type population size right after the deterioration of a patch (but the pop size depend on fold, don't they? it seems that this then only matters for about one generation in the just deteriorated patch?). A time-dependent establishment probability could account for these effects but unfortunately is not amenable to approximations in our framework. Uecker et al. (2014) considered scenarios with an accessible time-dependent solution: 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 ranking of the different dispersal scheme is overall conserved from the previous steps of our analysis (Fig. 3). Differences between the dispersal schemes are more marked when the fecundity of the mutant in old-habitat patches is lower (Fig. 5c,d), including when the mutant cannot reproduce at all in old-habitat patches ($\omega_m^{\text{old}} = 0$). It is comparatively better for rescue that the mutant preferentially disperses into new-habitat patches, where it is fitter, and for the wild-type to also preferentially disperse into new-habitat patches, thereby releasing competition in old-habitat patches.

When mutant fecundity in old-habitat patches is comparatively low (Fig. 5c,d), the probability of evolutionary rescue often reaches a local (or global) maximum at intermediate emigration probabilities. This finding extends previous results (Tomasini and Peischl, 2019; Uecker et al., 2014) to arbitrary dispersal schemes affecting the immigration process.

Habitat of origin of the rescue mutant and standing genetic variation

Similar to what we found for the probability of adaptation, rescue mutants mainly originate from old-habitat patches (Fig. 6a). Mutations are more likely to appear in the more populated patches (old-habitat). However, a low mutant fecundity in old-habitat patches ω_m^{old} decreases the chance of establishment of these mutants that appear in old-habitat patches (compare black and yellow symbols in Fig. 6a). Here again, we cannot rule out that multiple mutant lineages having appeared in the same habitat type established. Only when mutants from both habitat types are present can we be sure that at least two lineages contributed to establishment (i.e., there was a soft sweep). In this case, the probability of rescue with a mix of origins was very low in our simulations (circles in Fig. 6a). Note that our choice of a small mutation rate implies a hard selective sweep regime ($\theta K_{\text{old}} M = 0.08 < 1$) (Hermisson and Pennings, 2017;

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

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

(c) $\omega_m^{\text{old}} = 1.1$

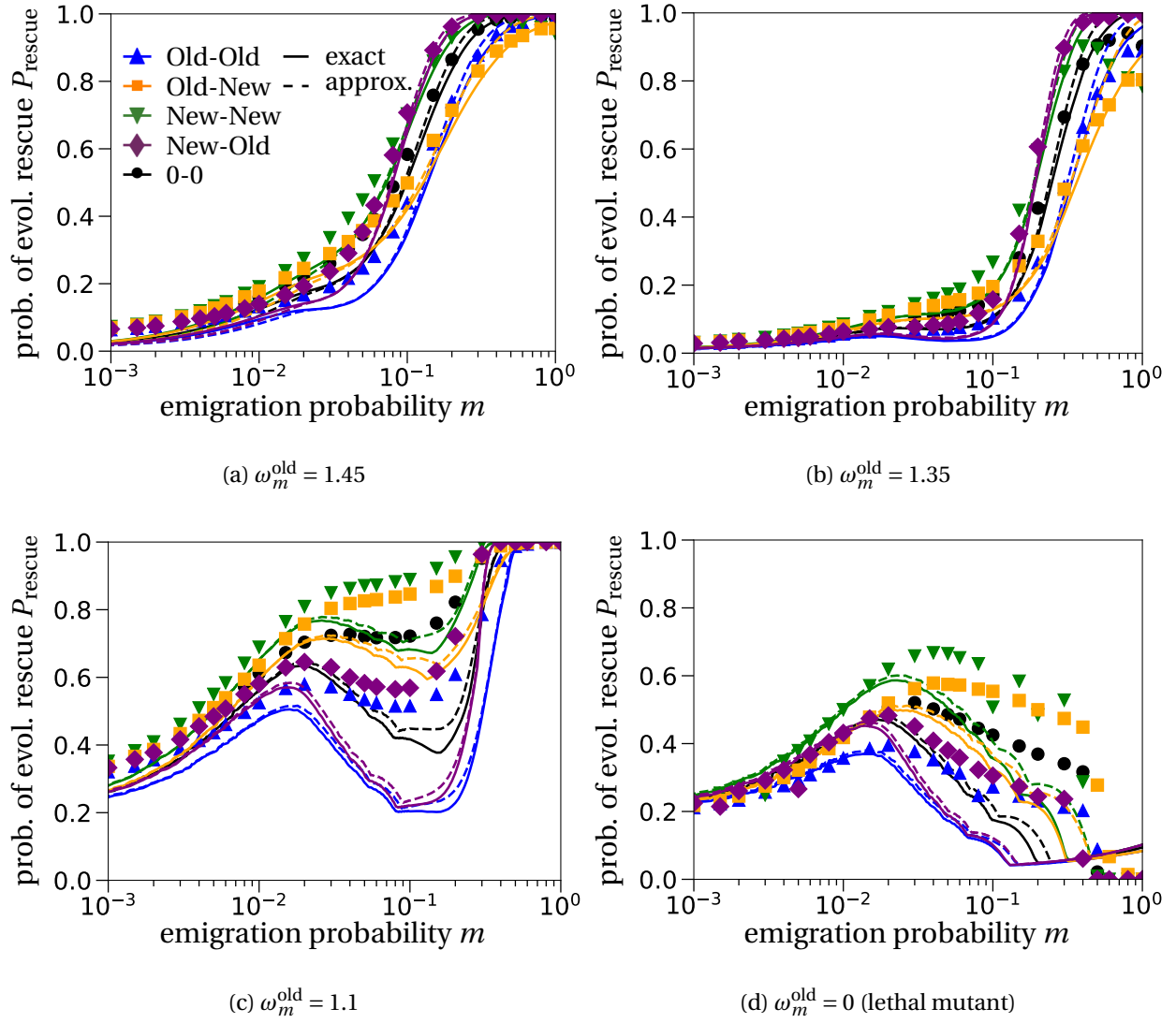(d) $\omega_m^{\text{old}} = 0$ (lethal mutant)

Figure 5: **The probability of evolutionary rescue compared to simulation results.** Our predictions, computed with eq. (12), match the qualitative behavior of the simulated data for the probability of evolutionary rescue. All rankings of the dispersal schemes align well. Quantitatively though, we find that our predictions tend to underestimate the simulated data. In (a,b) the mutation probability is set to (θ instead of u?) $u = 1/(25MK_{\text{new}})$ while in (c,d) it is (θ instead of u?) $u = 1/(MK_{\text{new}})$. The label 'exact' refers to the exact solution of eq. (7) which is then plugged into the approximation of the probability of evolutionary rescue in eq. (12).

Wilson et al., 2017a).

508 So far, we have considered settings where evolutionary rescue is exclusively due to de novo mutations.
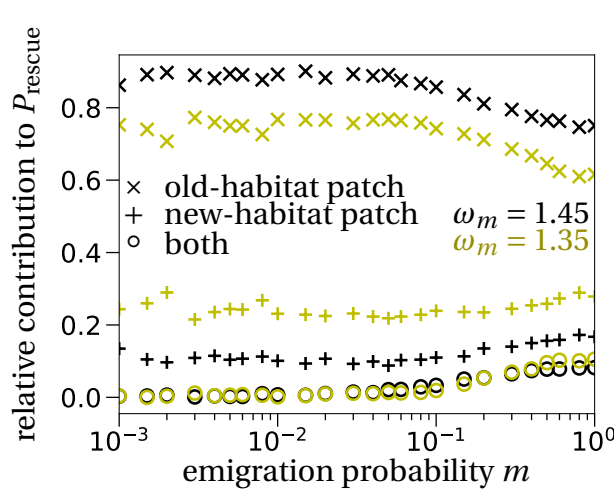
(a) Habitat of origin of the rescue mutants
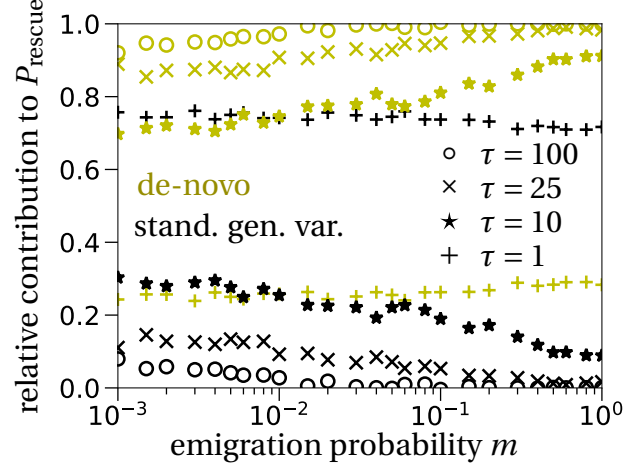
(b) Contribution of de novo mutations compared to standing genetic variation

Figure 6: **Habitat of origin of the rescue mutation and the impact of standing genetic variation.** (a) We compare the source of successful mutations for different mutant fecundity in the old-habitat patches (black vs. yellow). Decreasing the fecundity of the mutant results in more successful mutations emerging in new-habitat patches (+) compared to the contribution from old-habitat patches (×). Dispersal is unbiased ($\pi_m = \pi_w = 0$). (b) For slower environmental degradation, i.e. $\tau = 200$(this value does not appear in the figure?), 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 $\omega_m^{\mathrm{old}} = 1.45$. The relative contribution is then determined by $(P_{\mathrm{rescue\ with\ sgv}} - P_{\mathrm{rescue\ only\ de\ novo}})/P_{\mathrm{rescue\ with\ sgv}}$.

To explore the role of standing genetic variation[23], we ran simulations where we let the system evolve for

510 1,000 generations before the first degradation event happened. Fig. 6b shows the relative contribution of de novo mutations and of standing genetic variation, i.e. mutations that appeared before the first

512 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

514 deteriorated that the probability of adaptation, P_{adapt}, becomes non zero, compare to Fig. 3(b,d) and Fig. SX(which figure?) in the SI. Reducing the time between two consecutive degradation events (reducing

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

τ) also reduces the overall time span of the entire environmental change. Therefore, the proportion of rescue mutants due to standing genetic variation increases as τ decreases.

The relative contribution of standing genetic variation declines as the emigration rate m increases. With high m and a high proportion of old-habitat patches f_{old}, mutants are almost exclusively found in old-habitat patches (see Fig. SX in SI (which figure?)). Thus, mutants that existed prior to the first deterioration event are very unlikely to survive even for a rapidly changing environment. (I do not understand what you mean and could not rephrase this paragraph. Missing a logical step– how come is it detrimental for the mutant to be in old-habitat patches (higher estab proba))

Discussion

We have studied the probabilities of establishment, adaptation and evolutionary rescue under four non-uniform dispersal schemes and compared them to unbiased dispersal. 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 dispersal schemes affect population dynamics and consequently the parameter regions corresponding to the three phases.

Dispersal and adaptation

Theoretical studies that investigated the effects of spatial subdivision on the adaptation of a population in a heterogeneous environment can be classified into two types, depending on how they treat demography. One type of models, classically analyzed in a population genetic framework, assumes constant population sizes in all patches, independent of their local habitat type and of dispersal strength (which we later call implicit demography). 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 "gene swamping" effect is due to the dispersal of non-adapted individuals in the habitat where the rare mutant is beneficial , decreasing the local frequency of the mutant (Lenormand, 2002; Tomasini and Peischl, 2018). In our model, gene swamping was rarely observed; the

31

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), which we also observe. When the mutant is just slightly less fit than the wild type in the old habitat (Fig. 2c), the probability of adaptation monotonically increases with dispersal. When the mutant's fecundity is lower, however, establishment probabilities reach a local maximum at intermediate dispersal rates, and increase again at large dispersal rates thanks to relaxed competition (Fig. 2a(a)). When the fecundity of the mutant is even smaller, the local maximum remains but relaxed competition no longer occurs (cf. Fig. S2).

Compared to models with implicit demography, explicitly modelling the population dynamics allows for relaxed competition at high dispersal rates, which increases the probability of establishment. To illustrate this point, Fig. S5 is the non-demographic version of Fig. 2 (all patches are always at carrying capacity in Fig. S5). (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.)(I am also confused by the increases in orange and purple.)

Standing genetic variation and evolutionary rescue

We also studied the contribution of standing genetic variation to evolutionary rescue. This contribution increases with the speed of environmental change (i.e., with smaller interval between degradations τ), (Fig. 6b). This observation has also been made in a quantitative genetics setting where the adaptive trait is continuous (and not discrete as in our model) (Matuszewski et al., 2015). Experimental results with *Caenorhabditis elegans* also indicate that the impact of standing genetic variation is small under slow environmental change(Guzella et al., 2018).

---

[24](not sure we should keep this last sentence)

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 on (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 compared to unbiased dispersal. This is in line with our findings: when each type favors patches where they are relatively fitter (Old-New scheme), probabilities of establishment and evolutionary rescue are higher than under unbiased dispersal (0-0) (Figs. 2, 3, 5). (I kept the sentence in case I missed something, but this does not seem to be the case?? orange can be below black)

We identified two types of effects of the different dispersal schemes. First, by changing population densities in both habitat types, the dispersal schemes alter the growth rate of the mutant in old-habitat patches a_{old}. This is the primary reason for the ranking of the dispersal schemes[25]. Secondly, the different dispersal schemes 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 lineage (see also Fig.). As the genetic background may vary across patches, the origin of a successful mutation will also affect which mutations will hitchhike with it. 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.

Generality of our theoretical analysis and future directions

Our mathematical results rely on the simplifications that the wild type population does not change over time and that the mutant is rare enough that mutants live independently of each other, and do not

---

[25] (really need a figure!)

33

affect wild-type individuals. This allows us to summarize mutant population dynamics with the λ terms

590 presented in eq.(4). Furthermore, for our approximation in eq. (8) to generate accurate predictions, it is

essential that growth rate differences between the wild type and the mutant are weak and dispersal is low

592 – these conditions are however not needed when we numerically solve system (7). Formally, just two of

these parameters need to be small, as discussed also in Tomasini and Peischl (2018).

594   Our approach 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-

596 dependent carrying capacities, explicit spatial structure or rapidly changing environments. The latter is

the reason for our less accurate approximate in the context of evolutionary rescue (Fig. 5)[26]. Additionally,

598 in order to obtain analytical solutions(but it is still possible if we do things numerically, right? if so, I would

remove the two following sentences), it is important that the stationary population sizes of the wild type

600 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

602 et al., 2018).

    Our model can readily be extended and include a cost of dispersal or a different life cycle. In particular,

604 the variation of the life cycle could yield distinct results regarding adaptation (Holt and Barfield, 2015)[27]

and, more generally, in the context of the evolution of dispersal (Massol and Débarre, 2015).

606

Conclusion

608 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

610 population. 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

612 unifying approach allows us to identify the forces responsible for the different predictions obtained in

---

[26](I would remove this sentence)(I am ok with the sentence)

[27](+ cite Debarre and Gandon hard soft selection please :-))

34

the population genetics literature and under source-sink dynamics. 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[28]. 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.

Acknowledgements

References

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

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

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

---

[28] (reconsider these sentences given the results in S5??)

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

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

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

Bell, G., and A. Gonzalez. 2009. Evolutionary rescue can prevent extinction following environmental 642 change. Ecology Letters 12:942–948.

———. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental 644 deterioration. Science 332:1327–1330.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on 646 the future of biodiversity. Ecology Letters 15:365–377.

Benkman, C. W. 2017. Matching habitat choice in nomadic crossbills appears most pronounced when 648 food is most limiting. Evolution 71:778–785.

Bestion, E., J. Clobert, and J. Cote. 2015. Dispersal response to climate change: scaling down to intraspecific 650 variation. Ecology Letters 18:1226–1233.

Bolnick, D. I., L. K. Snowberg, C. Patenia, W. E. Stutz, T. Ingram, and O. L. Lau. 2009. Phenotype-dependent 652 native habitat preference facilitates divergence between parapatric lake and stream stickleback. Evolution 63:2004–2016.

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

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

36

658　Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters
660　12:197–209.

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

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

Diniz-Filho, J. A. F., K. S. Souza, L. M. Bini, R. Loyola, R. Dobrovolski, J. F. M. Rodrigues, S. Lima-Ribeiro, L. C.
666　Terribile, T. F. Rangel, I. Bione, R. Freitas, I. F. Machado, T. Rocha, M. L. Lorini, M. M. Vale, C. A. Navas, N. M. Maciel, F. Villalobos, M. A. Olalla-Tarraga, and S. Gouveia. 2019. A macroecological approach to
668　evolutionary rescue and adaptation to climate change. Ecography .

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

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

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

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

Fedorka, K. M., W. E. Winterhalter, K. L. Shaw, W. R. Brogan, and T. A. Mousseau. 2012. The role of gene
680　flow asymmetry along an environmental gradient in constraining local adaptation and range expansion. Journal of Evolutionary Biology 25:1676–1685.

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

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

García-Ramos, G., and M. Kirkpatrick. 1997. Genetic models of adaptation and gene flow in peripheral populations. Evolution 51:21.

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

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

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

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

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

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

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

Haccou, P., P. Jagers, and V. A. Vatutin. 2005. Branching Processes: Variation, Growth, and Extinction of Populations. Cambridge Studies in Adaptive Dynamics. Cambridge University Press.

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

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

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

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

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

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

Jacob, S., E. Laurent, B. Haegeman, R. Bertrand, J. G. Prunier, D. Legrand, J. Cote, A. S. Chaine, M. Loreau, J. Clobert, and N. Schtickzelle. 2018. Habitat choice meets thermal specialization: Competition with specialists may drive suboptimal habitat preferences in generalists. Proceedings of the National Academy of Sciences 115:11988–11993.

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

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

———. 2000. Adaptation to marginal habitats: contrasting influence of the dispersal rate on the fate of

alleles with small and large effects. Proceedings of the Royal Society of London. Series B: Biological Sciences 267:1315–1320.

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

Kirkpatrick, M., and N. Barton. 1997. Evolution of a species' range. The American Naturalist 150:1–23.

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

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

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

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

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

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

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

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

40

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

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

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

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

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

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

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

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

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

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

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

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

41

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

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

———. 2019. When does gene flow facilitate evolutionary rescue? bioRxiv .

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

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

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

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

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

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

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

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

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

Appendix

Table of Contents

A   Deriving the model dynamics

_{S22}   In this section we provide the mathematical details of the model that is verbally described in the main

text. We start by deriving the population dynamics when only the wild type is present. This will allow us to

_{S24}   compute the local growth rate of a rare mutant.

Before we go into the details of the computation, we recall the form of the dispersal rates. A dispersing

_{S26}   wild-type individual immigrates to a new-habitat patch with probability

$$\mu_w^{\text{new}} = \frac{1 - f_{\text{old}}}{1 - f_{\text{old}} + e^{\pi_w} f_{\text{old}}} = 1 - \mu_w^{\text{old}}, \tag{A1} \quad \texttt{\{Seq:dispers}$$

where f_{old} is the frequency of old-habitat patches and π_w is the wild-type bias towards old-habitat patches.

_{S28}   The complement, μ_w^{old}, is the probability that the dispersing wild-type individual instead immigrates into

an old-habitat patch.

_{S30}   All the subsequent computations can be checked with a symbolic programming language (e.g. *Mathe-*

matica). A *Mathematica* notebook is deposited on Gitlab[29].

_{S32}   *A.1   Stationary wild-type population sizes*

We denote by $\widehat{N}_w^{\text{old}}$ and $\widehat{N}_w^{\text{new}}$ the deterministic stationary population sizes of the wild type in old- and

_{S34}   new-habitat patches. We assume that the population is always at carrying capacity in old-habitat patches,

so that $\widehat{N}_w^{\text{old}} = K_{\text{old}}$. We now compute $\widehat{N}_w^{\text{new}}$ recursively: it is given by the solution of the following equation:

_{S36}

$$\widehat{N}_w^{\text{new}} = \left(1 - m + m\mu_w^{\text{new}} \frac{(1 - f_{\text{old}})M}{(1 - f_{\text{old}})M}\right) \omega_w^{\text{new}} \widehat{N}_w^{\text{new}} + m\mu_w^{\text{new}} \frac{f_{\text{old}}M}{(1 - f_{\text{old}})M} \omega_w^{\text{new}} \widehat{N}_w^{\text{old}},$$

where the first term on the right-hand side corresponds to individuals born in a new-habitat patch

_{S38}   and staying in it or migrating and landing in a new-habitat patch, and the second term corresponds to

individuals born in an old-habitat patch and migrating to a new-habitat patch. Simplifying, using eq. (A1)

---

[29]https://gitlab.com/pczuppon/evolutionary_rescue_and_dispersal

to replace μ_w^{new} and replacing $\widehat{N}_w^{\text{old}}$ by K_{old} , we obtain

$$\widehat{N}_w^{\text{new}} = \frac{m\omega_w^{\text{new}} f_{\text{old}} K_{\text{old}}}{1 - f_{\text{old}} + e^{\pi_w} f_{\text{old}} - \omega_w^{\text{new}}(1 - f_{\text{old}} + e^{\pi_w} f_{\text{old}}(1 - m))} \ . \tag{A2}$$

This value cannot be larger than K_{new}, the carrying capacity of new-habitat patches. So,

$$\widehat{N}_w^{\text{old}} = K_{\text{old}} \tag{A3a}$$

$$\widehat{N}_w^{\text{new}} = \min\left(K_{\text{new}}, \frac{m\omega_w^{\text{new}} f_{\text{old}} K_{\text{old}}}{1 - f_{\text{old}} + e^{\pi_w} f_{\text{old}} - \omega_w^{\text{new}}(1 - f_{\text{old}} + e^{\pi_w} f_{\text{old}}(1 - m))} \right). \tag{A3b} \quad \texttt{\{Seq:Nhatnew}$$

A.2   *Wild-type population sizes after dispersal*

We denote by $\widetilde{N}_w^{\text{old}}$ and $\widetilde{N}_w^{\text{new}}$ the numbers of wild-type individuals *after the dispersal step.* These quantities are needed to explicitly compute the growth rate of the mutant in old-habitat patches, and to approximate the probability of adaptation. They are given by

$$\widetilde{N}_w^{\text{old}} = \left(1 - m + m\mu_w^{\text{old}} \frac{f_{\text{old}} M}{f_{\text{old}} M}\right) \widehat{N}_w^{\text{old}} + m\mu_w^{\text{old}} \frac{(1 - f_{\text{old}})M}{f_{\text{old}} M} \widehat{N}_w^{\text{new}} \ , \tag{A4a} \quad \texttt{\{Seq:Ntildeo}$$

$$\widetilde{N}_w^{\text{new}} = \left(1 - m + m\mu_w^{\text{new}} \frac{(1 - f_{\text{old}})M}{(1 - f_{\text{old}})M}\right) \widehat{N}_w^{\text{new}} + m\mu_w^{\text{new}} \frac{f_{\text{old}} M}{(1 - f_{\text{old}})M} \widehat{N}_w^{\text{old}} \ . \tag{A4b} \quad \texttt{\{Seq:Ntilden}$$

We then replace $\widehat{N}_w^{\text{old}}$ by K_{old} (since old-habitat patches are assumed to be at carrying capacity after density regulation), and $\widehat{N}_w^{\text{new}}$ by the formula given in eq. (A3b).

A.3   *Wild-type population sizes during the environmental change*

(I suggest moving this subsection at the end of Appendix A) Lastly, compute the (deterministic) wild-type population size over time during the environmental change. This value is used in the approximation of the probability of evolutionary rescue in eq. (12) in the main text, more precisely to estimate the number of rescue mutants that appear during the deterioration of patches.

At the moment a patch deteriorate, its population size is still given by the carrying capacity of the old habitat, K_{old}, but only each adult has now on average $\omega_m^{\text{new}} < 1$ offspring. As the size of the local population decreases, there is not need for density regulation anymore. Neglecting dispersal for the moment, in

S56 generation τ after the degradation of a patch[30] , we would have

$$N_w^{\text{new}}(\tau) = K_{\text{old}}(\omega_w^{\text{new}})^\tau \tag{A5}$$

wild-type individuals in this patch. Including dispersal between the patches then results in the following

S58 number of wild-type individuals in a patch i at time τ post-degradation, given that there are $k-1$ other

new-habitat patches

$$N_w^{i,k}(\tau) = \omega_w^{\text{new}}\left((1-m)N_w^{i,k}(\tau-1) + \frac{m_w^{\text{new}}}{k}(M-k)K_{\text{old}} + \frac{m_w^{\text{new}}}{k}\sum_{l=1}^{k}N_w^{l,k}(\tau-1)\right). \tag{A6}$$

S60 The first term represents the remaining individuals after emigration, the second and third term are

immigrants from old- and new-habitat patches (distributed equally among the k new-habitat patches),

S62 respectively.

A.4   Local per capita growth rates

S64 *A.4.1   The local per capita growth rate a_{old}*

As stated in eq. (2) in the main text, we define the per capita growth rate of rare mutant in the old habitat

S66 by

$$1 + a_{\text{old}} = K_{\text{old}}\frac{\omega_m^{\text{old}}}{\omega_w^{\text{old}}\widetilde{N}_w^{\text{old}}}, \tag{A7}$$

where we replace $\widetilde{N}_w^{\text{old}}$ by the formula given in (A4a).

S68 *A.4.2   The local per capita growth rate a_{new}*

In new-habitat patches, we assume that the carrying capacity K_{new} is not reached during the establishment

S70 phase of the mutant. In other words, we assume that there is no density regulation in new-habitat patches.

As a result, the local per capita growth rate of the mutant only depends on its fecundity:

$$1 + a_{\text{new}} = \omega_m^{\text{new}}. \tag{A8}$$

---

[30] (is this just said/shown for the sake of pedagogy, or do you actually need this equation? If not, I suggest removing it.)

s72   Of course, there may be parameter configurations, typically high emigration rates m and a bias of the wild type towards the new habitat ($\pi_w < 0$), where our assumption of density-independent reproduction
s74   is violated. Then our approximation and the numerical solution of eq. (7) in the main text strongly deviate from the simulation results (e.g. the New-New dispersal scheme in Fig. 2(d)).

B   Approximation of the establishment probability

We compute the survival probability of the lineage of a single mutant starting either in an old- or in a new-habitat patch. We call this probability the establishment probability because it implies the successful establishment of a mutant population within the metapopulation. It is denoted by φ_k, k indicating the initial habitat type of the mutant (old or new).

Our method is the same as the one used in Tomasini and Peischl (2018), with the exception that our per capita growth rate in old-habitat patches, a_{old}, depends on the demography of the population. The method in general is based on the theory of multi-type branching processes, cf. Chapter 5.5 in Haccou et al. (2005). We refer the reader to the Supplementary Information of Tomasini and Peischl (2018) for a detailed application of the theory.

The mean reproduction matrix $\mathcal{M}$ of a mutant gives the average number of offspring in a certain habitat, dependent on the habitat type in which the mutant resides (see also eq. (??) in the main text):

$$
\mathcal{M} = \begin{array}{c} \text{old patch} \\ \text{new patch} \end{array}
\begin{array}{cc} \text{old patch} & \text{new patch} \end{array}
\left(\begin{array}{cc}
\left(1 - m\mu_m^{\text{new}}\right)(1 + a_{\text{old}}) & m\mu_m^{\text{new}}(1 + a_{\text{new}}) \\
m\mu_m^{\text{old}}(1 + a_{\text{old}}) & \left(1 - m\mu_m^{\text{old}}\right)(1 + a_{\text{new}})
\end{array} \right),
\tag{B1}
$$

{eq:repromat

$$
\mathcal{M} = \begin{array}{c} \text{old patch} \\ \text{new patch} \end{array}
\begin{array}{cc} \text{old patch} & \text{new patch} \end{array}
\left(\begin{array}{cc}
\left(1 - m_m^{\text{new}}\right)(1 + a_{\text{old}}) & m_m^{\text{new}}(1 + a_{\text{new}}) \\
m_m^{\text{old}}(1 + a_{\text{old}}) & \left(1 - m_m^{\text{old}}\right)(1 + a_{\text{new}})
\end{array} \right),
\tag{B2}
$$

{Seq:mean_re

where the rows denote the parent locations, and the columns the patch type of the offspring.

Our goal is to apply Theorem 5.6 from Haccou et al. (2005) which states that for a slightly super-critical branching process, i.e. where the survival probability is slightly above zero, the establishment probability can be expressed in terms of the largest eigenvalue ρ and the corresponding left- and right-eigenvectors of the mean reproduction matrix $\mathcal{M}$, denoted by u and v, respectively. The eigenvectors should be normalized in the following way: $u_1 + u_2 = 1$ and $\sum_{i=1}^2 u_i v_i = 1$. The establishment probabilities are then

given by

$$\varphi_i = \frac{2(\rho - 1)}{B} v_i + O(\varepsilon), \qquad (B3) \quad \texttt{\{Seq:theory\}}$$

with

$$B = \sum_{i=1}^{2} u_i \sum_{j=1}^{2} v_j \mathcal{M}_{ij} + \rho(1 - \rho) \sum_{j=1}^{2} u_j v_j^2. \qquad (B4)$$

B.1 Computing the largest eigenvalue

We first approximate the largest eigenvalue of $\mathcal{M}$ denoted by ρ. It is given by (see *Mathematica* notebook)

$$\rho = \frac{1}{2}\Big(2 + a_{\mathrm{old}} + a_{\mathrm{new}} - m - m_m^{\mathrm{new}} a_{\mathrm{old}} - m_m^{\mathrm{old}} a_{\mathrm{new}}$$
$$+ \sqrt{4(m-1)(1 + a_{\mathrm{old}})(1 + a_{\mathrm{new}}) + (2 + a_{\mathrm{old}} + a_{\mathrm{new}} - m - m_m^{\mathrm{new}} a_{\mathrm{old}} - m_m^{\mathrm{old}} a_{\mathrm{new}})^2}\Big) \qquad (B5)$$

In order to make analytical progress and to identify under which conditions the process is slightly super-critical, i.e. $\rho > 1$, we rescale the parameters by a small parameter ε. We set $a_{\mathrm{old}} = \varepsilon$, $a_{\mathrm{new}} = \varepsilon\xi$ and $m = \varepsilon\mu$. Assuming that ε is small enough, i.e. effectively a weak selection assumption in old-habitat patches, we can neglect higher orders of ε and find

$$\rho \approx 1 + \frac{1}{2}\varepsilon\left(1 + \xi - \mu + \sqrt{(\xi - 1 + \mu_m^{\mathrm{new}})^2 + 2(1 - \xi + \mu_m^{\mathrm{new}})\mu_m^{\mathrm{old}} + (\mu_m^{\mathrm{old}})^2}\right)$$
$$= 1 + \frac{1}{2}\varepsilon\left(1 + \xi - \mu + \sqrt{\frac{\gamma}{1 - f_{\mathrm{old}} + e^{\pi_m} f_{\mathrm{old}}}}\right), \qquad (B6) \quad \texttt{\{eq:eigenval}$$

where γ is the rescaled version of the constant C in the main text (eq. (8c)), i.e.

$$\gamma = (1 - f_{\mathrm{old}})(\xi - 1 + \mu)^2 + e^{\pi_m} f_{\mathrm{old}}(\xi - 1 - \mu)^2. \qquad (B7)$$

For $\varepsilon \to 0$ we find that $\rho \to 1$ (eq. (B6)) which means that the branching is slightly super-critical if $\rho > 1$ and real. A sufficient condition for this to be true is

$$1 + \xi - \mu > 0 \quad \Leftrightarrow \quad a_{\mathrm{old}} + a_{\mathrm{new}} - m > 0 \qquad (B8)$$

In case that the branching process is not super-critical the establishment probability in eq. (B3) becomes negative and as such is not a probability anymore. Hence, we can simply reject negative solutions of the establishment probability and by that implicitly justify that our approximation is valid.

S7

B.2 Computing the establishment probability

s110 For the solution of eq. (B3) it remains to compute the normalized eigenvectors. Their precise form is of not much insight. We therefore omit stating them explicitly but refer to the *Mathematica* notebook.

s112 Solving eq. (B3) to the first order of ε we find

$$
\begin{aligned}
\varphi_{\text{old}} &= \varepsilon + \frac{\varepsilon(1-\xi)}{\sqrt{\frac{\gamma}{(1-f_{\text{old}}+e^{\pi_m}f_{\text{old}})}}} + \frac{\varepsilon\left(\mu_m^{\text{old}} - \mu_m^{\text{new}} + 2\mu_m^{\text{new}}\xi\right)}{\sqrt{\frac{\gamma}{(1-f_{\text{old}}+e^{\pi_m}f_{\text{old}})}}}, \\
\varphi_{\text{new}} &= \varepsilon\xi + \frac{\varepsilon\xi(\xi-1)}{\sqrt{\frac{\gamma}{(1-f_{\text{old}}+e^{\pi_m}f_{\text{old}})}}} + \frac{\varepsilon\left(\xi\mu_m^{\text{new}} - \xi\mu_m^{\text{old}} + 2\mu_m^{\text{old}}\right)}{\sqrt{\frac{\gamma}{(1-f_{\text{old}}+e^{\pi_m}f_{\text{old}})}}}.
\end{aligned}
\tag{B9}
$$

Transforming back to the original variables and replacing γ by the constant C from the main text (eq. (8c))

$$
C = (1 - f_{\text{old}} + e^{\pi_m}f_{\text{old}})\left((1-f_{\text{old}})(a_{\text{new}} - a_{\text{old}} + m)^2 + e^{\pi_m}f_{\text{old}}(a_{\text{new}} - a_{\text{old}} - m)^2\right),
\tag{B10}
$$

s114 we obtain

$$
\begin{aligned}
\varphi_{\text{old}} &= a_{\text{old}} + \frac{(1 - f_{\text{old}} + e^{\pi_m}f_{\text{old}})a_{\text{old}}(a_{\text{old}} - a_{\text{new}})}{\sqrt{C}} + \\
&\quad m\frac{\left(e^{\pi_m}f_{\text{old}}a_{\text{old}} - (1-f_{\text{old}})a_{\text{old}} + 2(1-f_{\text{old}})a_{\text{new}}\right)}{\sqrt{C}}, \\
\varphi_{\text{new}} &= a_{\text{new}} + \frac{(1 - f_{\text{old}} + e^{\pi_m}f_{\text{old}})a_{\text{new}}(a_{\text{new}} - a_{\text{old}})}{\sqrt{C}} \\
&\quad + m\frac{\left(a_{\text{new}}(1-f_{\text{old}}) - a_{\text{new}}e^{\pi_m}f_{\text{old}} + 2a_{\text{old}}e^{\pi_m}f_{\text{old}}\right)}{\sqrt{C}}.
\end{aligned}
\tag{B11}
$$

Slightly re-ordering the terms, this gives the establishment probability of a single mutant individual, eq. (8)

s116 in the main text:

$$
\begin{aligned}
\varphi_{\text{old}} &\approx \quad a_{\text{old}} \quad + \quad a_{\text{old}}\frac{\left(1 - f_{\text{old}} + e^{\pi_m}f_{\text{old}}\right)}{\sqrt{C}}(a_{\text{old}} - a_{\text{new}}) \\
&\quad + \frac{m}{\sqrt{C}}\left(a_{\text{new}}(1-f_{\text{old}}) + a_{\text{old}}e^{\pi_m}f_{\text{old}} - (a_{\text{old}} - a_{\text{new}})(1-f_{\text{old}})\right), \\
\varphi_{\text{new}} &\approx \quad \underbrace{a_{\text{new}}}_{\text{(1) local growth parameter}} \quad + \quad \underbrace{a_{\text{new}}\frac{\left(1 - f_{\text{old}} + e^{\pi_m}f_{\text{old}}\right)}{\sqrt{C}}(a_{\text{new}} - a_{\text{old}})}_{\text{(2) effect of the heterogeneous environment}} \\
&\quad + \underbrace{\frac{m}{\sqrt{C}}\left(a_{\text{new}}(1-f_{\text{old}}) + a_{\text{old}}e^{\pi_m}f_{\text{old}} - (a_{\text{new}} - a_{\text{old}})e^{\pi_m}f_{\text{old}}\right)}_{\text{(3) effect of dispersal: new patches + old patches − loss to the other patch type}}.
\end{aligned}
\tag{B12}
$$

{Seq:estab_a

S8

For $m = 0$ we see that $\varphi_{\text{old}} = 0$, i.e. terms (1) and (2) cancel out. For the establishment probability in the new habitat we recover Haldane's result for the establishment probability of a slightly advantageous mutant: $\varphi_{\text{new}} = 2a_{\text{new}}$ (Haldane, 1927).

B.3 *Disentangling the contributions to the establishment probability*

We now proceed to explain the three regions of the establishment probability from Fig. 2(a) in the main text. These were defined by: (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.

For clarity, we re-plot Figs. 2(a,c) in Fig. S1(a,b), respectively. We try to explain the ongoing processes for each of the regions through the approximations of the establishment probabilities in eq. (B12), see also Fig. S1(c,d). Note that these explanations are only valid for the establishment probability of a mutant initially in an old-habitat patch, φ_{old}. For the intuition behind the shape of φ_{new} we refer to the corresponding section in the main text.

Region (i) is explained by the positive effect of dispersal. Mutants disperse from old- to new-habitat patches where they have a higher growth rate. This effect is mediated through the third term of the establishment probability in eq. (B12). Note that the first two terms of the approximation cancel out for small emigration probabilities m. While the third term increases with increasing emigration rate m, the second term in eq. (B12) decreases, cf. Fig. S1. In the formula this is mediated through the increase of the local growth rate in the old-habitat, a_{old}, i.e. it becomes less negative. Then both factors of the second term, a_{old} and the difference $(a_{\text{old}} - a_{\text{new}})$, increase (which in turn decreases term two). The intuitive reason is that due to larger emigration probabilities m, more individuals leave old habitats before the reproductive event. This relaxes competition in these patches and therefore increases the local growth rate of mutants in old-habitat patches. Finally, in region (iii) dispersal is so large that the population homogenizes. This results in even less competitive pressure in old-habitat patches. Eventually, this yields a positive growth rate a_{old} (first term in eq. (B12)). Therefore, this region is driven by the local growth rate in old habitats.

S9

Note that region (iii) can be shifted to the left by increasing the absolute number of offspring of

S144 mutants in old-habitat patches, ω_m^{old}, and therefore decreasing the local disadvantage of the mutant. If

shifted sufficiently to the left, like in Fig. S1(d), region (ii) might vanish due to this effect.

S146 Contrarily, if we set the fecundity parameter of the mutant in the old habitat to $\omega_m^{\text{old}} = 1.1$, we see that

region (iii) disappears for most dispersal schemes, cf. Fig. S2. Due to the low fecundity of the mutant,

S148 even under relaxed competition in old habitats, establishment of a mutant population is very unlikely.

The final increase of our approximation in the dispersal schemes New-New and New-Old is due to our

S150 density-independence assumption in new habitats. For these large values of m and the bias of the wild

type towards new-habitat patches, this assumption is violated in the simulations explaining the deviation

S152 from the simulation results and our prediction.

C Habitat of origin of the adaptive mutation

S154 Here, we provide further insight into the origin of the adaptive mutation. Therefore we plot the establishment probabilities φ_{old} and φ_{new} when varying the frequency of old habitats, f_{old}. In Fig. 4 in the

S156 main text we have seen that most successful adaptive mutations arise in old-habitat patches. Here, we show that this is explained mostly due to the large mutational input that is provided by the much larger

S158 wild-type population sizes in old habitats, see Fig. S3(b). The establishment probability though is always larger for mutants that arise in new habitats than in old habitats (Fig. S3(a)).

S160 (There was a figure where the contribution from new habitats was larger than from old habitats. With the changed fecundities, I only get this behavior if the fecundity of the mutant is larger in the new patches

S162 than in the old patches, i.e. $\omega_m^{\text{old}} < a_{\text{new}}$. Also, for some reason the approximations do not work that well in these scenarios (I did not investigate why the estimated lines are bad – soft sweeps still work fine but

S164 the other approximations don't.))

D   Probability of establishment for large frequencies of old-habitat patches

We plot the probability of establishment for a large frequency of old-habitat patches, f_{old}. As visible in Fig. S4 below, for high frequencies of old-habitat patches the probability of adaptation becomes very small, if not zero, for large emigration probabilities m. These high frequency of old-habitat patches are the patch configurations which mutants that were present before the first patch degrades, i.e. standing genetic variation mutants, experience. Therefore, it is very unlikely that the mutant, which will eventually rescue the population, was already present before the first degradation event. This supports the explanation that homogenizing the population (large m) reduces the impact of standing genetic variation on the probability of evolutionary rescue, see Fig. 6(b) in the main text where $\pi_w = \pi_m = 0$ was plotted.

E   Establishment probability in a model without demography

Here, we consider a variation of our original model in order to investigate the impact of demography on
the establishment probabilities φ_{old} and φ_{new}. The dispersal process and the dynamics in old-habitat
patches remain as studied before. In new-habitat patches we now assume that the population remains at
carrying capacity, i.e. there is no longer a declining wild-type population. This means that the local growth
rate a_{old} in eq. (??) takes the form for $\widehat{N}_w^{\text{new}} = K_{\text{new}}$. For simplicity we will also assume that $K_{\text{new}} = K_{\text{old}} = K$.
In order to maintain the divergent selection assumption, we assume that the fecundity of the wild-type in
the new habitat is below the fecundity of the mutant. Therefore, we need to adjust the local growth rate of
a single mutant, a_{new}. The local growth rate in old habitats, a_{old}, remains as outlined in eq. (??). We have

$$1 + a_{\text{new}} = K \frac{\omega_m^{\text{new}}}{\omega_w^{\text{new}} \widetilde{N}_w^{\text{new}} + \omega_m^{\text{new}}} \approx K \frac{\omega_m^{\text{new}}}{\omega_w^{\text{new}} \widetilde{N}_w^{\text{new}}}, \tag{E1}$$

which with the help of eq. (??) yields

$$a_{\text{new}} \approx \frac{\omega_m^{\text{new}}}{\omega_w^{\text{new}} \left(1 + \frac{m f_{\text{old}}(1 - e^{\pi_w})}{1 - f_{\text{old}} + e^{\pi_w} f_{\text{old}}}\right)}. \tag{E2}$$

Note, that we again used that during the establishment phase the wild type is much more abun-
dant than the mutant which explains the approximation in the two equations. Plugging this in the
approximation of the establishment probability from eq. (B12) we find the curves in Fig. S5.

We see that, as briefly mentioned in the main text, region (iii) of the establishment probability
disappears in these type of models except for the Old-New and the New-Old dispersal schemes. The
reason for the disappearance of the region is that relaxed competition only plays a subordinate role for
the symmetric dispersal schemes (Old-Old, New-New and 0-0). In other words, these dispersal schemes
maintain the local frequencies of the mutant at the same level as before the dispersal step and by that do
not change the population dynamics. In contrast, the Old-New dispersal scheme strongly increases the
frequency of mutants in new-habitat patches and by that increases the establishment probability. It is
worth mentioning though, that this is not an effect of relaxed competition but rather a biased dispersal of
the mutant into the habitat where it is favored. Solely for the New-Old dispersal scheme where individuals
prefer the habitat they are relatively less fit, we see a relaxed competition scenario in old-habitat patches.

For high dispersal rates m the majority of the wild-type individuals emigrate to new habitats and by that

leave space for the rare mutants in old-habitat patches to reproduce. This explains why this dispersal

scheme still shows the characteristic pattern of a three-stage establishment probability.

F   Habitat of origin dependent on the dispersal scheme

The habitat type of the origin of the rescue mutation is largely independent of the considered dispersal

scheme. For $\omega_m^{\text{old}} = 1.35$ we have plotted the relative contribution of each natal habitat type to the

probability of evolutionary rescue, Fig. S6. We do not see large differences between the three symmetric

dispersal schemes (0-0, Old-Old, and New-New) and the Old-New dispersal scheme. Only for the New-Old

dispersal schemes we see an increase in the contribution of mutants emerging from old-habitat patches

for very high emigration probabilities m. A possible explanation is the large probability of establishment

for a mutant emerging in old-habitat patches for this parameter set (cf. Fig. S1(a)).
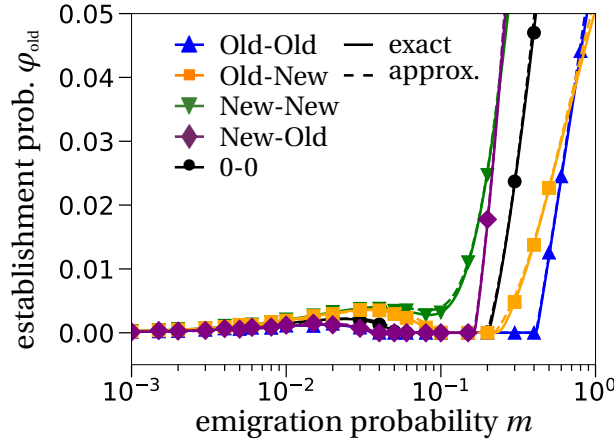
(a) $\omega_m^{old} = 1.35$ (large fecundity difference)
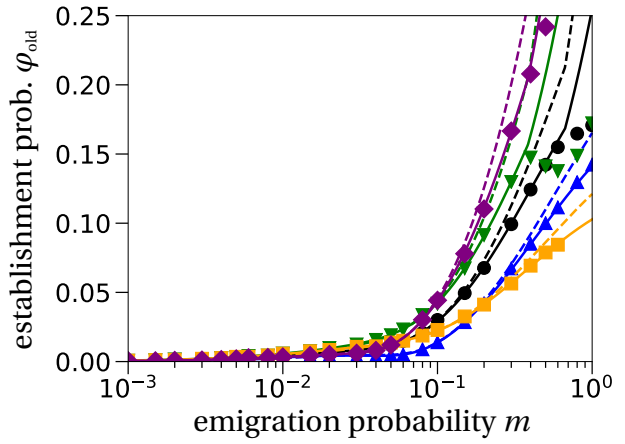
(b) $\omega_m^{old} = 1.45$ (small fecundity difference)
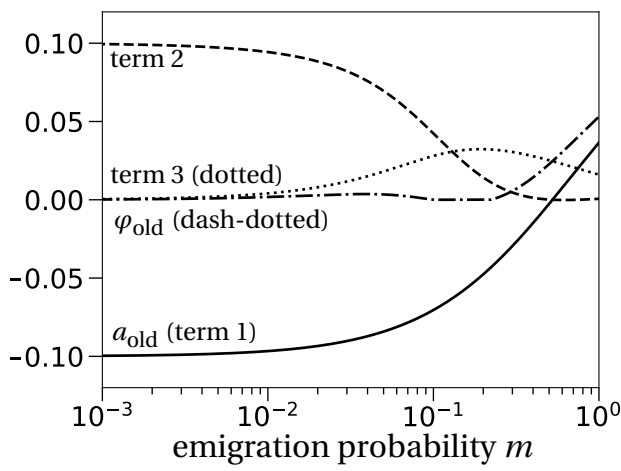
(c) $\omega_m^{old} = 1.35$ (large fecundity difference)
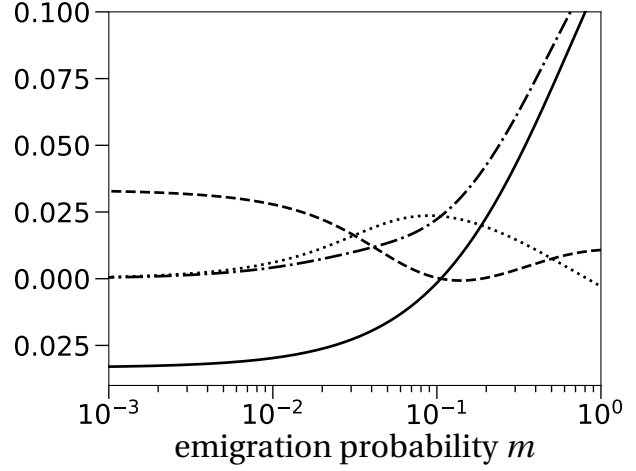
(d) $\omega_m^{old} = 1.45$ (small fecundity difference)

Figure S1: **Contribution of the different terms in eq.** (B12) **to the establishment probability φ_{old}.** Subfigures (a,b) are the same as Figs. 2(a,c) in the main text. They show the establishment probability for a single mutant individual arising in an old-habitat patch for varying emigration probabilities m. In subfigures (c,d) we plot the terms from eq. (B12) separately ($\pi_w = 0.5, \pi_m = -0.5$). Term 1, the mutant growth rate in old habitats (solid), increases with increasing dispersal rates as a consequence of relaxed competition. Term 2, the environmental effect (dashed), captures the differences between the growth rates in the habitats. The larger the difference, the larger its contribution to the overall establishment probability. Term 3, the effect of dispersal (dotted), (largely) increases with increasing dispersal rates m. The sum of the three terms is plotted as a dash-dotted line.

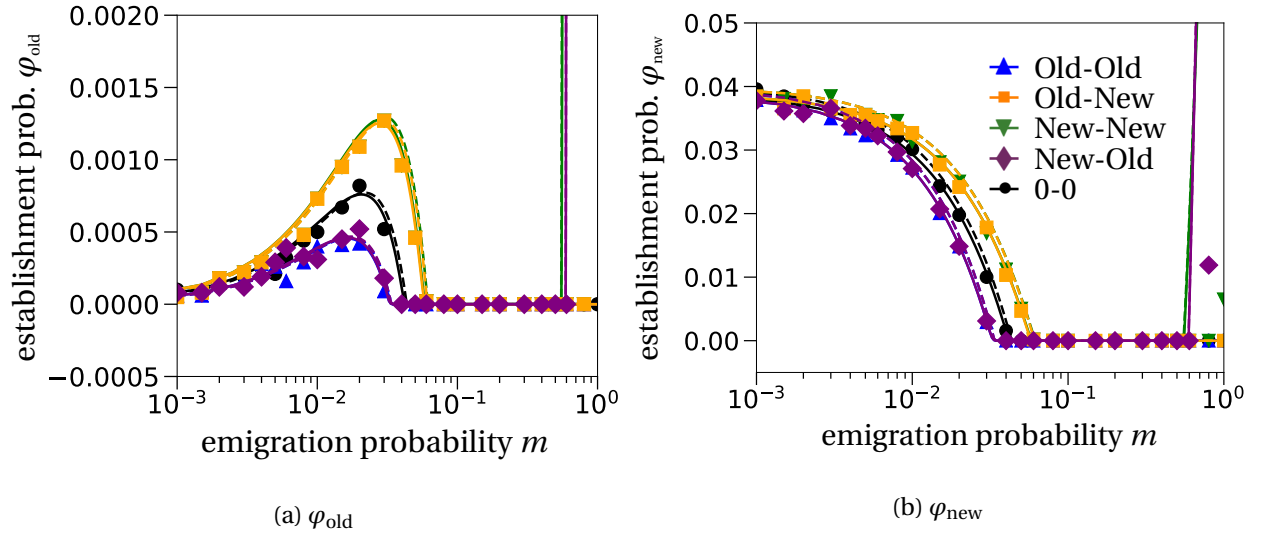(a) φ_{old}

(b) φ_{new}

Figure S2: **Disappearance of region (iii) for large fecundity differences in the old habitat.** If the mutant fecundity in old-habitat patches is too low, here $\omega_m^{\text{old}} = 1.1$, the effect of relaxed competition is not strong enough to have an impact on the establishment probability for high dispersal rates. The establishment probability remains at zero.
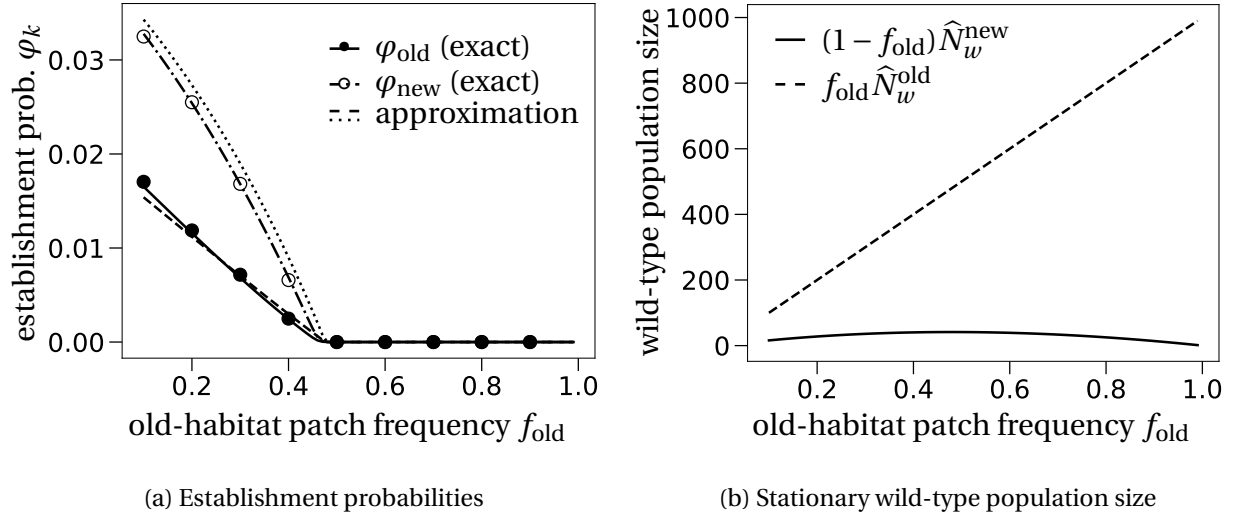
(a) Establishment probabilities

(b) Stationary wild-type population size

Figure S3: **Establishment probability and stationary wild-type population size when varying the old-habitat frequency.** In the simulations we have used the standard set of parameters as given in Table 1 and the unbiased dispersal scheme ($\pi_w = \pi_m = 0$). In (a) we additionally chose the large fecundity difference scenario ($\omega_m^{\text{old}} = 1.35$).
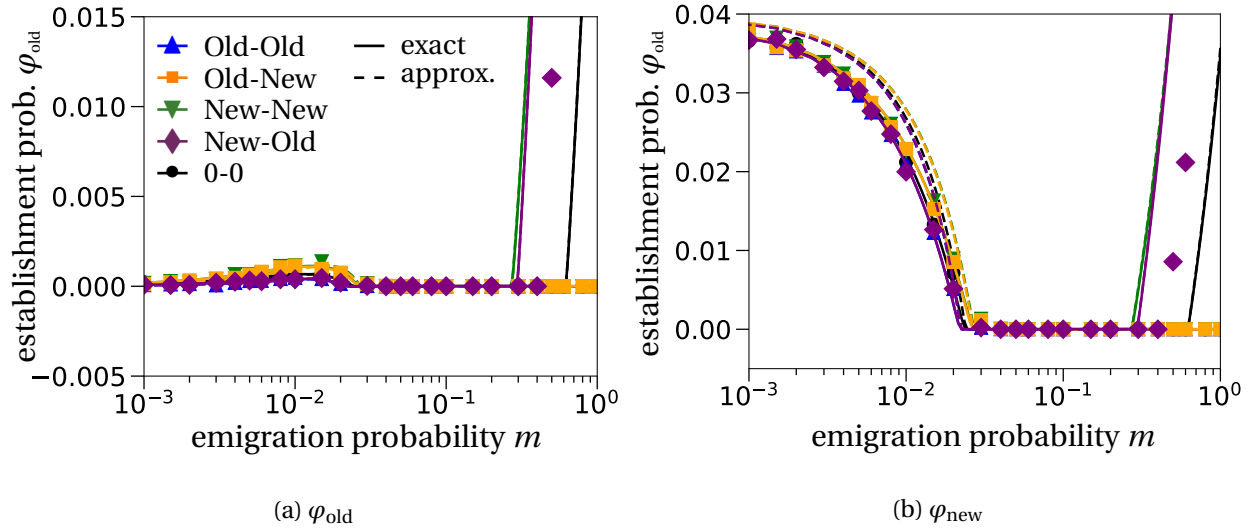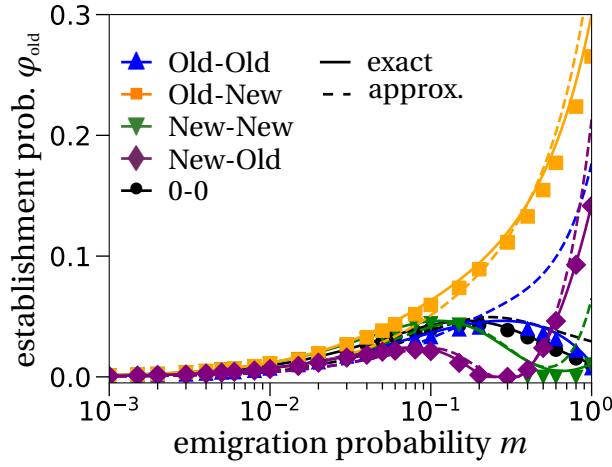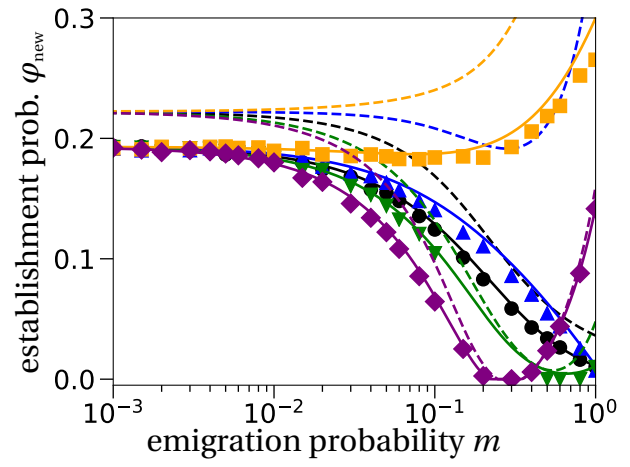

(a) φ_{old}

(b) φ_{new}
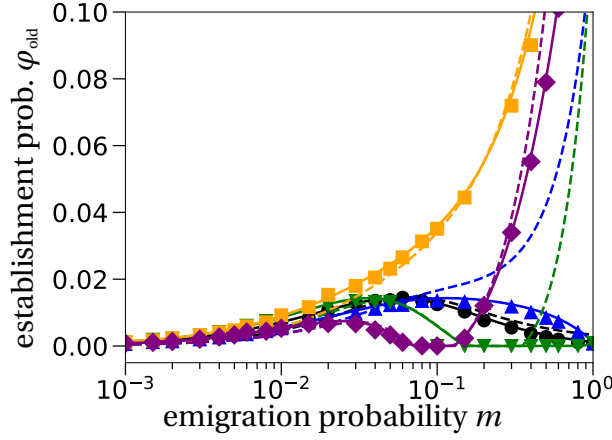
Figure S4: **Probability of adaptation for a large frequency of old-habitat patches ($f_{\text{old}} = 0.9$).** The fecundity of the mutant in old-habitat patches is set to $\omega_m^{\text{old}} = 1.45$. Note also the difference between the scales of the y-axes in the two panels.
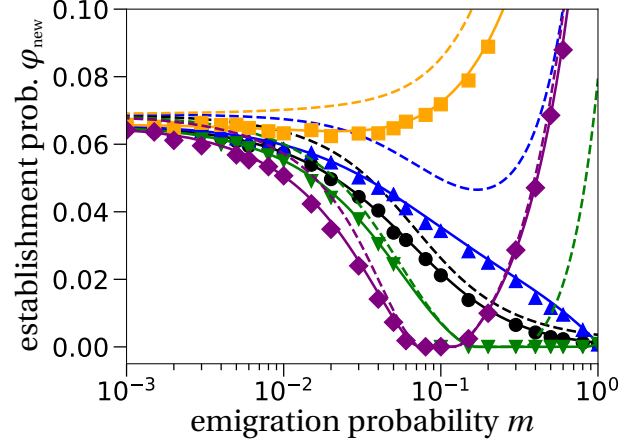
(a) φ_{old} with $\omega_m^{\mathrm{old}} = 1.35$ (large fecundity difference)

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

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

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

Figure S5: **Establishment probability when populations in both habitats are at carrying capacity.** We plot the establishment probability for a single mutant either initially in an old-habitat patch (a,c) or in a new-habitat patch (b,d). The numerical solution (solid lines) still approximates the simulated data reasonably well. The analytical approximation (dashed lines) however deviates strongly from the data due to large growth rates ($a_{\mathrm{new}} \approx 0.2$) so that the conditions for the approximation to hold are violated. In this case, in eq. (B12) higher order corrections would need to be taken into account. The fecundity values in the new habitat are given by $\omega_w^{\mathrm{new}} = \omega_m^{\mathrm{old}}$ and $\omega_m^{\mathrm{new}} = \omega_w^{\mathrm{old}}$ and the carrying capacity is $K_{\mathrm{new}} = K_{\mathrm{old}} = K = 500$. Missing data points (mostly for the negative density-dependent dispersal scheme – green triangles) are explained by too large computation times. All data points are averages from 10^4 independent runs. Note the varying y-axes scales.
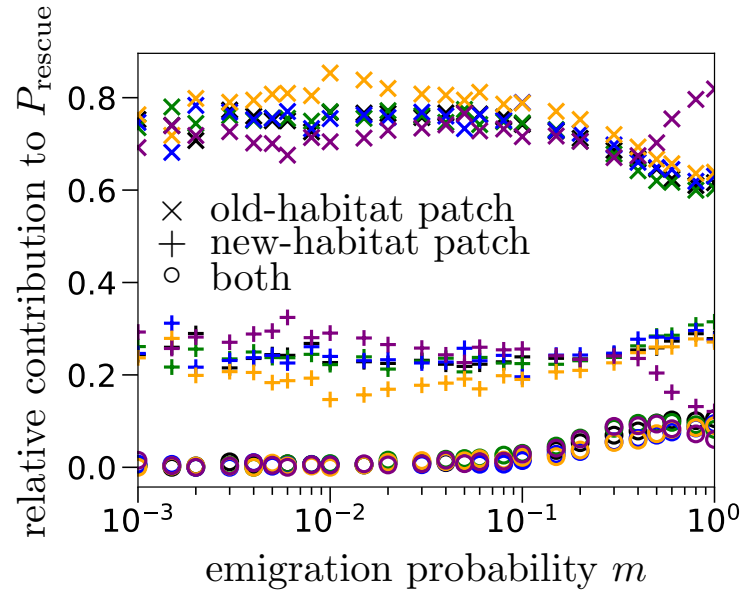
Figure S6: **Habitat type of the origin of the rescue mutant dependent on the dispersal scheme.** Varying the emigration probability m we plot the relative contributions of each habitat type to the probability of evolutionary rescue. The color-coding is as in the main text: black for 0-0, blue for the Old-Old, green for the New-New, orange for the Old-New, and purple for the New-Old dispersal scheme.