E-Article

Transient Eco-Evolutionary Dynamics and the Window of Opportunity for Establishment of Immigrants

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abstract: To what extent does landscape genetic structure bear the signature of arrival order of lineages during population assembly? Rapid genetic adaptation of resident populations founded by early colonists to local conditions might prevent establishment of later-arriving lineages, resulting in an evolution-mediated priority effect. This might result in a limited window of opportunity for establishment during which the resident population did not have sufficient time yet to monopolize the patch through local adaptation. The length of this window of opportunity is expected to depend on the degree to which early colonists and immigrants are preadapted to local habitat conditions. We present an intraspecific competition model of the initial transient population and evolutionary dynamics that quantifies the window of opportunity for establishment for asexual species. The model explicitly addresses the long-lasting effects of evolution-mediated priority effects by tracking lineages through time. Our results show that the difference in initial preadaptation between early colonists and late immigrants and the speed of evolution codetermine the window of opportunity for establishment. Our results also suggest that local populations should often be dominated by descendants of just a few early colonist lineages and that landscape genetic structure should often reflect the legacy of colonization history.

Keywords: evolution-mediated priority effects, evolutionary population dynamics, monopolization, transient dynamics, rapid local adaptation.

During a certain time period after the initialization of a population in a suitable patch, for instance, when a newly formed island or local habitat patch in a regional metapopulation is colonized, there will not be a population genetic equilibrium. Instead, the population genetic structure will be dominated by early colonists due to founder effects (Mayr 1942). However, little is known about the persistence of these founder effects, and therefore they are often assumed to be absent (e.g., Bohonak 1998, 1999). In empirical studies on population and landscape genetic structure, this assumption has led to the expectation that genetic differentiation between populations is the result of a balance between gene flow, genetic drift, mutations, and selection.

Boileau et al. (1992) presented a model on the persistence of early colonist dominance in the context of population dynamics and its consequences for population and landscape genetic structure. They found that if the establishment of a population is followed by rapid population growth toward carrying capacity, the founder effect resulting from the numerical advantage of the early colonists over later immigrants might last for long periods of time. The model presented by Boileau et al. (1992) only considers the neutral case. Fitness differences and rapid local genetic adaptation were not considered. Lineages that are better preadapted to local conditions might be able to invade and replace founding lineages (Fukami 2015). Conversely, local genetic adaptation can reduce establishment success of new immigrants (Urban and De Meester 2009; De Meester et al. 2016). The latter is often ignored on the basis of the assumption that evolution is too slow to play a role in ecological processes like colonization, an assumption that is challenged by many studies (Thompson 1998; Yoshida et al. 2003; Hairston et al. 2005; Carroll et al. 2007; Post and Palkovacs 2009; Hendry 2017). Some degree of local adaptation in habitat patches (e.g., islands, bodies of water, or forest fragments or host individuals in the case of parasites and gut mutualists) is expected to occur if the

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selection coefficient is substantially larger than the immigration rate (Haldane 1930; Richardson et al. 2014). If resident populations established by early colonist lineages can sufficiently rapidly adapt to local habitat conditions and thus obtain a fitness advantage over later-arriving immigrants, the establishment success of later-arriving immigrants is reduced, resulting in an evolution-mediated priority effect ("monopolization"; De Meester et al. 2002, 2016). This can result in high genetic differentiation among populations, similar to the persistent founder effect described by Boileau et al. (1992), but which are mediated by contemporary evolution. Local adaptation enhances these priority effects, and it could lead to them being fairly permanent relative to the length of time a population persists (see app. A; apps. A–E are available online). If local adaptation does not happen quickly enough, however, the immigration of preadapted lineages could result in the replacement of the founding lineage (Fukami 2015; De Meester et al. 2016). We therefore expect that there is a time window between the arrival of the founding propagule and subsequent immigrant propagules in which the immigrant lineages will still be able to form a substantial part of the population at equilibrium. By means of a minimal model of intraspecific competition, we here explore how the length of the window of opportunity for establishment depends on the initial fitness of the founding and subsequent immigrant lineages and on the rate of evolution. We compute the contribution of early and late immigrants to the population through time and show that once the population density and fitness is at equilibrium, populations are likely to be dominated by descendants of only a few early colonists.

Model

The specific scenario in which we theorize that there is a window of opportunity for establishment is as follows: a population formed by the colonization of one or a few immigrants in a habitat patch converges, through (*a*) population growth, (*b*) selection, (*c*) inflow of preadapted immigrants, and (*d*) mutations, on a regime in which the population is equally or better adapted to local conditions than any immigrant can be preadapted and has a much larger population size than the immigrant propagule. From then onward, and potentially even earlier, the system can be considered closed to immigrants, except for chance effects (i.e., the rare cases in which an immigrant is as preadapted to the local conditions as the resident population or is sufficiently close to it to have a reasonable chance to establish through genetic drift) or strong disturbances (including strong changes in environmental conditions). In appendix A, we demonstrate that through these chance effects alone, the replacement of resident lineages by new immigrant lineages is a very slow process. The time period before the system has converged on a regime, which in the remainder of the article we will call "equilibrium," is characterized by the establishment of new immigrants and an increase in degree of local adaptation and population size or density of established lineages and newly arriving immigrants. It is this preequilibrium period of the scenario that we want to capture with our model.

To capture the transient population and evolutionary dynamics after the founding of a new population, we use an approach that takes into account that evolution and ecology can occur at the same timescale. Traditional invasion analysis (also known as adaptive dynamics; see, e.g., Metz et al. 1995; Geritz and Éva 2000; Dieckmann et al. 2007) assumes that population dynamics are in equilibrium at the timescale at which mutations occur and is thus less suitable for our question. Here we model a growing and evolving asexual population by simulating the dynamics in population density of different competing heritable phenotypes (i.e., parts of the population with the same degree of maladaptation). Because of mutations, part of the offspring of a given phenotype will be of different phenotypes. Moreover, due to mutations, descendants of immigrants with different phenotypes can have the same phenotype. Only keeping track of phenotypes would thus obscure the impact of different immigrants on the population genetic structure. To deal with this, we also track immigrant lineages. We here define a lineage as an immigrant and all its descendants. By partitioning the population by both phenotype and lineage, we can model population growth as determined by fitness (phenotype) while at the same time track the success of lineages.

Intraspecific Competition Model

A key feature of our minimal model of intraspecific competition is that we can track immigrant history (i.e., lineages). Lineages can, however, evolve through mutations and thus consist of multiple phenotypes. Therefore, our model tracks the population density over time of all descendants of a lineage (i.e., same immigrant ancestor) that share the same phenotype P_i (with $i \in \{1, \ldots, a\}$ and $a =$ number of possible phenotypes). For this, we used the $(a \times n)$-matrix $\boldsymbol{N}$ with elements $N_{i,j}$, where i indexes the different possible phenotypes P_i and j indexes the different lineages. Note that n is the maximum number of possible immigration events (and thus lineages) during a simulation. In our implementation of the model in Matlab, n was a parameter that had to be predetermined to preallocate memory space to store the model output (for code, see https://doi.org/10.5281/zenodo.4723810; Kilsdonk and De Meester 2021).

In our model, the changes over time in population densities $dN_{i,j}/dt$ are calculated by summing three processes:

(1) resource-independent production of new offspring, (2) mortality due to (intraspecific) competition, and (3) additional mortality independent of resource competition. The implementation in our model of these three processes is discussed below.

We assumed competition has no effect on birth rate, and offspring are thus produced at rate b. While this assumption will often not hold, the assumption that reproduction is independent of competition likely is conservative with respect to the occurrence and persistence of evolution-mediated priority effects. If reproduction would depend on competition, the ability of lineages to evolve through mutations would be higher during the initial phase of colonization when population densities are low and would become lower (because of lower birth rates) for later immigrants.

We did not explicitly model genotypes and mutations in our model. Instead, we indirectly accounted for the effect of mutations on offspring phenotype by letting some offspring contribute to the population density of a phenotype one row higher or one row lower than the parent phenotype. More specifically, we ordered phenotypes as (P_1, P_2, … , P_a) and assumed a fraction μ (the mutation rate) of offspring of individuals with phenotype P_i had phenotype P_{i-1} (which increases the value of $N_{i-1,j}$) and the fraction μ of the offspring of individuals with phenotype P_i had phenotype P_{i+1} (which increases the value of $N_{i+1,j}$). The remaining fraction $1 - 2\mu$ of the offspring of individuals with phenotype P_i have the same phenotype as the parent. These fractions are the elements of the mutation matrix $\boldsymbol{Q}$, a $(a \times a)$-tridiagonal matrix:

$$\boldsymbol{Q} = \begin{bmatrix} 1-\mu & \mu & & & \cdots & & 0 \\ \mu & 1-2\mu & \mu & & & & \\ & \ddots & \ddots & \ddots & & & \vdots \\ & & \mu & 1-2\mu & \mu & & \\ \vdots & & & \ddots & \ddots & \ddots & \\ & & & & \mu & 1-2\mu & \mu \\ 0 & & \cdots & & & \mu & 1-\mu \end{bmatrix}.$$

Since the rate of reproduction by phenotype P_g (g indexes the parent phenotype) of lineage j equals $bN_{g,j}$, the rate at which reproduction adds to $N_{i,j}$ (i.e., the first process in our model) equals $\sum_{g=1}^{a}(\boldsymbol{Q}_{i,g} bN_{g,j}) = b(\boldsymbol{QN})_{i,j}$. As we expressed time in units of b (so that $b = 1$), $b(\boldsymbol{QN})_{i,j} = (\boldsymbol{QN})_{i,j}$, and we call the unit of time in the model generation time. Note that we assume that phenotype is perfectly heritable.

We model the mortality rate of $N_{i,j}$ due to competition with the function $-N_{i,j}\sum_{g,f} N_{g,f}/k$, where $\sum_{g,f} N_{g,f}$ is the total population density (i.e., the sum over all elements of $\boldsymbol{N}$) and k is the carrying capacity, which is the maximum population density given the available resources. Note that k is not the same as the equilibrium population density, as there can be additional resource-independent mortality (i.e., the third process in our model). By scaling population density in our model by k, the function of mortality due to competition simplifies to $-N_{i,j}\sum_{g,f} N_{g,f}$. To model the additional resource-independent mortality, we used $-d_i\boldsymbol{N}_{i,j}$, where d_i is the per capita rate of additional mortality of phenotype i.

The parameter influenced by the differences in phenotypes is thus d. The value of d_i depends on the mismatch between an individual's phenotype (P_i) and the environment of the habitat patch, that is, the degree of maladaptation. We used a unidimensional axis to represent both variation in phenotype and variation in environment. As phenotypic value of P_i on this axis, we used its index i (i.e., phenotypic value $= i$ with $i \in \{1, \dots, a\}$). We used the same set of possible values (i.e., $\{1, \dots, a\}$) for E, the environmental value of a given habitat patch. Thus, P_E denotes the optimum phenotype for a patch with environmental value E. The phenotype-environment mismatch—that is, the mismatch between P_i and the local environment scaled by the maximum possible mismatch between them—is given by

$$v_i = \frac{|i - E|}{a - 1}. \tag{1}$$

The maximum possible mismatch is $v_{\max} = 1$ and only occurs in the most extreme environments, where $E = 1$ or $E = a$. The per capita rate of additional mortality of each phenotype d_i is a linear function of v_i and has as minimum value $d_{\min}$ and as maximum value $d_{\max}$; thus, $d_i = v_i(d_{\max} - d_{\min}) + d_{\min}$. In our simulations, we used $d_{\min} = 0$ and $d_{\max} = 1$. Hence, in our simulations $d_i = v_i$ (in app. B, we show results for alternative $d_{\max}$ and $d_{\min}$ values). Note, however, that under $d_{\min} = 0$, total mortality is still higher than zero due to the resource-independent mortality.

Summing the three abovementioned processes gives the main equation of our model:

$$\frac{dN_{i,j}}{dt} = (\boldsymbol{QN})_{i,j} - N_{i,j}\sum_{g,f} N_{g,f} - d_i N_{i,j}, \tag{2}$$

with $i \in \{1, \dots, a\}$ and $j \in \{1, \dots, n\}$. If we ignore mutations (which has little effect on $dN_{i,j}/dt$ since $(\boldsymbol{QN})_{i,j} \approx N_{i,j}$), the only difference between phenotypes in their per capita rate of change in population density is d_i. Therefore, the (relative) fitness of a phenotype is a monotonically decreasing function of d_i.

Instead of differences between phenotypes in their d_i, we could have chosen to use differences in b or k. However, introducing variation in both b or k between phenotypes would introduce further complexities in the interpretation. Differences in birth rate (b) could result in an additional evolutionary advantage for phenotypes with a high birth

rate, as they produce more (mutated) offspring and thus can evolve faster. And competition has little effect on population density during the initial phase of colonization when population densities are low. Thus, introducing variation in both b or k between phenotypes would introduce further complexities in the interpretation, and hence we decided they were beyond the scope of this study. A consequence of tracking population densities instead of population size is that population sizes (but not densities) are effectively infinite. Two key consequences of this assumption are that even very small densities of a given phenotype can evolve and that there is no genetic drift. We address these concerns in appendix D. For all simulations (except those explained in app. D), we used Matlab solver ode45 with relative tolerance 5×10^{-6} and absolute tolerance 10^{-8}, and we set $\boldsymbol{N} = 0$ as the initial value. For each immigration event m (m between 1 and n) with phenotype P_i, $N_{i,m}$ is set from zero to the propagule density (s) at the time of immigration.

Migration Setups

By numerically solving the model, we obtain the densities of all phenotypes linked to their immigration history (phenotype × lineage combination). By performing simulations in which we inoculate immigrants of varying phenotypes (each starting up their own lineage) at different time spans after the arrival of the first colonist (founding migrant), we can assess how the densities of each lineage at population equilibrium are dependent on arrival order and time, as well as on the level of preadaptation to local habitat conditions of the immigrants.

For a detailed analysis of the relation between the phenotypes of founders and subsequent immigrants and the length of the window of opportunity for establishment, we performed simulations with a dual-migration setup in which we systematically varied phenotypes of the founding migrants and the invading immigrants to determine the time span following the arrival in the patch of the founder during which establishment of the invading immigrant is successful. We subsequently modeled a setting with multiple immigrants migrating from a regional gene pool, randomly picking phenotypes and arrival times for the propagules we introduced, to study to what extent natural populations are expected to be dominated by descendants of early colonists.

For both the dual- and multiple-migration setups, we used a propagule density of $10^{-3}k$ (i.e., a propagule density of 0.1% of k, which is reasonably large when translated to many real populations) and a mutation rate of $10^{-5}b$ (i.e., 0.001% of the offspring mutate per generation). Prior screening with up to 1,000 times smaller propagule densities and 10 times lower and higher mutation rates revealed that the window of opportunity for invasion is rather insensitive to these two factors (see app. C). Our sensitivity analysis for the number of possible phenotypes did reveal a clear positive relationship between the number of phenotypes and the length of the window of opportunity (see app. B). In the remainder of the article, we present the results of simulations using 20 phenotypes (i.e., 19 mutation steps between least and most adapted).

Dual-Migration Setup

We here assume that there is only one invading immigrant propagule following the founder (i.e., first immigrant) and determine the window of opportunity for establishment of this invading immigrant for all possible combinations of phenotypes of the invading immigrant and founder at their arrival in the patch—in the following we will refer to the original phenotypes of the lineage at the time of arrival in the patch as the ancestral phenotypes and corresponding phenotype-environment mismatch (in contrast to the distribution of phenotypes and mismatches among its descendants). Successful establishment was determined by a threshold T that determines the density that an invading lineage needs to reach in the population for the invasion to be considered successful. This threshold is needed because we use an infinite population size model. The threshold T was set at 0.05 (i.e., 5% of the population at equilibrium). To find the length of the window of opportunity for each combination of the ancestral phenotype of the invading immigrant and of the founder, we followed an optimization procedure (see https://doi.org/10.5281/zenodo.4723810; Kilsdonk and De Meester 2021). In brief, we drew on our observation, based on a wide variety of simulations, that the density of the invading immigrant lineage at population equilibrium is a strictly decreasing function of the lag in arrival time between the invading and the founding lineage (given time lags >0). Therefore, if the density of the invading lineage at the end of a run with a specified arrival time lag of the invading lineage was lower/higher than T, we can conclude that the window of opportunity for establishment was shorter/longer than that time lag. We first determined whether with a zero lag in arrival time, establishment of the invading lineage was successful, in order to test whether establishment of the invading lineage is possible at all. Whenever establishment was possible, we used the built-in Matlab optimization function fzero to find the lag in arrival time where the density of the invading lineage at the end of a run equaled T. By iterating this over all different combinations of founder and invader phenotypes, we generated a matrix with as elements the window of opportunity for each of these combinations.

The results of this analysis are shown in figure 1. The conceptual scheme in figure 1*A* illustrates that for a specific phenotype-environment mismatch of the founder—that is, the ancestral mismatch of the founding lineage (here

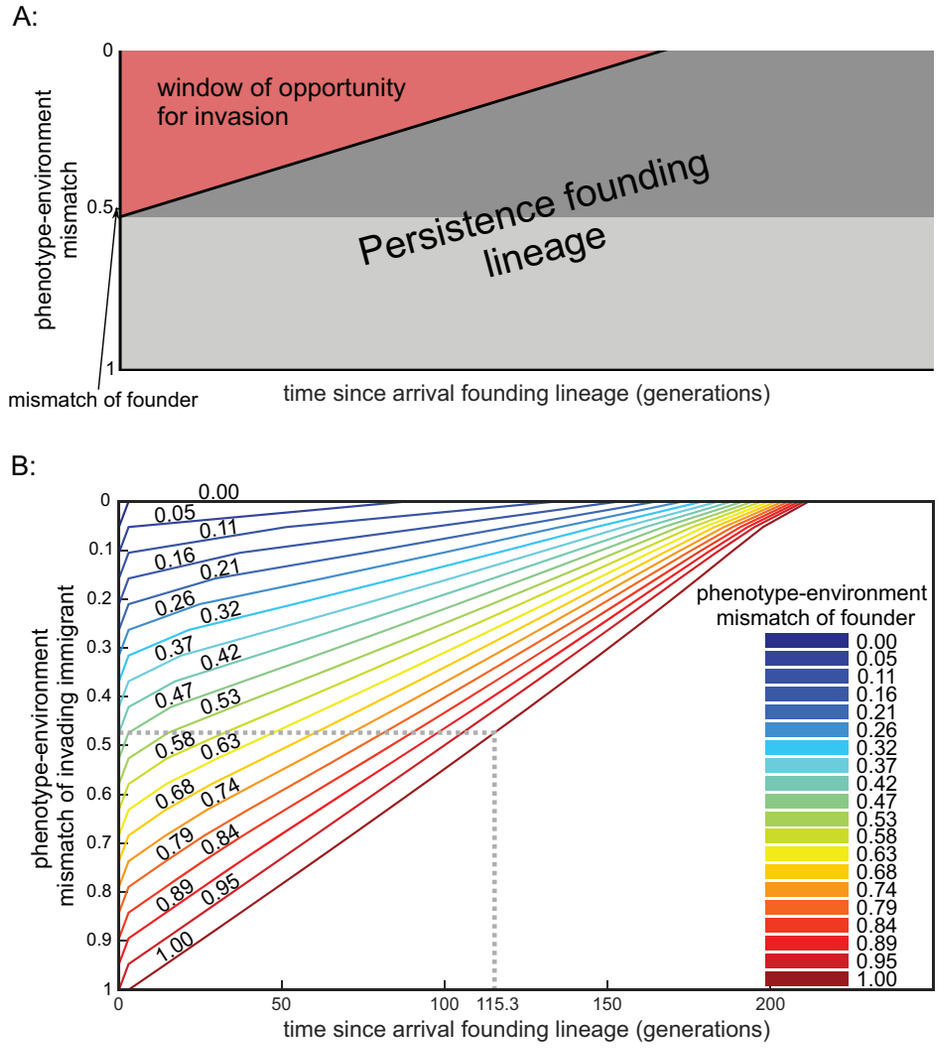

Figure 1: *A*, Visualization of the window of opportunity for establishment success (in red) for a certain ancestral phenotype-environment mismatch (v) of the founder. The light gray area is that where immigrants have a higher phenotype-environment mismatch (i.e., lower fitness) than the founder (i.e., the first immigrant, which started the founding lineage) and thus are not able to establish. The dark gray area is that where invading immigrants have a lower mismatch (i.e., higher fitness) than the ancestral phenotype-environment mismatch of the founder but could nevertheless not establish due to local adaptation of the founding lineage, resulting in a higher fitness of its descendants. *B*, Result of simulations to determine the window of opportunity for establishment success ($T = 0.05$) for scenarios with different ancestral phenotype-environment mismatches of the founder. The phenotype-environment mismatches of the founders corresponding to each line are indicated both on the line as well as by line color. We used $a = 20$ and $E = 1$. The dashed line is an example; it shows that the window of opportunity for establishment of an invading immigrant with a phenotype-environment mismatch $v = 0.47$ in a population founded by an immigrant with an ancestral phenotype-environment mismatch $v = 1.00$ equals approximately 115.3 generations.

assumed to be $v_{\hat{i}} = 0.5$; the mismatch of the intermediate phenotype P_i with $\hat{i} = E \pm (a - 1)/2$)—one can determine the period in which establishment is still possible for an invading lineage with a certain ancestral phenotype-environment mismatch. The red triangular area indicates the conditions under which the invading immigrant phenotype can establish (i.e., reach a density higher than T in the final population; $T = 0.05$). If the ancestral phenotype-environment mismatch of the founder is 0.5, only immigrants with a phenotype-environment mismatch close to or lower than 0.5 can establish. On arrival, the founding lineage starts to grow and adapt. As a result, the invading lineage has to be increasingly more preadapted to be able to establish as time since the arrival of the founder progresses. Any invading immigrant with a distinctly lower fitness (i.e., higher d_i in our model) than the founder will not be able to establish in a deterministic setting (light gray area in fig. 1*A*). Moreover, immigrants with a higher fitness (lower d_i) than the

original founder have only a limited window of opportunity to invade, due to local adaptation of the resident population (see red area in fig. 1*A*). Thus, for any given ancestral phenotype-environment mismatch of the founder, a window of opportunity can be determined, that is, the parameter space in which the phenotype-environment mismatch of the invading immigrant is low enough and the lag in arrival time is short enough for establishment to succeed. Figure 1*B* shows these windows for different phenotype-environment mismatches v_i of the founder (note that $v_i = d_i$, as $d_{\max} = 1$ and $d_{\min} = 0$). Each line in figure 1*B* divides the parameter space into establishment success (area above line, corresponding to the red area in fig. 1*A*) and establishment failure (area below line, corresponding to the gray areas in fig. 1*A*). For instance, an invading immigrant with a $v_i = 0.47$ (horizontal gray dashed line in fig. 1*B*) has a window of opportunity of 115.3 generations to successfully invade a resident population that started with the highest phenotype-environment mismatch (i.e., $d_{a-1} = 1$ for the ancestral phenotype of the founder) but had the capacity to locally adapt.

Multiple-Migration Setup

There are many systems in which not two but many immigration events take place. In these systems, we are no longer primarily interested only in whether the second immigrant can replace the founder lineage but also whether later immigrants do. For example, if an unsuccessful first invasion can have a negative effect on the resident population, it may enable a second immigrant to be successful. Moreover, evolution-mediated priority effects can manifest themselves as the persistence of a group of early colonist lineages and not exclusively the first-arriving lineage. To estimate in a metapopulation context the persistence of early colonist lineages in a patch with several immigration events, we used a multiple-migration setup in which multiple lineages with different phenotypes are introduced at different points in time. We assumed that the phenotype of each propagule was randomly drawn from the distribution of phenotypes in the regional gene pool; that is, we assumed no specific spatial configuration of patches with specific environments in the landscape. The phenotype and the arrival time of each lineage was derived from two metapopulation parameters: (1) the migration rate (or immigration probabilities) to the habitat patch of interest and (2) the differences in environmental conditions between the habitat patch of interest and the surrounding patches. We ran simulations for different immigration frequencies I (0.05, 0.2, and 0.8 propagules per generation, unless otherwise specified), representing the probability per time step that a propagule with density $10^{-3}k$ arrives in the target patch. For each time interval of 0.25 generations, we randomly drew from a Bernoulli distribution with Pr(immigration event) $= I \times 0.25$ to determine whether an immigration event had occurred. In our model, the environmental value E of a habitat patch can only have the discrete set of values $\{1, 2, \ldots, a\}$. Therefore, we used the binomial distribution to describe S_E, the probability distribution of E for habitat patches in the metapopulation, as the closest discrete approximation of a normal distribution (fig. 2*A*):

$$\begin{aligned} S_E &= B\left(E-1, a-1, \frac{1}{2}\right) \\ &= \binom{a-1}{E-1}\left(\frac{1}{2}\right)^{E-1}\left(1-\frac{1}{2}\right)^{(a-1)-(E-1)} \\ &= \binom{a-1}{E-1}\left(\frac{1}{2}\right)^{a-1}, \end{aligned}$$

with B denoting the probability mass function of the binomial distribution and the binomial coefficient

$$\binom{\eta}{x} = 0$$

if $x > \eta$ or $x < 0$. We assume that in the patches surrounding the new patch, the populations were already fully adapted to the local conditions of that patch. Therefore, the probability of phenotypes P_i in immigrants is $S_i = S_E$ for all $i = E$.

We simulated two different types of settings, where the environment in the target habitat (to be invaded) is rare or common at the regional scale (for results with an intermediate environment, see app. E). As we allowed for 20 possible phenotypes and environments (i.e., $a = 20$), this corresponds to values for E in the target habitat of 1 and 11, respectively (see fig. 2*B*; for $E = 6$, see app. E).

We performed simulations for all six combinations of the mentioned values for E (i.e., 1 and 11) and I (0.05, 0.20, and 0.8 propagules per generation). Based on preliminary test runs to examine the time needed for ecological and evolutionary dynamics to stabilize, we decided to run each simulation for 500 generations. We repeated each simulation 200 times, randomly assigning arrival time and phenotype of each propagule. As early-arriving colonist lineages with an optimally preadapted phenotype can also persist through non-evolution-mediated priority effects, we also repeated all simulations with a mutation rate of zero (i.e., without mutations) for comparison.

Arrival Rank of Lineages and Their Contribution to the Population at Equilibrium. Besides scenarios in which the founder is able to prevent establishment success of the immigrants, it is also possible that the founder is replaced by another early immigrant, which then prevents establishment

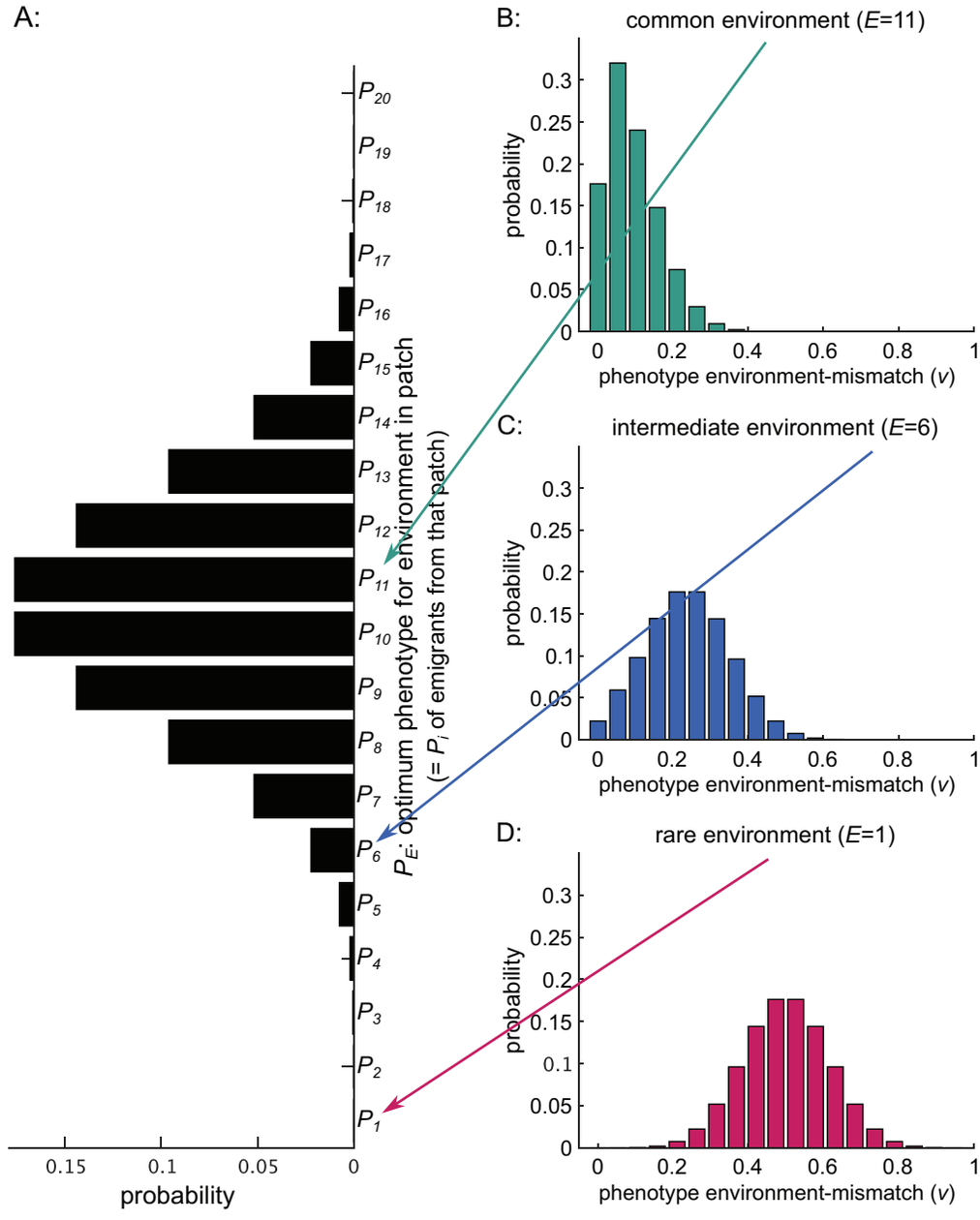

Figure 2: The three tested scenarios with different environments in the target habitat: $E = 1$, $E = 6$ (see app. E), and $E = 11$. These conditions are shown in red, blue, and green, respectively. *A*, Probability distribution of optimum phenotypes for patches in the landscape S_E, corresponding to the hypothetical distribution of environments in the landscape. Because we assume that populations in all nontarget patches are locally adapted and contain only the optimum phenotype, this is also the distribution of phenotypes among immigrants S_i. The arrows indicate the optimum phenotype P_E of the three different environments that we picked as examples for our simulations. *B–D*, Distributions of phenotype-environment mismatches v_i ($= d_i$) that immigrants randomly drawn from the metapopulation would have if the target patch has values for $E = 11$ (*B*), $E = 6$ (*C*), and $E = 1$ (*D*).

success of subsequent immigrants. This would still constitute an important priority effect viewed from the perspective of a situation in which there are regular immigrants during the whole time period. To study priority effects, we ranked migrant lineages (i.e., parts of the population with the same immigrant ancestor) based on the arrival order of those lineages in the population. Figure 3 shows the percentage in the population of the different

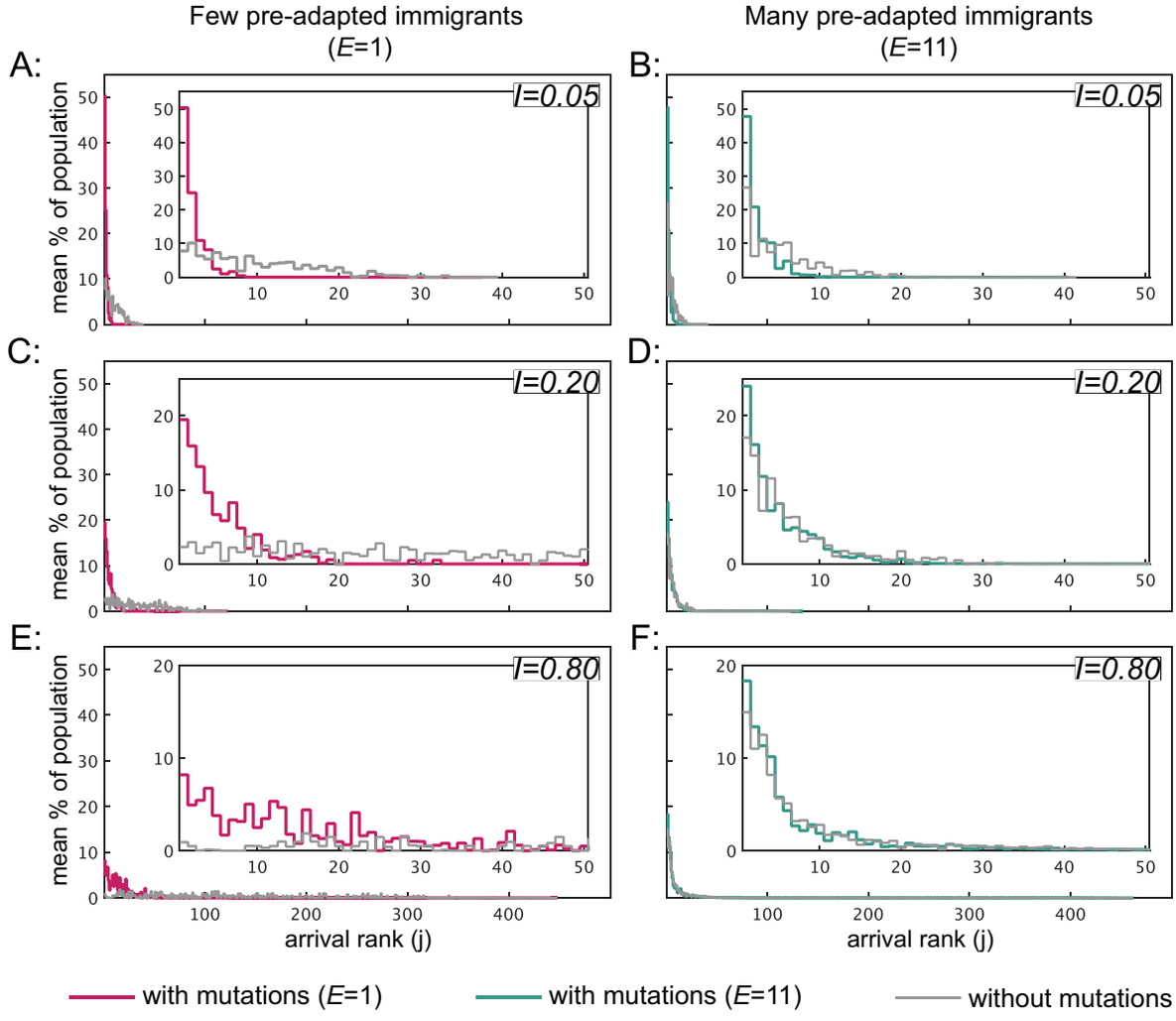

Figure 3: Evolution of migrant lineages increases the percentage of early-arriving lineages in the population 500 generations after the arrival of the founder immigrant, especially in rare environments for which few immigrants are preadapted. For each of the six tested combinations of environment in the target patch ($E = 1$ and $E = 11$ shown in the left [*A*, *C*, *E*] and right [*B*, *D*, *F*] panels, respectively; for $E = 6$ see app. *E*, fig. E1) and propagule immigration frequency ($I = 0.05$, $I = 0.20$, and $I = 0.80$; panels in the upper, middle, and lower rows, respectively), a panel shows the fraction of the population with different arrival ranks averaged over 200 replicates. Each panel also has an inset plot showing a close-up of the first 50 arrival ranks, which captures most of the pattern. The population in each replicate run has a mean arrival rank. The grand mean arrival ranks (i.e., the mean of these replicate means) with mutations (i.e., evolution of lineages) are 1.99, 2.33, 5.18, 5.78, 16.55, and 24.14 for *A*, *B*, *C*, *D*, *E*, and *F*, respectively. The effect sizes, calculated as the difference in grand mean arrival rank between simulations without and with mutations, are 7.56, 2.91, 27.66, 1.58, 110.22, and 1.72 for *A*, *B*, *C*, *D*, *E*, and *F*, respectively.

*n*th arriving lineages (ordered by arrival order) averaged over 200 runs. At low propagule immigration frequencies, only the population densities of a few (often <10) early-arriving lineages usually reach a high proportion at equilibrium (i.e., 500 generations after the arrival of the founder). With increasing immigration frequencies, the number of later immigrants that can reach reasonable proportions increases but still remains within the group of the 20 first immigrants, in most cases. A high immigration frequency (0.8 propagules per generation) combined with a low number of preadapted phenotypes results in a further spreading of establishment success of immigrants, but here still nearly all successful lineages are within the 50 first immigrants. In the scenarios with many preadapted phenotypes, the clustering of successful lineages toward early immigrants is also quite pronounced in the absence of evolution of lineages, but for scenarios with a low number of preadapted immigrants, the successful lineages are

much more spread across time in the absence of evolution of lineages, especially when immigration frequencies are high (fig. 3).

Lineage Richness at Equilibrium. Despite the fact that many lineages seem to persist when population frequencies are averaged over 200 replicate runs (see fig. 3), it is possible that in many individual runs, only one lineage persists and that the spread in the distribution of mean arrival ranks is due to variation between replicate runs instead of high lineage richness within each run. Therefore, we show lineage richness in figure 4. Because, due to the nature of the model, no lineage can truly become extinct (instead lineages can have an exponential decay with as limit zero), a cutoff value below which a lineage density is considered too low to be counted into the lineage richness is needed. A logical option is to exclude lineages that have not increased in density after their arrival. Specifically, we used 1.05 times the propagule density s ($1.05s = 1.05 \times 10^{-3}k$) as cutoff value and thus only included lineages with a density at least 5% higher than the propagule density.

Both with and without mutations, we find that fewer preadapted immigrants and a lower immigration frequency results in a lower lineage richness (fig. 4). With few preadapted immigrants ($E = 1$), for all the tested immigration frequencies (ranging from 0.05 to 0.8 propagules per generation), the mean lineage richness is below 2 (fig. 4). With many preadapted immigrants ($E = 11$), the mean lineage richness is between 2 and 13 for all tested immigration frequencies (fig. 4). In all tested conditions, the lineage richness is almost equal in simulations without compared to simulations with mutations (fig. 4). The standard deviation in lineage richness between replicates is more pronounced when the lineage richness is higher (fig. 4).

Dynamics Preceding Population Equilibrium

Thus far, we have focused on the length of the window of opportunity for establishment. However, exploring the dynamics occurring during growth and evolution of the population toward the equilibrium can help us explain why the window of opportunity closes and the equilibrium population is mainly composed of descendants of early colonizers.

In the dual-migration setup, depending on the arrival time and ancestral phenotype of both founder and invader, there are three outcomes possible: (1) the founding lineage prevents a second lineage from invading, (2) the second lineage manages to invade but does not replace the founding lineage, or (3) the second lineage replaces the founding lineage. An example of the transient dynamics in each of these three scenarios is shown in figure 5 using Muller plots (Muller 1932; Crow and Kimura 1965). The only setting altered

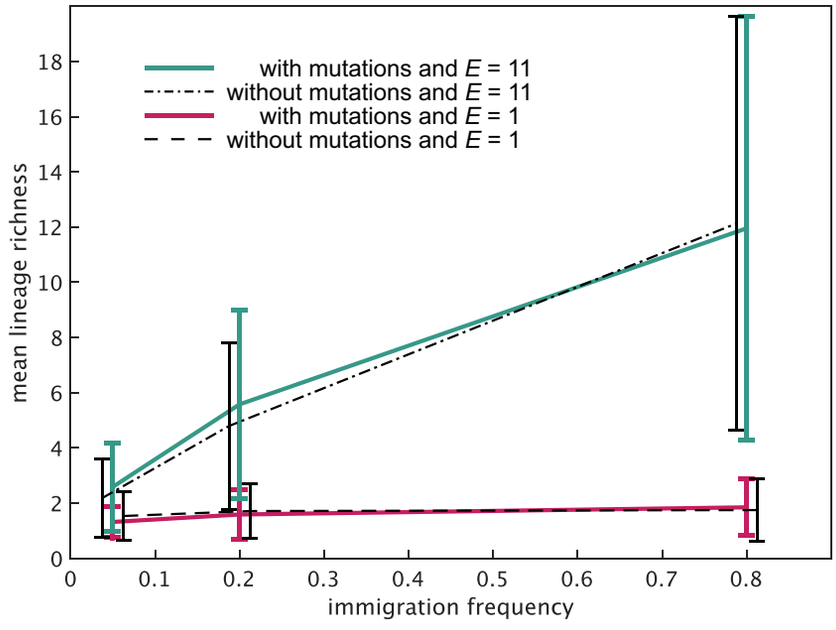

Figure 4: Lineage richness averaged over all 200 replicates for simulations with different immigration frequencies for both rare environments ($E = 1$) and common environments ($E = 11$) and with and without evolution of lineages (i.e., mutations). Only lineages with a density at least 5% higher than the propagule density were included in the count. Error bars depict the standard deviation. Both low immigration frequencies and rare environments result in low lineage richness. Evolution of lineages has little effect on the mean lineage richness per run.

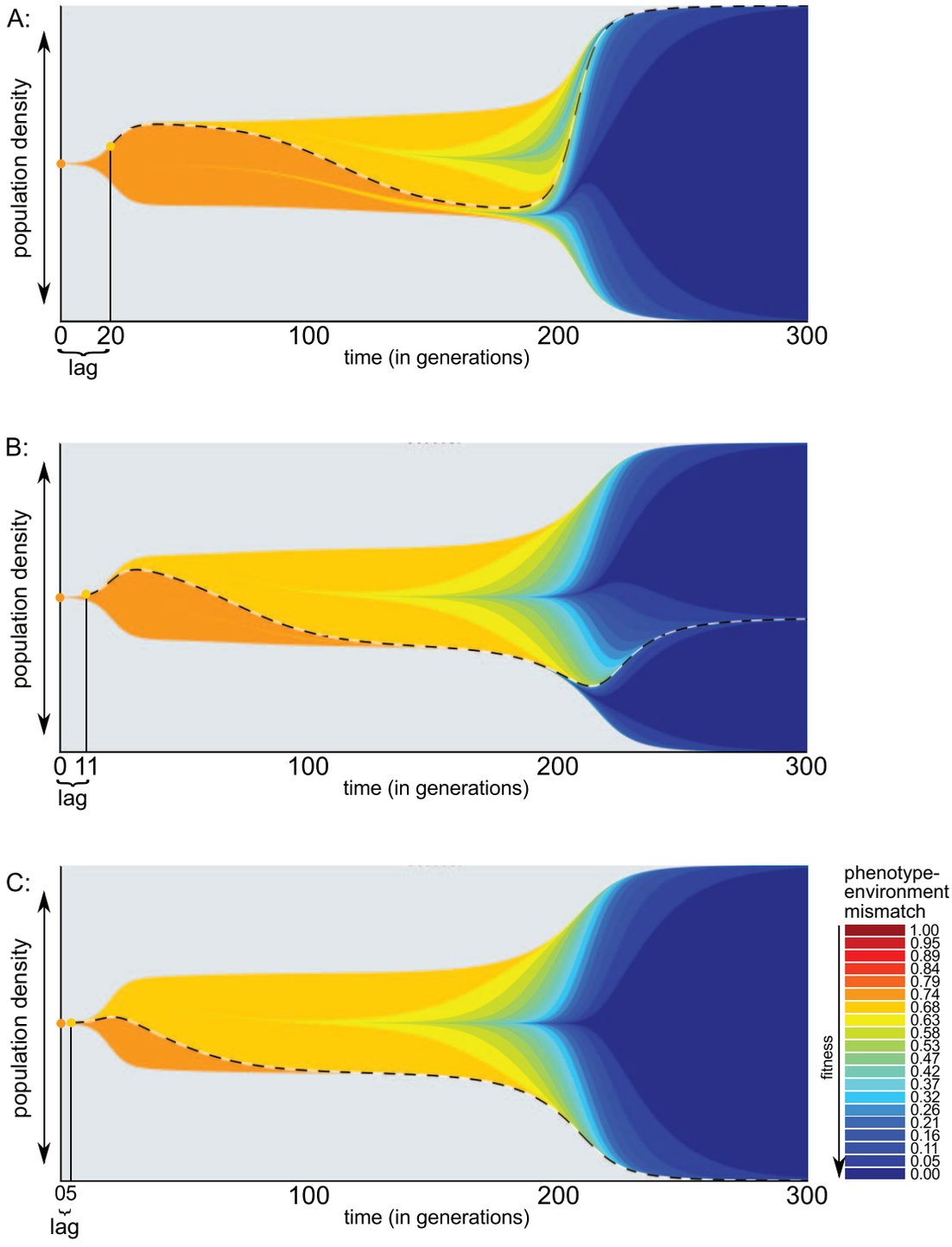

Figure 5: Three examples of the preequilibrium dynamics of runs with the dual-migration setup. In this setup, there is one founding lineage (i.e., descendants of the first immigrant) and one invading lineage (i.e., descendants of the second immigrant). In all three simulations, $a = 20$ and $E = 1$; that is, there are 20 possible phenotypes P_i (see color legend), where $i = \{1, 2, \ldots, 20\}$ with 20 corresponding phenotype-environment mismatches ν_i. At time $= 0$, the first lineage (with P_{15}: $d_{15} = \nu_{15} \approx 0.74$) is introduced (see circle at time $= 0$), and after a certain time lag (as indicated by curly brackets, these lags are 20, 11, and 5 generations for *A*, *B*, and *C*, respectively; note that even the longest time lag shown is still relatively short compared with the time at which the population reaches equilibrium) a second invading lineage (with P_{14}: $d_{15} = \nu_{14} \approx 0.68$) is introduced (see second circle). A dashed line separates the two lineages (with the density of the invading lineage above the line). Over time, mutations lead to new phenotypes (see change in color) in both lineages. The population densities are represented by the vertical width. The actual location on the vertical axis, apart from whether it is above or below the dashed line separating lineages, carries no information.

between the three examples in figure 5 is the lag in arrival time between the founder and the immigrant. In figure 5*A*, the invading lineage arrives too late to prevent the founding lineage from taking over the entire patch. In figure 5*B*, the invading lineage arrives in the window of time in which it ends up partially taking over, and in figure 5*C*, the invading lineage arrives in time to de facto outcompete and replace the founding lineage.

In each of the three runs in figure 5, we see an initial rapid increase in population density that levels off toward the fitness-dependent carrying capacity. Subsequently, as the population is locally adapting, the resource-dependent per capita mortality rate of the population decreases and the carrying capacity of the population increases gradually, until it eventually reaches the carrying capacity of an optimally adapted population. Early on during the simulation, optimally and close to optimally adapted phenotypes are already present in the population but at extremely low densities. The descendants of these genotypes take over and replace less well-adapted lineages in a predictable way, given that our model is entirely deterministic. For results of simulations with finite populations, we refer to appendix D. We return to this in the discussion section.

For the multiple-migration setup, figure 6 shows the grand mean arrival rank and mean lineage richness (cutoff value $= 0.00105k = 105\%$ of the propagule density) over the 200 replicate runs during the growth and evolution of the population toward an equilibrium during the first 750 generations. Both with and without mutations, all four different scenarios showed an initial increase in grand mean arrival rank and mean lineage richness. In the simulations with mutations, this initial increase was followed by a decrease and then stabilization of grand mean arrival rank and mean lineage richness in the scenarios with few

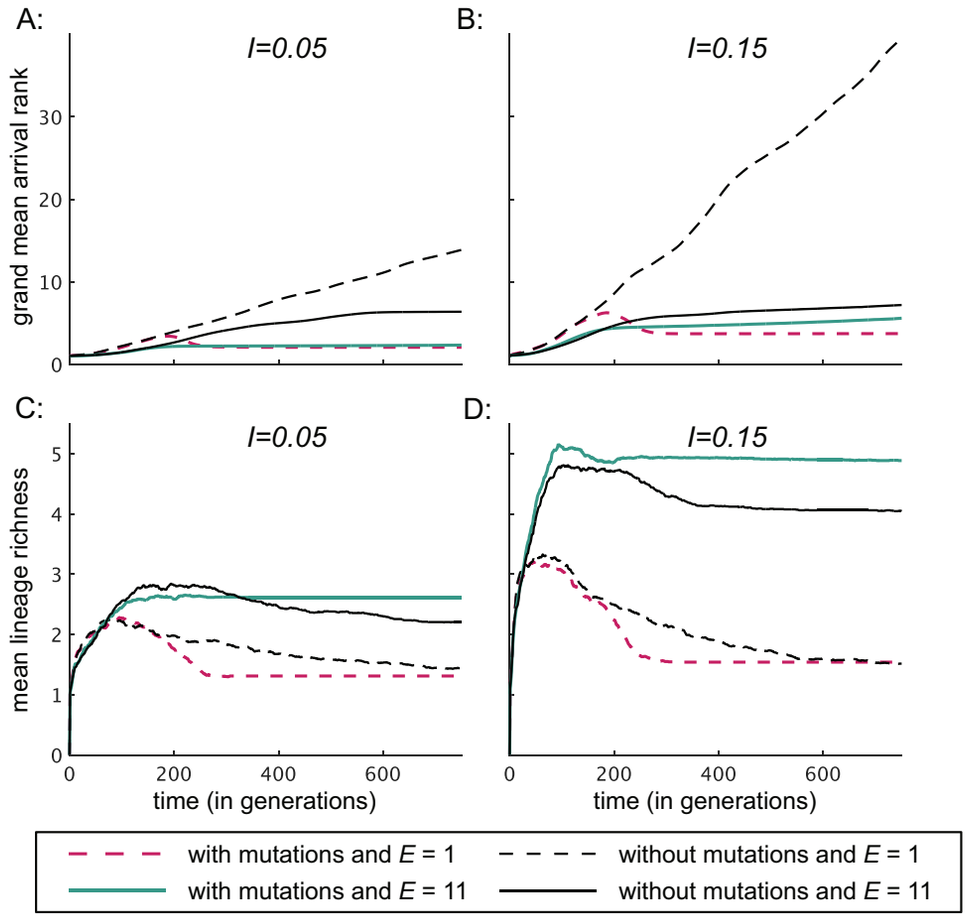

Figure 6: Arrival rank and lineage richness over time using a multiple-migration setup. Only lineages with a density >105% of the propagule density were included in the calculation of lineage richness. The first founding propagule was set to arrive at $t = 0$ in each simulation. The immigration frequencies tested ($I = \{0.05, 0.15\}$ propagules per generation) are shown in each panel. The environments tested are rare ($E = 1$) and common ($E = 11$; shown in dashed red and solid green, respectively). The black lines show the results for identical scenarios but without mutations (solid for $E = 11$ and dashed for $E = 1$).

preadapted immigrants (fig. 6). In the simulations without mutations, the initial increase in mean lineage richness was followed by a continuous gradual decrease in all scenarios. Considering this decrease was still ongoing at the end of the simulations without mutations, the final mean lineage richness in the scenarios without mutations is always similar to or lower than in scenarios with mutations. However, the main difference between the settings with and without mutations is that in the latter case, the grand mean arrival rank is much higher at equilibrium due to a continuous replacement of lineages. In contrast, the mean arrival rank in all scenarios in which evolution of lineages is possible stabilizes within the first 300 generations at very low level (<5 in most scenarios).

Discussion

Standard population and landscape genetic analyses often ignore the legacy of colonization history and therefore tend to interpret patterns of genetic structure as a function of the balance between contemporary gene flow, genetic drift, mutations, and selection. In this scheme, priority effects, including evolution-mediated priority effects, are often ignored (Boileau et al. 1992; De Meester et al. 2016). In the model presented here, priority effects can be identified as the model keeps track of the dynamics of each lineage and explicitly considers the nonequilibrium conditions during the initial colonization phase. We included simulations with and without mutations to test for the effect of evolution of lineages on the strength of priority effects. We modeled both dual-migration and multiple-migration settings. Our simulations indicate that for an extensive range of preadaptedness of immigrants, arrival time, and parameters related to evolutionary rate (i.e., mutation rate and fitness differences per mutational step), priority effects are common and local populations at equilibrium are most often dominated by descendants of the first few immigrants only.

Our dual-migration setup simulations show that, in alignment with our expectations, the degree of preadaptation of both the founder and the invader (see fig. 1*B*), the time lag between the arrival of the founder and the invader (see fig. 1*B*) and the rate of evolution (see app. B) determine the success, measured as the relative abundance at equilibrium, of an invading lineage in a population that can adapt to local environmental conditions. High preadaptation in the founder, low preadaptation in the invader, and high evolutionary rates, which are among others dependent on the fitness gain per mutational step, result in a short window of opportunity for establishment of a lineage in a resident population. The potential of early-arriving lineages, even when not optimally adapted, to limit the establishment of later-arriving lineages, and the dependence of this process on the arrival time, has been reported in experimental studies on bacterial communities and gut microbiota (Martínez et al. 2018; Svoboda et al. 2018). The window of opportunity for establishment by a second immigrant was short. This leads to the prediction that populations at equilibrium will generally be dominated by descendants of a few early-arriving lineages only.

To explore whether evolving populations that are exposed to multiple immigration events are at equilibrium dominated by descendants of the first few colonists, we also explicitly modeled settings characterized by multiple invasions. Here, the added insight is that we could quantify lineage richness and mean arrival rank of the lineages at equilibrium. Both are expected to be low when priority effects are important and strong. We modeled different landscapes that differ in the degree to which the environmental conditions in the target patch are common at the landscape scale, as this determines the probability that immigrants are preadapted to the local patch. In all tested combinations (each replicated 200 times) of propagule immigration frequency and environmental rarity, populations at equilibrium had a low mean lineage richness (see fig. 4) and showed a negative correlation between the arrival rank and the mean population density (see fig. 3) and thus a low mean arrival rank. Hence, our model suggests that priority effects are expected to be common in the broad range of tested conditions.

To quantify the degree to which evolution of lineages can enhance priority effects—that is, to test the importance of population monopolization or evolution-mediated priority effects (De Meester et al. 2002, 2016; Urban and De Meester 2009)—we compared simulations with and without mutations. In most of the tested combinations of environmental rarity and immigration frequencies, the mean arrival rank of lineages that make up the population after 500 generations is lower in the presence of mutations than in the absence of mutations. Moreover, as in some simulations the most preadapted immigrant does not arrive within 500 generations, in the absence of mutations, the mean arrival rank in those simulations is not in equilibrium after 500 generations, and hence the difference in grand mean arrival rank can increase even further after this period (see fig. 6). Our results thus indicate that long-term priority effects are strongly dependent on the resident populations' potential to evolve if there are few preadapted immigrants. The resulting priority effects are strong, as the mean arrival rank of most populations at equilibrium is less than 6, clearly indicating that the population is dominated by the first few colonists even after 500 generations representing approximately 25 to 400 immigrants depending on the immigration rate. In contrast, in scenarios with many preadapted immigrants, letting lineages evolve merely

reduced the mean arrival rank by less than 3 ranks. This is not unexpected given that at high immigration frequencies in landscapes with many similar habitats, optimally adapted lineages have a high likelihood to arrive early, resulting in a strong priority effect without evolution of lineages. Evolution does, however, enhance priority effects in scenarios where the first-arriving lineages tend not to be optimally adapted. Hence, our results suggest that evolution-mediated priority effects might be common. Overall, we expected and found a larger monopolization effect (i.e., a large contribution of evolution to the priority effect) when immigration frequencies are low (as this causes larger average time lags between subsequent colonizers, allowing more time for evolutionary trait change) and when there are few preadapted immigrants. The latter should be reflected in stronger evolution-mediated priority effects in patches characterized by regionally rare environments than in patches with regionally common environments.

Next to the difference in arrival time and the ancestral environment-phenotype match of both the founder and invader, the rate of evolution is expected to influence the length of the window of opportunity for establishment of the invader. We tested for different rates of evolution of lineages by varying the mutation rate (range 10^4 to 10^6; see app. C) and the fitness gain or loss that is achieved through each mutation (see app. B). In contrast to varying the fitness gain or loss, varying mutation rate did not have a strong effect on the window of opportunity for establishment.

In conditions producing a large monopolization effect, we expected a lower lineage richness at equilibrium in simulations with mutations than those without mutations. Our results do not show such a difference in average lineage richness in simulations with and without mutations. Rather, the mean lineage richness was low in all simulations. Thus, our results suggest that population monopolization, despite resulting in a larger influence of early-arriving lineages on the population genetic structure at equilibrium, does not necessarily result in a lower lineage richness. Our simulations also show that lineage richness at equilibrium is, under a broad range of scenarios, lower than lineage richness after 100 to 200 generations (see fig. 6). This is likely the result of the fact that during the first generations population growth is exponential and allows multiple lineages to coexist due to gene surfing (Excoffier and Ray 2008; Hallatschek and Nelson 2008). As competition increases in our patch, local fitness becomes more important and gradually an equilibrium richness is reached, which is in most cases lower than the lineage richness at intermediate stages (see fig. 6).

Given the widespread occurrence of contemporary evolution, our results suggest that landscape genetic structure in nature may often largely result from the dynamics that occurred during colonization and the initial out-of-equilibrium population dynamics following colonization. In our simulations, most populations at equilibrium are indeed dominated by the descendants of only a few early-arriving immigrants. Estimates of gene flow often reported in population and landscape genetic and genomic studies should thus be interpreted with care, as they often might not only reflect current levels of gene flow but also might be strongly impacted by colonization dynamics (Orsini et al. 2013). This introduces an important element of stochasticity in the observed landscape genetic structure, as among-population genetic differentiation might then to a large extent be determined by arrival order of genotypes during colonization of habitats.

Generality of Results

Our results are clear-cut and striking in their prediction that most populations would be dominated by the descendants of a few early-arriving lineages. We implemented a quite broad set of scenarios, varying immigration frequencies over several orders of magnitude and testing landscapes in which the target patch differs in terms of its uniqueness in environmental conditions. We also explored the effect of different fitness gain or loss per mutation (see app. B), mutation rates (see app. C), and population sizes (see app. D). We deliberately kept our model very general, and a number of key simplifying assumptions were made.

First, we made strong simplifications on the evolutionary mechanism underpinning adaptation (i.e., asexual reproduction, haploid individuals, relatively large selection differentials, no horizontal gene transfer, no epistatic interactions, etc.). These assumptions can affect the rate of evolution (Muller 1932; Crow and Kimura 1965; Orr and Otto 1994; Orr 2000; Rice 2002). Overall, however, our results should not be overly sensitive to the precise evolutionary mechanism, but rather may depend on the potential rates of evolutionary trait change. Our key finding, that patches tend to be monopolized by the descendants of only a few early-arriving lineages, is linked to the fact that local adaptation of lineages always occurred and was rapid compared with the rate of immigration (Haldane 1930; Richardson et al. 2014). Rapid local adaptation has increasingly been reported for natural populations across a broad range of organisms including vertebrates, microbial organisms, and higher plants (Thompson 1998; Hendry and Kinnison 1999; Kinnison and Hendry 2001; Palumbi 2001; Zhao et al. 2019). Genetic architectures and life cycles that would slow down evolution considerably are expected to increase the window of opportunity.

Second, in the main model we assumed infinite deterministic population sizes; that is, we used densities and

not number of individuals. Therefore, mutations almost instantly add infinitesimally small densities to each phenotype. Several modeling studies (Gerrish and Lenski 1998; de Visser et al. 1999) show that the population size determines the supply rate of mutations, which affects the rate of adaptation. To explore potential biases introduced by the fact that we worked with a population of infinite size—that is, where the (1) supply rate of mutations is infinite and (2) stochasticity is absent—we also implemented our simulations in a stochastic ordinary differential equation model with finite population sizes (see app. D). We observed that with increasing population size, the rate of adaptation converges on that of the regular infinite population size model (see app. D, figs. D1, D2; figs. B1, B2, C1, D1–D4, and E1 are available online) and that in general the finite population size model gave qualitatively similar results to the infinite population model (see app. D, figs. D3, D4). Small populations show a higher mean arrival rank (fig. D3), because local adaptation takes longer (figs. D1, D2), leading to reduced priority effects. Overall, our observation that the landscape genetic structure in heterogeneous landscapes might largely be determined by the identity of the first few colonizers in each of the habitat patches likely holds for species that build up local population sizes of intermediate to large sizes (several thousand or more). While this excludes many of the larger-bodied species that have small local population sizes, our results thus likely hold for many smaller-bodied organisms for which local populations (e.g., herbivore insects on a single tree) often rapidly grow to thousands of individuals.

Third, our model is not spatially explicit; that is, it excludes migration-based feedback loops between patches. One interesting spatial setting to which our model applies is that of (environmentally rare) small peripheral habitat patches connected to one very large source patch, where effect of the peripheral patches on the common habitat patch is negligible. For this setting, our model predicts strong evolution-mediated priority effects for the peripheral populations, resulting in those populations being dominated by a few early-arriving colonist lineages. Indeed, studies of the bivalve mussel *Brachidontes* sp. in marine lakes with varying degrees of connection to the sea show widespread evidence suggestive of evolution-mediated priority effects even in well-connected lakes, including high genetic differentiation between nearby lakes, a correlation between lake temperature and genotype at the local scale, and an estimated bottleneck event roughly coinciding with the filling of the lakes (Maas et al. 2018; Leeuw et al. 2020). More spatially explicit models with migration-based feedback loops between patches or a sequential order of habitat patch colonization (Ramachandran et al. 2005; Excoffier and Ray 2008; Hallatschek and Nelson 2008) are beyond the scope of this article but might reveal additional patterns.

Finally, an important simplifying assumption we made is that the environmental conditions that determine which phenotype has the highest fitness in local habitats do not change over time. One can expect, however, that priority effects might still predominate in systems in which the rate of environmental change is sufficiently slow and gradual so that the resident population can genetically track the changes and stay well adapted (Loeuille and Leibold 2008). An example of a setting in which evolution-mediated priority effects persist despite environmental changes is in populations of the human gut bacteria *Bacteroides fragilis* (Zhao et al. 2019). Exploring the effect of changing environmental conditions on colonization dynamics in future work might provide a more realistic picture on when and in which environments populations will tend to be dominated by early-arriving colonist lineages. There are many settings in which rapidly fluctuating or otherwise changing biotic environments are common, such as in the case of host-parasite dynamics (Khibnik and Kondrashov 1997; Dybdahl and Lively 1998; Dercole et al. 2006; Decaestecker et al. 2007; Kouyos et al. 2007; Ebert 2008) or predator-prey cycles (Yoshida et al. 2003; Dercole et al. 2006). For host-parasite and predator-prey dynamics, many studies have reported that contemporaneous evolution can strongly impact ecological dynamics, similar to the eco-evolutionary dynamics impacting establishment success in our model (Hairston et al. 2005; Urban et al. 2008; Pantel et al. 2015; Hendry 2017). To what extent changing environmental conditions interfere with the persistence of evolution-mediated priority effects needs further study.

To conclude, despite our simplifying assumptions on the evolutionary and ecological mechanisms, our results suggest that under a broad range of immigration frequencies and uniqueness of local environmental conditions, local adaptation can sufficiently increase the fitness of resident populations so as to reduce establishment success of later-arriving lineages, thus enhancing priority effects (De Meester et al. 2002, 2016).

Conclusion

We studied the dynamics during the colonization of a new habitat patch using a minimalistic model of competition between evolving asexually reproducing lineages in which we can track the fate of all immigrant lineages. In general, we found that the window of opportunity for the establishment of late-arriving lineages is short due to local adaptation of the descendants from founding lineages and that the length of this window of opportunity critically depends on the ancestral fitness of both the founding and the invading immigrants. We tested the implications of this short window under a variety of propagule immigration frequencies and environmental landscape settings in which

the habitat patch to be invaded was rare or common. We consistently found that lineage richness is low in populations at equilibrium and that in simulations with evolution of lineages, equilibrium populations are dominated by descendants of early-arriving lineages, with the mean arrival rank being lower than 6 in most simulations (up to 25 in simulations with many preadapted immigrants). Evolution of lineages made a substantial difference, because in the absence of it in environmental settings with few or an intermediate number of preadapted immigrants, we found that the populations at equilibrium were no longer dominated by early-arriving lineages. These results have important implications for landscape genetic structure in heterogeneous landscapes, which is expected to be strongly influenced by colonization dynamics (isolation by colonization; Orsini et al. 2013).

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Statement of Authorship

Both authors jointly developed the concept of the study. L.J.K. was responsible for coding the simulations and model analyses, with input from L.D.M. L.J.K. wrote the manuscript, which L.D.M. edited and revised.

Data and Code Availability

Code for all simulations and associated figures is publicly available at https://github.com/LJ-Kilsdonk/Window.git (Kilsdonk and De Meester 2021; https://doi.org/10.5281/zenodo.4723810).

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