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Despite the amplified threats of extinction facing small founder populations, successful colonization sometimes occurs, bringing devastating ecological and economic consequences. One explanation may be rapid evolution, which can increase mean fitness in populations declining towards extinction, permitting persistence and subsequent expansion. Such evolutionary rescue may be particularly important, given Allee effects. When a population is introduced at low density, individuals often experience a reduction in one or more components of fitness due to novel selection pressures that arise from diminished intraspecific interactions and positive density dependence (i.e. component Allee effects). A population can avoid extinction if it can adapt and recover on its own (i.e. evolutionary rescue), or if additional immigration sustains the population (i.e. demographic rescue) or boosts its genetic variation that facilitates adaptation (i.e. genetic rescue). These various forms of rescue have often been invoked as possible mechanisms for specific invasions, but their relative importance to invasion is not generally understood. Within a spatially explicit modelling framework, we consider the relative impact of each type of rescue on the probability of successful colonization, when there is evolution of a multi-locus quantitative trait that influences the strength of component Allee effects. We demonstrate that when Allee effects are important, the effect of demographic rescue via recurrent immigration overall provides the greatest opportunity for success. While highlighting the role of evolution in the invasion process, we underscore the importance of the ecological context influencing the persistence of small founder populations.

Keywords: Allee effects; adaptive evolution; biological invasion; individual-based model

1. Introduction

A fundamental question for the preservation of biodiversity and ecosystem health is, 'what minimal numbers are necessary if a species is to maintain itself in nature?' [1]. The issue of how population size influences extinction risk is also fundamental in community ecology, because during community assembly (especially on islands and in patchy habitats), communities build up via colonization, and colonizing propagules are typically small in number. Larger populations are less likely to become extinct [46,49], particularly when there are Allee effects (positive density dependence at low densities, so fitness declines as density declines; [11,58]). Maintaining

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sufficient population size acts as a buffer from the decrease in fitness due to Allee effects, as well as from the extinction risks of demographic and environmental stochasticity. Given genetic variation, maintaining a larger population may also enhance the opportunity for adaptive response to novel selection pressures, further facilitating persistence [40].

During the introduction phase of a biological invasion into a novel environment, an invading population may be reduced to such a low density that it experiences a high risk of extinction. However, if demographic constraints and stochastic effects are not too severe, the population may persist long enough to adapt and recover (i.e. experience evolutionary rescue; [24,32,35]), or be rescued by additional immigrants [8]. Additionally, an influx of immigrants can significantly increase population viability by increasing population size, thereby reducing the demographic threats of extinction (i.e. demographic rescue), or by introducing adaptive genetic variation that facilitates selection to increase mean fitness (i.e. genetic rescue). However, introduced genetic variation can sometimes decrease mean fitness (e.g. because gene flow hampers local adaptation; [19,28,54,60]), reducing population viability. These various forms of rescue have often been invoked as possible mechanisms for specific invasions [57], but their relative importance to invasion more generally is not understood. In this paper, we explore a model that permits us to weigh the relative importance of each of these distinct mechanisms in determining the influence of population size on invasion success.

Intraspecific interactions are a primary factor influencing the relationship between these ecological and evolutionary processes, especially for sexually reproducing species. The ability to find a mate and reproduce in a sexual species is required to maintain and bolster population size, and moreover influences the genetic variation available for selection, and hence the evolutionary potential of the introduced population. Other examples of intraspecific mechanisms that affect population persistence and increase survival at higher densities include environmental conditioning, predator dilution, anti-predator behaviour, and group foraging [4,11,58 and references therein]. These mechanisms influence specific fitness components (e.g. mating success, fecundity, or survival), leading to a 'component Allee effect' [58]. If component Allee effects have a sufficient impact on overall individual fitness, then when combined with other local interactions and ecological processes, a demographic Allee effect can emerge and influence population dynamics [21,33]. Hence, a particular challenge for small founder populations is the reduction of these positive intraspecific interactions. This challenge can produce a systematic novel selection pressure during colonization, compared to established populations near their carrying capacity [13].

With genetic variability, some individuals may better cope with the negative ecological or genetic effects of low density, so natural selection can occur on component Allee effects [11,21,32]. Adaptation to low-density conditions across generations can effectively alleviate the ecological constraints of demographic Allee effects – as long as the population is not so limited by demographic stochasticity in the short term that it simply goes extinct [24]. Such adaptation can be viewed as a form of evolutionary rescue [24,26]. Some of the clearest examples of rapid evolution come from introduced species [12,39,41,51,54], despite the fact that founder events can reduce genetic variation and thus hamper evolutionary change [2,48]. It has been suggested that, in altered environments, 'rapid adaptation is the norm rather than the exception' [59], and such adaptation can, in principle, surmount the challenges posed by Allee effects at low densities, as well as challenges posed by novel environments.

Although evolutionary rescue in a single colonizing episode can facilitate successful establishment, there is substantial evidence that recurrent introductions into a given invasive population significantly increase its probability of establishment [57]. Additional migrants, if they arrive frequently enough, can bolster population size and thus help buffer against Allee effects, over-dispersal, and the impacts of demographic and environmental stochasticity [8]. However, even if an immigration event pushes the population above its demographic Allee threshold (so that

expected births exceed expected deaths), this may not be sufficient to rescue the population as the spatial structure of a population is critical to how density is experienced by individuals and how component Allee effects scale to demographic Allee thresholds. Further, high dispersal rates can decrease local density and thereby amplify Allee effects and so hinder invasion [15,32,33,37,45,66]. In cases where increased propagule pressure does not on its own suffice for demographic rescue, the addition of conspecifics can still potentially introduce beneficial alleles and facilitate adaptive evolution and evolutionary rescue [25,63]. The strength of this effect depends on the degree of genetic divergence between the founder and immigrant populations, and the degree to which genetic variation is limiting evolution; the net effect of immigrants involves both demographic and genetic effects [60].

To better illustrate the interplay between ecological and evolutionary processes that influence persistence of a founder population subject to Allee effects, we consider a conceptual framework that demonstrates the relative effects and consequences of evolutionary, demographic, and genetic rescue. Since selection pressure and individual fitness are assumed to be governed by intraspecific interactions and population density, we consider the evolution of an ecologically important quantitative trait that directly influences the relationship between local population size and individual fitness at low densities (where Allee effects are expected). The trait is a phenotypic measure of the overall strength of component Allee effects, measured in terms of the minimum number of conspecifics within a given neighbourhood that an individual requires for the expected value of its lifetime offspring production to exceed 1 (i.e. it is analogous to an individual 'Allee threshold'). This is the most direct way to model evolution with Allee effects. For example, the trait could influence the ability of an individual to detect conspecifics in its area, in which case, individuals with decreased detection ability require a higher density of conspecifics to find a mate, and therefore would have a higher individual Allee threshold if the component Allee effect is based on mate finding. As seen in Figure 1, an individual would be considered maladapted with reduced fitness if its trait value is larger than the local population size, and better adapted otherwise; hence, the trait value and local population size are measured and displayed on the same scale. Variation around the mean phenotype (Figure 1, arrow a) is important, because more heritable variation increases the probability that there will be some well-adapted individuals in the population (with trait values in region b, below the local population size), even if on average it is maladapted. Since individuals with lower trait values have higher fitness, the trait distribution should shift in the direction of a smaller threshold population size (indicated by arrow d), which could lead to evolutionary rescue (though because population size is initially decreasing, it might not). With the addition of more immigrants, rescue may be more likely and hastened; if there is a sufficient increase in population size (arrow c), so that it is beyond the mean phenotype, demographic rescue is likely to occur. However, even if population size does not increase dramatically, immigrants can widen the trait distribution by infusing new variation (arrow a) or actually shifting the mean phenotype with the introduction of beneficial alleles (arrow d), resulting in genetic rescue. Conversely, if immigrants all have maladapted trait values, the mean phenotype could be increased, moving away from the threshold and hindering evolutionary rescue. We here consider the relative importance of these effects in contributing to rescue from extinction, given ecological constraints on population growth, and incorporating effects of mutation and recombination on the trait variation (arrow a), using a simulation modelling approach.

We developed a spatially explicit individual-based model that incorporates both demographic and genetic stochastic processes to gauge the relative importance of the different forms of rescue in mitigating Allee effects in a small founder population. We track multi-locus genotypes of individuals to investigate how initial genetic variation, coupled with the effects of mutation and recombination, affects the rate of adaptive evolution when selection pressure on the Allee threshold varies with population size. Additionally, we assess the influence of recurrent immigration events on demographic and genetic processes and determine the relative contribution
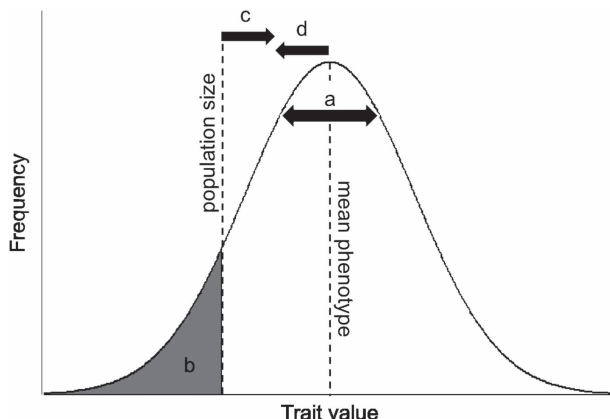
Figure 1. Conceptual representation of the basic elements driving evolutionary, genetic, and demographic rescue. A trait is assumed to determine each individual's Allee threshold, so the population's mean trait value (phenotype) is the average Allee threshold. The variance of the phenotype distribution determines its width (arrow a). The distance between the local population size of an individual and its phenotype is its degree of maladaptation, if the population size is lower. The individuals in shaded region b have phenotypes below the local population size, and therefore are well adapted. If those individuals successfully reproduce enough prior to population extinction, the population size can eventually increase (arrow c) and the mean phenotype should decrease (arrow d), beginning the trend towards evolutionary rescue. Demographic rescue is caused by the addition of new immigrants that push the local population size (arrow c) beyond the mean phenotype. Genetic rescue occurs when the contribution of immigration increases the variance (arrow a) and primarily shifts the mean phenotype to the left (arrow d). All of these forces can operate simultaneously.

of these factors to the overall likelihood of rescue and subsequent invasion. Finally, we determine how much evolutionary rescue depends on initial genetic variance versus mutation and recombination.

2. Model description

We expanded on an individual-based framework previously used to examine the effect of endogenous spatial heterogeneity (the local spatial structure of individuals within a population due to their movement, births and deaths) on intraspecific interactions [33] by explicitly incorporating quantitative genetic structure (following [9,27]). Computer simulations were performed incorporating multiple stochastic and genetic effects (e.g. mutation, recombination, dispersal, and the demographic birth–death process) in order to better understand the relative importance of the different dimensions of rescue in invasive populations.

2.1. *Ecological assumptions*

In each run of the model, a small population of diploid, sexually reproducing, hermaphroditic individuals was introduced into a continuous space environment with explicit spatial locations. We used Gillespie's Direct algorithm to simulate a continuous time birth–death process [5,17,23,33,52]. For each individual (i), its current birth (b_i) and death (d_i) rates were determined by the number of conspecifics (N_i) in its local neighbourhood (the region within a distance of 1 unit from i), its phenotypic value for strength of component Allee effects via the individual Allee threshold, a_i, and the local carrying capacity, K [33]. The birth and death rates are assumed to be given by

$$b_i = \frac{N_i}{a_i} + \frac{N_i}{K} = \frac{N_i(a_i + K)}{a_i K}, \quad d_i = 1 + \frac{N_i^2}{a_i K} = \frac{a_i K + N_i^2}{a_i K}. \tag{1}$$

These relations [33] match a well-studied reaction–diffusion model [14,15,32,34,37,45,50] that represents the standard dynamics of strong Allee effects. Specifically, a simple model for per capita population growth rate that includes an Allee effect is $r = r_0(1 - N/K)(N/a - 1)$, which is often used in deterministic models. Our intent was to craft an individual-based model that generated this particular expression for per capita growth rate, which has been used in much of the previous literature. The first part of the standard deterministic model represents logistic population growth with a carrying capacity of K. The last term models the Allee effect, making the growth rate increase with increasing N at low N; $N = a$ separates populations that grow from populations that do not (so a is a demographic Allee threshold). For a stochastic, individual-based model, we do not need the per capita growth rate, but instead its components, the individual per capita birth rate (b_i) and death rate (d_i), since births and deaths are to be simulated. One fairly general way to assign birth and death rates so that $b - d$ equals the r above is given in Ackleh *et al.* (2007), in which d is the sum of a constant and a term that grows as N^2, and b is the sum of a constant and terms that depend on N and N^2. This general model has three parameters in addition to K and a that can be adjusted to model different scenarios. We chose two of these parameters so that b_i is a linear function of N_i by setting the constant term to zero (certainly reasonable for a sexual species, since an individual cannot reproduce in the absence of conspecifics) and also setting to zero the N_i^2 term (this term can cause the birth rate to saturate and eventually fall with increasing N_i, so these possibilities are not as relevant to the initial invasion process of interest here). At low densities, a linear b_i might be reasonable if births are mostly limited by difficulty in mate finding; the more mates that are in an individual's vicinity, the faster it can find a mate and reproduce. We also set r_0 to 1, which amounts to re-scaling the time variable. Future extensions to our work could include a broader span of functional forms for component density dependence, such as saturating effects of density on births. With this form of birth and death rates, both birth and death rates increase with increasing N_i. Therefore, the Allee effect is due to increasing births with increasing population size, such as when growth rates are limited by ability to find mates, and not by decreasing death rates, such as those due to cooperative behaviours.

In this model, the individual Allee threshold evolves directly with the trait while the carrying capacity remains constant. An alternative would have been to define a trait and birth or death rate functions that depend on the trait, and then calculated the individual Allee threshold and an individual carrying capacity, both of which could then change as the trait evolves. This would be an interesting extension to this work, but the current model has the advantage that the quantity we are most interested in (the individual Allee threshold) changes directly with the trait (and our results are not confounded by changes in K).

Births and deaths were assumed to be independent Poisson processes. These rates were summed over all individuals to give an overall event rate E at each time (this is also a Poisson process, so the time until the next birth or death had an exponential distribution with mean $1/E$). The event was chosen to be a birth or death based on the relative values of total birth and total death rate for the population; an individual was then chosen to reproduce or die based on the magnitude of that individual's respective birth or death rate. If the event was a death, the chosen individual was deleted. If the event was a birth, the chosen reproducing individual, i, randomly chose a mate, j, within its local neighbourhood (the region within a distance of 1 unit from i, but see [33] for a deeper analysis of this assumption). Each parent produced a gamete according to the genetic assumptions described below, and one offspring was produced from those gametes at the location of parent i. Each individual in the population then moved randomly, the distance in each coordinate direction having a zero-mean normal distribution with variance $2D\Delta t$ (where D is the diffusion coefficient and Δt is the inter-event time, which was small enough to approximate continuous movement; see Table 1 for parameters; [5,33,65]). This process continued until the population either went extinct or grew sufficiently large that persistence was reasonably certain. From preliminary results, persistence was reasonably certain when the population size exceeded

Table 1. Parameters, definitions, and values explored and used.

Parameter	Definition	Range	Default
n	Number of loci	1–10	5
$n\mu$	Mutation rate per haplotype	$0, 10^{-6}$–0.1	0.01
α^2	Mutational variance	0.01–0.1	0.05
σ_g^2	Initial genetic variance per haplotype locus	0, 0.01–0.25	0.05
$\bar{a}$	Initial mean phenotype, Allee threshold	25	25
$\bar{a}_{imm}$	Mean phenotype, Allee threshold of immigrants	20–30	20, 25, 30
I_t	Time of immigration event	1–10	1
I_n	Number of immigrants per event	1–25	15
K	Carrying capacity	100	100
D	Dispersal rate	0.001–0.1	0.01
$\hat{K}_0$	Initial modified Ripley's K	− 0.2 to 0.2	0

100 individuals (which is the carrying capacity), and we used reaching this value as our cut-off for assessing establishment.

When an immigration event was incorporated, immigrants (after their introduction) reproduced, died, and moved following the same algorithms. Since other work has investigated invasion risk with multiple introductions of varying spatial proximity to the original release point [15], we fixed the introduction site (to match the initial population) and manipulated the number of immigrants and arrival times to explore other dimensions of immigration effects (Section 2.3).

2.2. *Genetic assumptions*

We modelled the fitness-governing quantitative trait (a_i) assuming multi-locus heritability because many traits of ecological importance in natural populations are polygenic [18]. The value of a_i was determined by summing over n diploid loci, with additive allelic effects within and among loci (i.e. with no dominance or epistasis). Earlier studies with similar assumptions have found little quantitative difference among simulation results with different n, as long as $n \geq 5$ [27]; we thus set n equal to 5. The phenotypic value for each individual was simply the sum of the allelic values (with a negligible environmental contribution, and no plasticity).

We examined the impact of recombination by allowing loci to either be completely linked, or to freely recombine. In simulations with recombination, each parent randomly contributed one allelic value for each locus from its diploid genome to its gamete. Without recombination, one haplotype was randomly chosen from each parent. New alleles were generated through mutation. The mutation rate per haplotype was $n\mu$, where μ was the mutation rate per locus [9,27]. Following segregation, up to one mutation occurred (per haplotype) at a randomly chosen locus. The mutation effect size was normally distributed with mean zero and variance α^2 and was added to the previous allelic value.

2.3. *Parameters and initial conditions*

For the results presented here, we started each simulation with 25 individuals randomly placed in the unit circle around the origin (see below for discussion on varying the initial population size and how we controlled the initial dispersion). For simulations with non-zero initial genetic variance, allelic values for each initial individual were chosen independently from a normal distribution with mean $\bar{a}/(2n)$ and variance σ_g^2, which gave each individual an expected phenotypic value of $\bar{a}$ (set to 25 unless otherwise noted), and an initial genetic variance of $2n\sigma_g^2$; with no initial variance, all initial alleles were $\bar{a}/(2n)$. Therefore, if each individual was (initially) in

the local neighbourhood of all others, the introduced population would have been at the demographic Allee threshold (the unstable equilibrium for critical size in our model; [32,33]). We kept the mutation rate and mutation effect variance constant after exploring the range of values indicated in Table 1 (and used values based on [27], where $n\mu = 0.01$ and $\alpha^2 = 0.05$) and standardized the initial genetic variance across simulations (at $\sigma_g^2 = 0.05$; see Appendix 1 for the effect of varying this).

To consider the impact of immigration on genetic rescue, we present broad comparisons between the founder population alone and with a fixed immigrant population size of 15 individuals introduced after one time unit (see Appendix 2 for the effect of varying these parameters). Genetic variance, mutation and recombination parameters, and initial spatial distribution (see below) for immigrants matched the founder population; however, we did vary the expected mean phenotype of the immigrant population from well adapted (i.e. $\bar{a}_{imm} = 20$) to the same as the founder population (i.e. $\bar{a}_{imm} = 25$) to maladapted (i.e. $\bar{a}_{imm} = 30$).

Kanarek *et al.* [33] found that the interaction between dispersal rate (diffusion coefficient) and initial spatial structure can qualitatively influence population dynamics during introductions; we explored multiple combinations of these characteristics in [33], but use particular fixed values for the results presented here. The diffusion coefficient, D, was set at 0.01. The initial spatial structure, measured by Ripley's K, a clustering statistic [53], was similar across runs and approximately fit complete spatial randomness for a homogeneous Poisson process. This was achieved by placing the initial individuals randomly in the unit circle, but only using initial populations for which the magnitude of the modified Ripley's K, $|\hat{K}_0(1)|$, was less than 0.02 [33]. These values describe an ecological context in which individuals were neither initially over-dispersed, nor thereafter dispersed too quickly, giving a sufficient demographic window for evolutionary rescue (see 'null' model below).

The model embodies multiple sources of stochasticity. To average across such stochasticity, 1000 replicates were performed for each choice of parameter values, so as to tease apart the relative contribution of various model components and better understand the sensitivity of the outcomes to different assumptions (see appendices A and B). We then fixed particular parameters to draw comparisons and elucidate the primary drivers of population success (we did assess the model over the ranges of parameter values listed in Table 1, but note that we are reporting only a subset of the simulations performed). We present results for three main model types for populations with and without initial genetic variance: (1) without mutation or recombination (what we call the 'null' model), (2) with mutation only, and (3) both with mutation and recombination (hereon referred to by just 'recombination'). We used this same comparison structure to assess the impact of immigration. We quantified the proportion of successes (i.e. establishment and persistence through positive population growth) and assessed average time to extinction (of the populations that went extinct). We also tracked initial trait distributions, and changes in population size, mean phenotype, and phenotypic variance over time.

3. Results and discussion

We evaluated the individual fitness as a function of the trait, a_i, and the local population size, N_i, to gain a better sense of the ecological and evolutionary forces influencing model results. We used the difference between the probability that the next event for an individual will be a birth $[b_i/(b_i + d_i)]$ and the probability that it will be a death $[d_i/(b_i + d_i)]$ as a measure of individual fitness (r_i). In Figure 2, the dot represents an individual with the default mean initial phenotype in the model, $a_i = 25$, and with local population size $N_i = 25$ (as it would be in the centre of the introduced population). Hence, the initial probability that the individual reproduced before dying was 0.5, matching the probability that it died first, giving it a fitness of 0. The fate of an individual
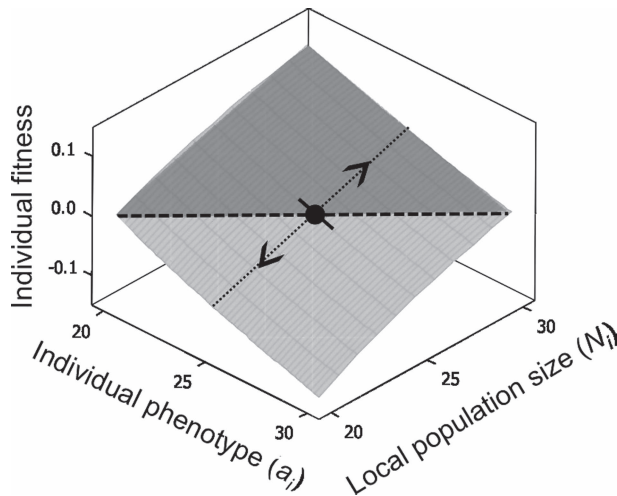
Figure 2. Individual fitness surface where fitness, the difference between birth and death probabilities, is a function of the individual phenotype (a_i) and local population size (N_i). An individual, represented by the dot, has an equal probability of birth or death when the trait value equals the population size (along the dashed line). The error bar represents the range based on one standard deviation of phenotypic values an individual could be initialized with. Fluctuations in local population size will move the individual along the dotted line, indicated by the arrows. Individuals in the darker region are well adapted, while those in the lighter region are maladapted.

with this trait was highly sensitive to its local, neighbourhood population size due to the density-dependent fitness function. Because of constant fluctuations in the individual's local population (as birth, immigration, death, and movement occur), the individual's fitness was always changing along the dotted line (where a_i remains constant). This fast-paced ecological process caused by demographic feedbacks is by definition how Allee effects are expressed (i.e. as an increase in fitness with population size, [11]). If the individual's local population size exceeded its trait value, the individual had a better chance of reproducing than dying and therefore a positive fitness. The demographic processes that impact the individual described in Figure 2 scale up to impact the probability of demographic rescue at the population level (and mirrors the effect of varying the initial population size relative to the mean Allee threshold). To better understand how individual fitness affects evolutionary and genetic rescue, we must consider multiple individuals on this fitness surface. Given the default values for expected genetic variance (Table 1), at the start of a simulation with variation, the majority of individual phenotypic values would likely fall within one standard deviation of the mean shown with the error bar on the point in Figure 2 for constant $N_i = 25$. Because phenotypic variation in a_i is generally small and does not change as rapidly as does local population size, the relative impact of phenotype (a_i) and ecological processes (N_i) with respect to individual fitness foreshadows the importance of demographic rescue versus other types of rescue at the population level. Overall, an individual has an expected fitness greater than 0 if $a_i < N_i$ (the darkly shaded region of Figure 2, where $b_i > d_i$).

Scaling up from individual-level fitness to population dynamics, we first highlight the relative effect of each type of rescue, given various sources of genetic variation, by presenting comparisons of mean behaviour. We then illustrate major trends with representative model runs.

We used the baseline null model (no mutation or recombination) to understand the impact of the stochastic birth–death process on persistence; 10% of the introduced populations succeeded with no evolution (Figure 3(A), see also [33]). It should be noted that the conclusions we draw on the impact of different forms of ecological and evolutionary processes on rescue, drawn from the probability of successful establishment and persistence relative to this baseline scenario, reflect the initial conditions of our simulations. In particular, the trade-off between initial population size and the strength of initial Allee effects primarily drives the response to selection
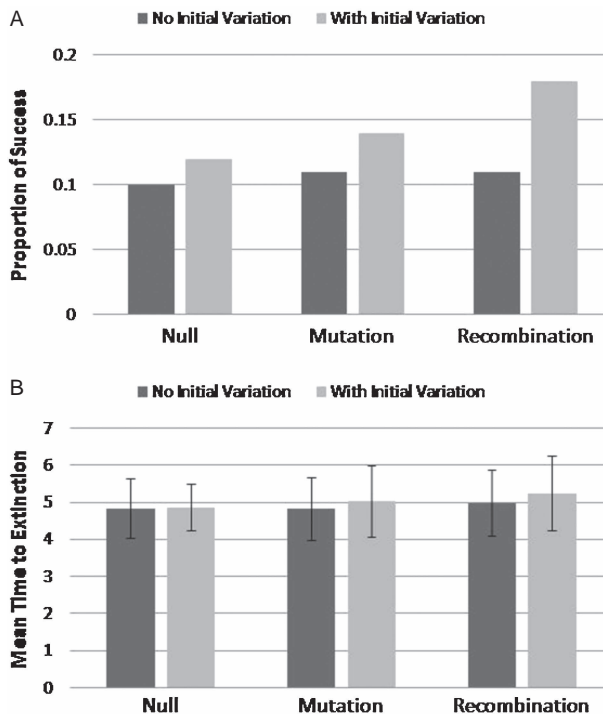
Figure 3. Comparisons between different sources of new genetic variation without (dark grey bars) or with (light grey bars) initial genetic variance. The null model has no variance-generating processes. (A) The proportion of 1000 replicate populations that succeeded. (B) The average time to extinction of populations that went extinct (error bars are one standard deviation).

and the likelihood of success; and when we varied the initial population size above and below the mean Allee threshold, we confirmed this general behaviour – where the probability of success was, on average, inversely proportional to the degree of maladaptation. Based on the forms of the birth and death rates, the interplay between the population size, carrying capacity, and individual phenotype has a relatively straightforward effect on probability of establishment, but becomes less predictable with the added influence of spatial structure, dispersal rate, and interaction kernel (see [33] for the full analysis of the interaction of these parameters; and the online appendix for the results of varying parameter values for the additional genetic and immigration components). Thus, we expect our results to hold qualitatively for populations faced with similar selection pressure (e.g. functional forms for birth and death rates and demographic and genetic assumptions); however, further investigation would be needed to draw conclusions regarding the robustness of our results for a wider range of ecological and evolutionary conditions (e.g. non-random movement, non-hermaphroditic individuals, epistasis, and dominance).

With no initial genetic variance, neither mutation nor recombination contributed strongly to evolutionary rescue as the proportion of successes did not increase meaningfully under these models (Figure 3(A), dark bars). This makes sense, given that these processes infuse genetic variance slowly, relative to the demographic processes determining persistence or extinction. There was a small increase in mean time to extinction with recombination (Figure 3(B), dark bars), indicating that the generation of new genetic variation allowed populations that inevitably went extinct to persist slightly longer (but note that mutation alone had almost no effect).

By contrast, founder populations with substantial initial genetic variation did generate a higher proportion of successes, even with no mutation or recombination, suggesting that evolutionary

rescue does occur (i.e. null model with initial variation compared to without, Figure 3(A)). The fraction that went extinct decreased, but for those populations that did not persist, the mean time to extinction was unaffected (Figure 3(B)). Mutation added to initial variation resulted in a greater number of successes (Figure 3(A), light bars) and (possibly) a slightly increased mean time to extinction (Figure 3(B)). Not surprisingly, if there is initial genetic variation, recombination facilitated success because it generates the most genetic variation over a short time scale of all the processes considered (Figure 3(A)).

In assessing the added impact of immigration of 15 individuals after one time unit, we first note that approximately 40% of the model replicates succeeded for populations without initial variation and with the addition of genetically identical immigrants (Figure 4(A)). Compared with the null model (without variation) in Figure 3(A), this means that demographic rescue accounted for a 30% point increase in the likelihood of persistence. In a similar way, we use the results from Figure 3 to interpret the additional genetic impact of immigrants and assess the occurrence of genetic rescue. Overall, similar general trends appear in the mutation and recombination models with and without initial variation and with and without immigration, if immigrants have the same initial mean trait value as residents (first two bars for each model type, Figures 3 and 4). The immigrant population labelled 'with variation' had allelic values drawn from the same distribution as did the initial resident population and was not more or less adapted. Thus, it is not surprising that in this case, when immigrants had the same initial mean trait value and variation as residents, immigration had little evolutionary impact. We observed approximately the same
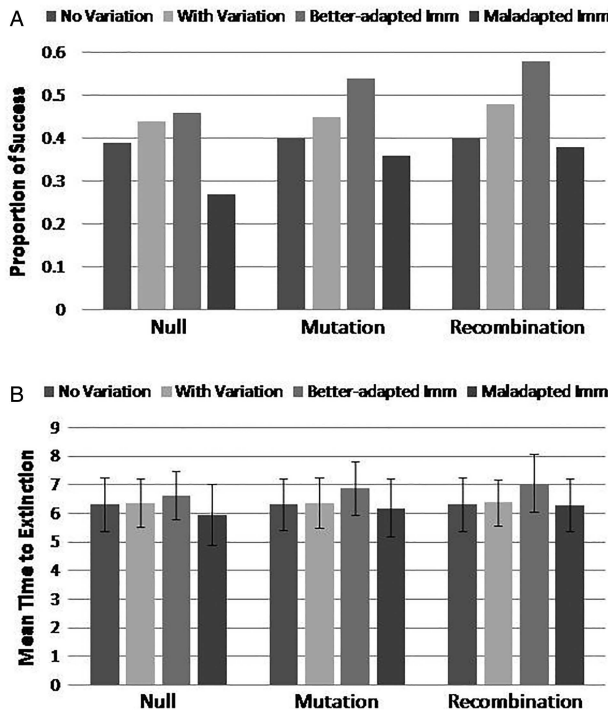

Figure 4. Comparisons between different sources of new genetic variation with or without initial genetic variation and with immigration of 15 individuals one time unit after population establishment ($\bar{a}_{imm} = 25$ for 'no variation' and 'with variation' results, and $\bar{a}_{imm} = 20$ for better adapted immigrants and $\bar{a}_{imm} = 30$ for maladapted immigrants; there was initial variation in the latter two cases). Selection acts on the variants within the three models: (1) the null model has only standing variation, (2) mutation only, or (3) mutation and recombination contribute to variation. (A) shows the proportion of populations that have succeeded of 1000 replicates and (B) gives the average time to extinction (error bars are one standard deviation).

30% point increases in the proportion of successes (Figure 3(A) compared with left two bars in Figure 4(A)), and we consider this a combination of demographic rescue with adaptive evolution rather than purely genetic rescue.

The effect of the genetic contribution from the immigrant population was primarily demonstrated when the immigrant initial mean trait values differed from that of the original founders. In Figure 4, the latter two bars for each model type show the results for better adapted immigrants and maladapted immigrants with the same initial variance as the founder population. In the case of better adapted immigrants, the increases in the proportion of success due to the combination of effect on mean phenotype and mean time to extinction represent genetic rescue (Figure 4(A) and (B)). The additional introduction of maladapted individuals is detrimental and constrains adaptive evolution; the positive demographic effect is now outweighed by the negative genetic effect. We further evaluate the impacts of phenotypic divergence in the immigrants and the effect of timing of immigration in Appendix 2. Note that immigration, even in the worst case, facilitates ultimate persistence, compared to isolated populations (compare left sides of Figures 3(A) and 4(A)).

We specifically illustrate some of the dynamics that gave rise to the results for evolutionary, demographic and genetic rescue in order to better understand these broad comparisons. Figure 5 shows characteristic examples of evolutionary rescue. In each scenario, there was no initial genetic variation in order to show how variation emerges through mutation and recombination. The null model population driven by demographic stochasticity only goes extinct. The
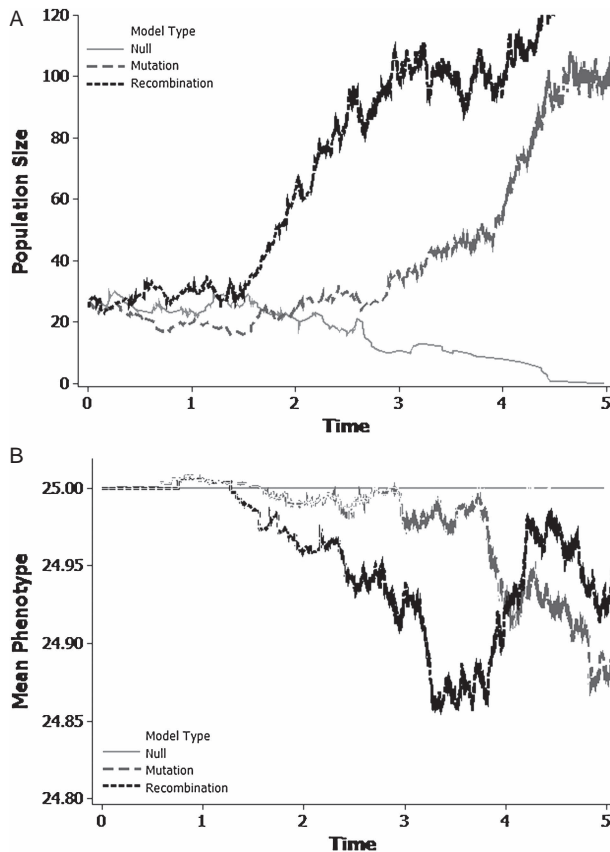

Figure 5. Representative trajectories for (A) population size and (B) mean phenotype (Allee threshold) with no initial genetic variance or immigration. In (B), dark lines show dynamics of the mean and light lines indicate the associated range denoting standard error.
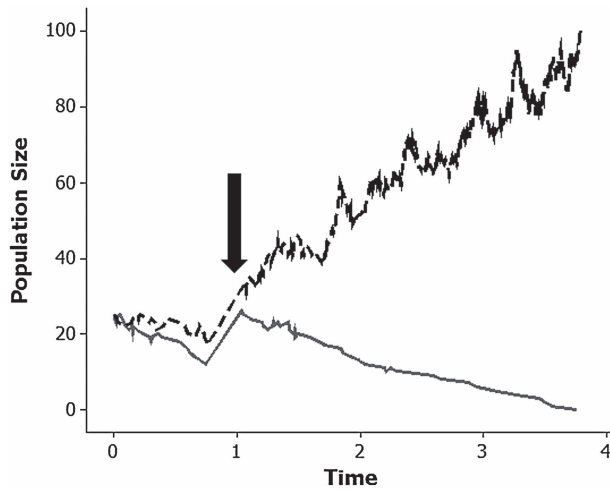
Figure 6. Representative trajectories of population size over time with an immigration event of 15 individuals (with the same mean phenotype as the founders (i.e. $\bar{a} = 25$) and no standing genetic variation) occurring at approximately time 1 as indicated by the arrow. The dashed line illustrates demographic rescue. There was no genetic variation and hence, no evolution.
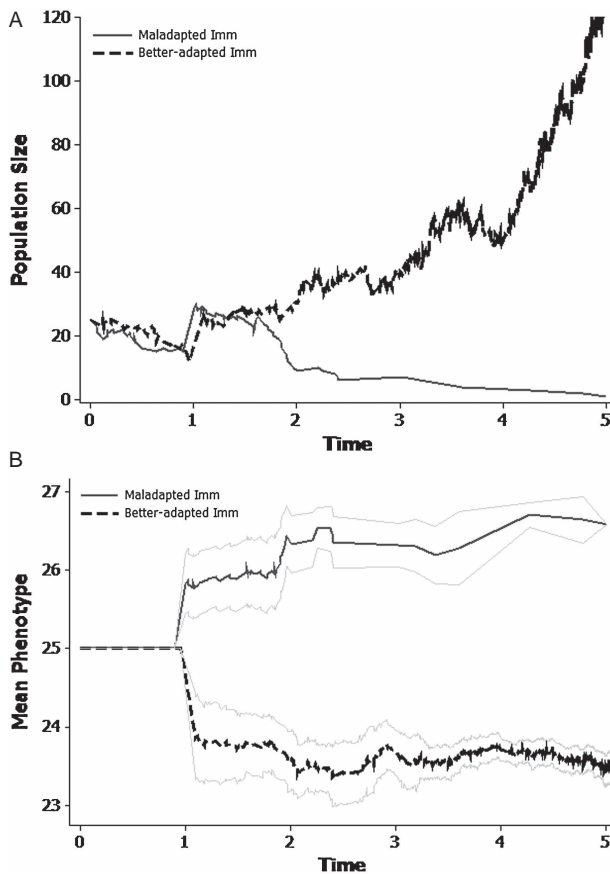

Figure 7. Representative trajectories of (A) population size and (B) mean phenotype and standard error (light grey lines following means) over time with immigration at time 1. These simulations included mutation and recombination and further variation was introduced by immigration. The dashed trajectories illustrate genetic rescue.

mutation and recombination models showed extended time lags before adaptation related to the rate at which genetic variation was generated by each process. Once the population size approximated the carrying capacity, selection for decreased Allee threshold was negligible, allowing it in some cases to increase due to mutation and drift (Figure 5(B), recombination curve).

Demographic rescue (population rescue with no genetic variation and therefore no evolution) is not just based on the number of immigrants and time of introduction, but also hinges on the trajectory of population size and how the invasion develops (e.g. spatial distribution; Figure 6). The impact of the ecological conditions is illustrated by the very different trajectories under potential demographic rescue of the two populations that had the same simulation parameters [33]. Figure 7 shows an example of genetic rescue (and one of failure). In these examples, we manipulated which individuals were chosen as immigrants to clearly illustrate the consequences of the level of adaptation of the immigrants. We started with a founder population with no initial genetic variation, and, after one time unit, introduced immigrants with the same mean phenotype as the founders (i.e. $\bar{a} = 25$), but with standing variation. In one model run (solid lines), we chose immigrants with maladapted phenotypes ($a_i > 25$), and in the other (dashed lines), we chose well-adapted immigrants ($a_i < 25$). Both founder populations had similar behaviour until the immigration event (Figure 7(A)). At that time, the trait means diverged significantly with roughly the same standard error (Figure 7(B)). Maladapted immigrants (solid lines) increased the mean phenotype, which caused reduced growth rates due to an elevated necessity for intraspecific interactions and stronger component Allee effects, and resulted in extinction. Well-adapted immigrants (dashed lines) genetically rescued the population by introducing beneficial alleles, facilitating evolution (these immigrants also facilitated rescue through their demographic effect).

4. Conclusions

A small introduced population with Allee effects can only succeed if it is faced with favourable ecological conditions, or experiences rapid adaptive evolution, or simply has good luck. Our stochastic simulations produced all three possibilities and allowed us to quantify their relative importance for invasion success. Beyond the 10% of successes not attributable to any rescue effect (i.e. sheer luck), additional immigration had a stronger impact on overcoming density dependence than evolution alone due to the rapid and consistently favourable effect that additional individuals have over changes in the mean phenotype (see individual fitness surface Figure 2). For example, the addition of 15 immigrants early on had the same effect on establishment success as a founder population with five times more additive genetic variance than the default value (compare Figure 4(A), light grey bars and Appendix 1, Figure A1 at a genetic variance of 0.25). The impact of immigration was largely through demographic rescue, as opposed to genetic rescue. Once demographic rescue occurred, additional immigration did not notably enhance local adaptation. Local adaptation ceases following demographic rescue in our model because intraspecific interactions are the source of endogenous selection pressure. Once populations are above the Allee threshold by any means, the direct selection pressure on this demographic parameter is reduced, and it ceases entirely when numbers are at carrying capacity. Thus, there was little difference between evolutionary change with or without an immigration event, except when the immigrants were divergent enough to shift the mean phenotype and generate a genetic rescue effect. Overall, the increased effect of demographic rescue over evolutionary and genetic rescue is a general consequence of strong Allee effects as illustrated conceptually in Figures 1 and 2, and we feel that this general conclusion is broadly applicable beyond the detailed assumptions we have made in our simulation explorations.

In our model, not only is there an abbreviated time scale during which evolution can occur, because of the high risk of extinction, there are other implicit genetic consequences of small populations and Allee effects. The most obvious is the potential reduction of diversity due to genetic drift and founder effects; however, there is much recent evidence that indicates that the typical loss of additive genetic variance in introductions is minimal [41,56,67]. Kramer and Sarnelle [38] even suggest that Allee effects may lead to resistance to significant changes in heterozygosity and genetic distance by imposing limits on minimum population size. Specifically, they found that 70–75% of populations of an alpine copepod that maintained the minimal population size lost < 10% of allelic richness. Although it seems plausible that the ecological limitations that Allee effects impose on critical density can actually indirectly maintain genetic variation, we suspect that the spatial constraints influencing population growth often instead limit genetic variation through restricted mating options. This is consistent with Kramer and Sarnelle's [38] finding that increased habitat size of a founder population at critical density also increased the proportion of original allelic richness. Thus, in the race against time for evolution to reduce component Allee effects through heritable fitness-related traits, endogenous spatial heterogeneity that emerges ecologically to mitigate component Allee effects [33] may indirectly limit the amount of genetic variation available for selection, reducing the scope for the process of evolutionary rescue. Even though there may be sufficient genetic variance in the founder population, spatial structure may render it inaccessible to evolution, in effect leading to a tug of war between ecological and evolutionary survival mechanisms.

The mounting empirical evidence of adaptive evolution following invasions [6,7,12,22,30,42, 43,47,49,55,62] must be reconciled with these results. One reasonable reconciliation is that establishment and persistence are relatively rare compared with the number of introductions that fail [69], yet the empirical data are necessarily biased towards the former (it is easier to record long-lasting 'successes', than rapid 'failures', in invasions). Our results then suggest that because of demographic constraints on the evolutionary dynamics, the probability of evolutionary rescue is low and the observed examples are rare events. This explanation is consistent with the paradox of evolutionary rescue, where stronger selection gives rise to faster evolution while also imposing a greater demographic cost and risk of extinction [35]. We chose to exemplify this scenario by incorporating strong (as opposed to weak) Allee effects that produce an extinction threshold with negative growth [4]. Thus, extinction is drastically hastened as soon as the population size falls below the mean phenotype (i.e. Allee threshold). Evolutionary processes would play a more dramatic role in this simulation framework if a weak Allee effect or a more substantial fitness advantage from a small phenotypic change were incorporated. Hence, an alternative reconciliation of our results with empirical evidence is that strong Allee effects are necessarily rare in successful introductions. Alternatively, evolution may occur following invasion, without being causally strongly responsible for the invasion success in the first place.

To further assess the relevance of evolutionary processes to colonizing success, it might be helpful to take a more empirical approach in characterizing how density dependence operates at low densities and determining the following: Which mechanisms generating Allee effects are under selection? What is the probability of adaptation given the mating system? Do these adaptations allow persistence at low density or serve to increase density [21,28]? There are a number of examples of the selective pressures that Allee effects exert on invasive species. The evolutionary response can be primarily thought of as adaptations that facilitate reproduction by altering mating systems (e.g. self-fertilization, [61]; reproductive timing, [3]; induced ovulation, [31]; parthenogenesis, [29]; masting, [36]; gamete morphology and performance, [44]; and other life history traits, [21]). In addition, there are adaptations that affect survival, including detection of conspecifics as well as dispersal characteristics [64,68]. In one of the most direct studies, Elam *et al.* [16] found in self-incompatible invasive wild radishes that population size and genetic relatedness influence maternal reproductive success, and suggested that multi-seeded fruits are

an apparent adaptation to overcome the challenge of an Allee effect. Overall, understanding the ecological attributes of the mating system and dispersal mode can offer powerful insight into evolution, invasiveness, and establishment likelihood of small populations.

Our results are broadly applicable to a wide variety of taxa and emphasize the complex reality facing a small founder population. Our model captures the evolutionary phenomenon of adaptations influencing intraspecific interactions (rather than responding to the exogenous environment) in order to demonstrate the demographic challenge posed by Allee effects. When fitness is depressed at small population sizes, the ecological, evolutionary, and genetic obstacles that successful invaders need to overcome are exacerbated. Our results not only highlight potential mechanisms and conditions facilitating or hampering rapid adaptive evolution and establishment success of small founder populations but also provide phenomenological insights into how Allee effects contribute to the paradox of invasion. For species with strong Allee effects, invasion outside their basic ecological niches appears difficult.

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Appendix 1. Impact of initial genetic variance

In general, directional selection leads to an increase in mean fitness that is proportional to the additive genetic variance in a population [18]. Similar to Kanarek and Webb [32], we found that an increase in the initial genetic variance (σ_g^2) had a strong influence on the rate of evolution, resulting in an increased chance of survival (Figure A1). This is illustrated by a 40% point increase in the proportion of successful founder populations (out of 1000 replicates) between those that cannot evolve (null model with no genetic variance) and simulated populations that undergo recombination and mutation with $\sigma_g^2 = 0.25$. Comparing the three model types provides further evidence of how mutation and recombination influence genetic variation and affect the evolutionary processes in overcoming Allee effects. The light grey solid trend line indicates the null model with initial genetic variation. Because variation introduces both well-adapted and maladapted individuals around the mean phenotype, it is unsurprising that a wider spread will increase the likelihood of evolutionary rescue. The darker grey long dashed line shows that with added mutation (using defaults in Table 1), more variation was introduced and the proportion of successes was increased. The black short dashed line demonstrates that random recombination can allow more effective removal of deleterious alleles [20] contributed by increased initial variation and accumulated with mutation, increasing mean fitness, and population growth.

Appendix 2. Time and number of immigrants

Shifting the focus to the process of demographic rescue without genetic variation and evolution, Figure A2 demonstrates that the size of the immigrant population and temporal proximity to the introduction of the initial population influenced
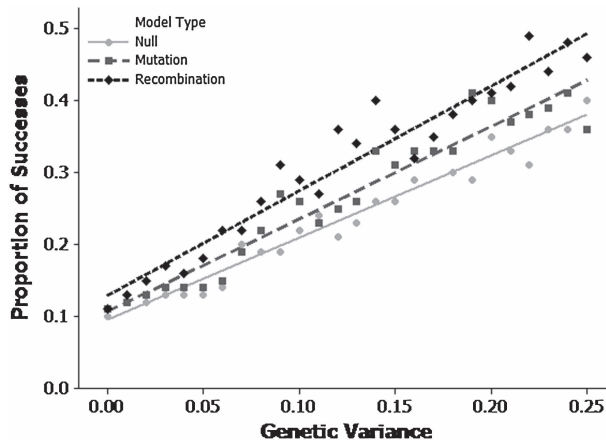
Figure A1. The proportion of successful populations of 1000 replicates according to the amount of initial genetic variance (varied from 0 to 0.25 incremented by 0.01).

both the likelihood of establishment and time to extinction (note, the immigrants had the same mean phenotype as the founders (i.e. $\bar{a} = 25$) and no standing genetic variation). The proportion of successes increased with the number of immigrants as long as they were introduced before the founder population became too dispersed or depauperate, and as long as the total population size was close to or exceeded the Allee threshold just after introduction. Even if the number of immigrants did not dramatically increase the total population size, additional individuals contributed to the lag phase and extended the time to extinction.

Figure A3(A) shows the probability of success resulting from the addition of 15 individuals at different points in time for each model type. The degree of adaptation of the mean immigrant phenotypes was higher than (mean Allee threshold of 20), equal to (25), or lower than (30) that of the initial population. Figure A3(B) further indicates the implications for genetic rescue based on the mean phenotype of the immigrants and genetic processes contributing to genetic variation. In this case, even a small number of immigrants (i.e. 5), for which there is little demographic rescue effect, can provide the opportunity for adaptive evolution in population recovery, if immigrants are better adapted and introduced early (solid lines). It should be noted that because of number of simulations presented in this figure, we used the LOWESS method of smoothing [10] over the time of immigration for clarity.

Comparison of Figure A3 with Figure Figure A2 demonstrates the additional contribution that genetic variation has on population success with evolution. For each model type in Figure A3, the original founder population and immigrant populations were initialized with expected genetic variance given in Table 1. Hence, the proportion of success increases with adaptive evolution (mean phenotype 25, long dashed lines Figure A3(A) versus dark grey short dashed line Figure A2 for 15 immigrants). A noteworthy effect is observed with the introduction of just five immigrants. Figure A3(B) shows that with added variation (in both the founder and immigrant populations), success increases compared to the low
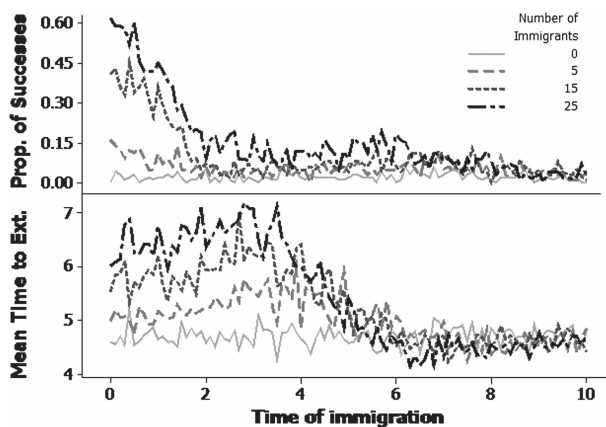

Figure A2. The proportion of successes and the average time to extinction based on the timing and size of an immigrant population upon introduction, with no initial genetic variation or evolution.
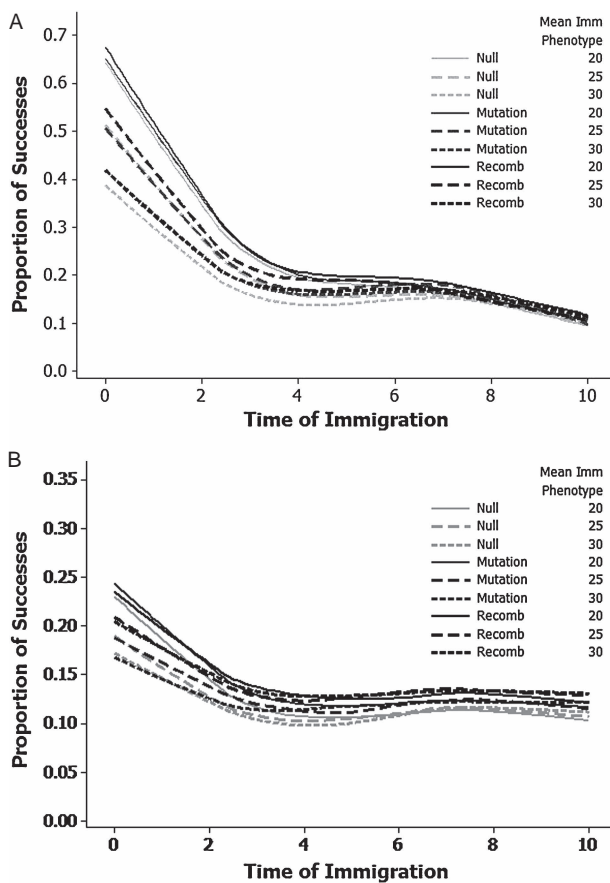
Figure A3. The proportion of successes based on the timing and mean phenotype of the immigrant population upon introduction for each model type. The immigrant population size is 15 in (A) and 5 in (B). Trend lines were generated with LOWESS smoothing across time of immigration (with degree 0.5 with 2 iterations).

proportion of successes in Figure A2 (grey long dashed line). Even with the introduction of maladapted immigrants, success is still enhanced due to evolutionary rescue in the founder population when the five immigrants are rapidly purged from the population (short dashed black lines on Figure A3(B); the negative effect of maladapted immigrants is more pronounced with more individuals in Figure A3(A)). However, five individuals can positively affect the mean phenotype when well adapted, resulting in genetic rescue (solid curves in Figure A3(B)).