Establishment in a new habitat by polygenic adaptation

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Abstract

Maladapted individuals can only colonise a new habitat if they can evolve a positive growth rate fast enough to avoid extinction, a process known as evolutionary rescue. We treat log fitness at low density in the new habitat as a single polygenic trait and thus use the infinitesimal model to follow the evolution of the growth rate; this assumes that the trait values of offspring of a sexual union are normally distributed around the mean of the parents' trait values, with variance that depends only on the parents' relatedness. The probability that a single migrant can establish depends on just two parameters: the mean and genetic variance of the trait in the source population. The chance of success becomes small if migrants come from a population with mean growth rate in the new habitat more than a few standard deviations below zero; this chance depends roughly equally on the probability that the initial founder is unusually fit, and on the subsequent increase in growth rate of its offspring as a result of selection. The loss of genetic variation during the founding event is substantial, but highly variable. With continued migration at rate M, establishment is inevitable; when migration is rare, the expected time to establishment decreases inversely with M. However, above a threshold migration rate, the population may be trapped in a 'sink' state, in which adaptation is held back by gene flow; above this threshold, the expected time to establishment increases exponentially with

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M. This threshold behaviour is captured by a deterministic approximation, which assumes a Gaussian distribution of the trait in the founder population with mean and variance evolving deterministically. By assuming a constant genetic variance, we also develop a diffusion approximation for the joint distribution of population size and trait mean, which extends to include stabilising selection and density regulation. Divergence of the population from its ancestors causes partial reproductive isolation, which we measure through the reproductive value of migrants into the newly established population.

1. Introduction

Can a population establish itself in a new habitat, adapting to the new conditions despite random drift and gene flow? This question is relevant in several contexts: the evolution of specialist host races, perhaps eventually leading to speciation; at the edge of a species' range, where adaptation to extreme conditions is necessary; and 'evolutionary rescue', following a catastrophic change in environment, or loss of adaptation by random drift.

In this paper, we focus on the initial establishment of a population by migrants, and its subsequent reproductive isolation. The source population is poorly adapted to the new environment, and would, on average, decline to extinction in the new conditions. However, migrants and their offspring may by chance be better adapted, and moreover, selection will cause further adaptation. Provided that gene flow is not so high as to swamp the incipient adaptation, growth rates may become positive, and a large, well-adapted population may be established.

As the population grows, the proportion of migrants decreases, as does random drift; these two positive feedbacks ensure rapid and secure establishment, that will ultimately be limited by density-dependent regulation of population size, and by stabilising selection on the trait, towards a new optimum. During establishment, we can ignore these two processes, focussing on the initial adaptation and growth via directional selection from low density. Subsequent evolution, perhaps based on new mutations, may allow further adaptation, and will lead to speciation if divergence (both adaptive and non-adaptive) is sufficient to cause strong reproductive isolation.

This problem has received considerable attention in recent years, since it is relevant to survival of endangered populations, delimitation of the species'

range, and invasion of non-native species (Gomulkiewicz et al., 2010; Gomulkiewicz and Shaw, 2013). The positive feedback between adaptation and population size was identified as a factor that can limit species' range by Haldane (1956); the consequent trapping of populations in a maladapted 'sink' state has been studied both in single demes (e,g, Holt et al., 2003; Holt and Barfield, 2011) and along one-dimensional environmental gradients (Kirkpatrick and Barton, 1997; Polechová and Barton, 2015). Such analyses have either been based on simulations of discrete loci, or on deterministic models that assume a constant additive variance for one or more traits. Here, we consider establishment despite initial maladaptation, using a model that takes into account the evolution of trait variance due to migration and random drift.

Adaptation to a new environment may sometimes involve one or a few changes of major effect - for example, a change in preference for a new host, or origin of a distinct and reproductively isolated polyploid. However, we deal here with the more common, and more challenging, case, where adaptation is polygenic, possibly acting via many biological mechanisms. We can simplify drastically by thinking of a single polygenic trait - log fitness at low density in the new habitat - which by definition is under directional selection. This fitness may be mediated via very many traits, but we can absorb the genetic component of all of these into a single value.

This approach may seem paradoxical, since existing theory apparently shows that gene flow should swamp polygenic adaptation. By analogy with the mutation load, migration reduces fitness by an amount equal to the mutation rate, for *each* locally adapted locus. If alleles at different loci are in linkage equilibrium (as will be the case if migration is much weaker than total selection), then the migration load is proportional to the number of locally adapted loci, and may become disastrously high. Looking at the problem in another way, selection at each locus must be stronger than migration to prevent local alleles from being swamped by gene flow, which implies that alleles of small effect cannot contribute to local adaptation.

However, these arguments only apply if locally favoured alleles are absent or very rare in the source population. If adaptation is instead based on standing variation, then alleles of indefinitely small effect can contribute. To see this, consider an additive trait in a population of diploids, with two possible alleles at locus i, having effect $\pm\alpha_i$ on the trait value. Writing p_i for the proportion of alleles of the first type in the new environment and p_i' for the corresponding proportion in the source population, migration contributes $m(p_i'-p_i)$ to the rate of change of p_i, but a selection gradient β on the trait causes selection $\beta\alpha_i$, and so contributes $\beta\alpha p_i(1-p_i)$. Thus selection

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can maintain a difference in allele frequency $\beta\alpha_i p_i q_i/m$ in migration selection balance. Summing over loci, we find a difference in trait mean between the new environment and the source population of

$$\Delta\bar{z} = \frac{\beta}{m}\sum_i 2\alpha_i^2 p_i q_i = \frac{\beta}{m}V_A,$$

where V_A is the additive genetic variance. This result can of course be obtained by a purely phenotypic argument, and is independent of the number and effects of individual loci. The difference in allele frequency at each locus may be small, but the cumulative effect can be large, shifting a set of traits by many standard deviations, to well outside their original range. A similar argument holds when random drift is included: slight changes in the neutral distribution of allele frequencies can have large effects on phenotype, even if drift and migration dominate selection at individual loci (Robertson, 1960; Kimura, 1981). We will consider the limiting infinitesimal model, which assumes a very large number of unlinked loci with additive effects. Then, the evolution of the trait distribution depends essentially only on the variance between offspring that is released by recombination. Within each family, the trait values of the offspring are normally distributed, with mean equal to the mid-parent value, and fixed variance V if the parents are unrelated. In a finite population, the within-family variance decreases in proportion to the parents' relatedness. We define the model more carefully below. For a more detailed introduction to the infinitesimal model, its derivation, and its application, we refer to Barton et al. (2016).

This simple model has proved remarkably accurate in practical animal breeding (Lynch and Walsh, 1998), in describing artificial selection experiments (Weber and Diggins, 1990), and in analysis of natural populations (Kruuk, 2004). Here, we use it to motivate an approximation to the joint evolution of population size and mean trait value in the new habitat, in which establishment can be described in a very general way, in terms of just two parameters: the change in trait needed to make growth positive, and the fitness of an average migrant, both expressed relative to the additive variance in the source population.

Once the new population is established, we can use the same approximation to calculate its reproductive isolation from the source. Again this depends on very few parameters: the divergence of the new population from the source, and its degree of inbreeding.

The infinitesimal model can be justified as the limit of a model of an additive trait that depends on a very large number of unlinked loci. Then,

knowing the trait of an individual provides very little information about the distribution of allele frequencies at any particular locus, which therefore changes only slightly as a result of selection. The sum of effects of slight changes in allele frequency across all the loci can produce a substantial change in the mean, but the within-family variance is determined by the degree of inbreeding of the parents, with the effects of changes in allele frequency only becoming important over a timescale longer by a factor proportional to the number of loci. Under strong selection, the distribution of trait values in the population may rapidly change its variance, and may certainly deviate from normality. However, these changes are due to the cumulative effects of linkage disequilibria amongst the loci, not to changes in the marginal allele frequencies. The establishment and adaptation of a small population under strong selection must occur quickly if it is to avoid extinction, and so we expect the infinitesimal model to be a good approximation to the evolution of polygenic traits.

After defining the model, and its implementation in individual-based simulations, we consider the fate of single migrants, finding (numerically) the probability that they can successfully establish a growing population. We then consider continued migration, and show that there is a threshold fitness of average migrants, above which establishment is rapid, but below which requires a rare fluctuation. This threshold behaviour is captured by a caricature of our model in which the trait distribution in the new population is assumed Gaussian with mean and variance evolving deterministically. In this regime of continued migration, we also develop a diffusion approximation for the joint evolution of the trait mean with population size, which extends to include stabilising selection and density regulation, and we use it to investigate the stationary distribution of the new population. Finally, we derive the reproductive isolation of the newly established population, assuming that it is at equilibrium under a balance between mutation and selection.

2. The infinitesimal model

Individuals are diploid, and may self-fertilise: thus, a single individual can found a new population. Generations are discrete, and do not overlap. We follow the 'breeding value' of a single additive quantitative trait, with individual value z. Non-inherited variation is not treated explicitly, but can be thought of as being absorbed into the relation between fitness and breeding value. Migrants (assumed unrelated) come from a large source population, which is in Hardy-Weinberg proportions and linkage equilibrium. The trait

is assumed to follow a Gaussian distribution in the source population with mean $\bar{z}_s$ and variance $2V$, composed equally of within and between family variance. This corresponds to the equilibrium distribution for a purely additive neutral trait in a large population under the infinitesimal model. To see why the variance is partitioned in this way, recall that under the infinitesimal model, offspring traits follow a Gaussian distribution around the mean of the parental traits with a fixed variance V. If the variance of the parental traits is V_1, say, then the variance of the mid-parent value is $V_1/2$, and so the variance across offspring is $V_1/2 + V$; at equilibrium we must have $V_1 = 2V$. By considering higher order cumulants, Bulmer (1980) shows that in the absence of selection, under this model the distribution of traits rapidly relaxes to a Gaussian.

Individuals migrate from the source population, independent of z, their number in each generation being Poisson distributed with expectation M. Immediately after migration, there are $N(t)$ individuals, which mate randomly, irrespective of whether they are newly arrived or native, and with the possibility of selfing. Offspring are produced, and survive into the next generation with probability that depends on their trait value, and which, if we incorporate population density regulation, will decrease with $N(t)$. The surviving offspring are joined by another Poisson distributed group of immigrants from the source population, resulting in $N(t + 1)$ individuals and the process repeats.

Although migrants are assumed to be unrelated to each other, and to the native population, the evolving population will become inbred. The variance amongst offspring is the sum of the variance contributed by haploid gametes from each parent, which in turn is generated by segregation at meiosis, in proportion to $(1 - F_{ii}), (1 - F_{jj})$ where F_{ii} is the probability of identity by descent between the two distinct genes of parent i, and similarly for F_{jj}. That is, the variance between offspring from diploid parents i, j is

$$v_{ij} = V \left(1 - \frac{(F_{ii} + F_{jj})}{2} \right). \tag{1}$$

The same formula applies with self-fertilisation.

We model directional selection on the trait by taking fitness to be $w = e^{\beta z}$. The number $N^*(t + 1)$ in the next generation, before migration, is Poisson distributed, with expectation $N(t)\overline{W}$, where $\overline{W}$ is the mean of $e^{\beta z}$ across offspring. Thus, the population is only expected to grow (as opposed to simply being maintained by immigration) if $\overline{W} > 1$. We focus on the case where the source population has $\bar{z}_s < 0$, so that some form of selection is

required for the trait to become positive in the new population, allowing it to grow.

It would be inefficient to simulate this model directly, by forming a large number of offspring, and culling them in proportion to their individual fitness. Instead, the average fitness of offspring from each possible pair of parents, w_{ij}, is calculated. Denoting the parental trait values by z_i, z_j respectively, with exponential directional selection, $e^{\beta z}$:

$$w_{ij} = \mathbb{E}\left[e^{\beta z}\right] = \exp\left(\beta\frac{(z_i + z_j)}{2} + \frac{\beta^2}{2}v_{ij}\right). \tag{2}$$

The number of surviving offspring, $N^*(t+1)$, is Poisson distributed with expectation $\sum_{i,j} w_{ij}/N(t)$. For each of these, parents i, j are drawn with probability proportional to w_{ij}. This choice is represented by a pedigree matrix P_{ki}, with dimensions $N^*(t+1) \times N(t)$; P_{ki} gives the probability that a gene in offspring k came from individual i in the parental population. Under the infinitesimal model, this is not distorted by knowing the trait values of the individuals involved. Thus, each row has either two entries of $1/2$, if that offspring has distinct parents, or one entry of 1, if it was produced by selfing. If offspring k has parents i, j, then its trait value is drawn from a normal distribution with mean $(z_i + z_j)/2 + \beta v_{ij}$, and variance v_{ij}. The relatedness in the new population is

$$P\left(F + \frac{1}{2}\left(I - F_{\text{diag}}\right)\right)P^T,$$

where F_{diag} is the diagonal matrix with entries from the diagonal of F. New migrants (assumed to be unrelated to these $N^*(t+1)$ individuals and to each other) are added, to arrive at the new generation of size $N(t+1)$. By representing P as a sparse matrix, a population of up to ~ 1000 can be simulated. For larger populations, the relatedness can be taken to be approximately equal between all pairs.

3. Establishment of a new population

In this section, we use simulations to explore establishment of the population in the new habitat, first considering the fate of a single migrant and then continuous immigration from the source population. In this second scenario, establishment is inevitable, but we still see two competing effects: migration introduces variance which feeds selection, but reproduction with

a migrant pulls back the mean trait value among offspring towards the value in the source population, thus impeding adaptation.

3.1. Single migrants

We begin by considering the fate of a single migrant, of trait value z_0. In the long term, density-dependent fitness must limit population size, and stabilising selection (or some other process) must limit trait evolution. However, we assume that the population is established before either of these are significant, and so take fitness to be simply $e^{\beta z}$. In the first generation, born of a single selfed migrant, before selection, the trait values of offspring are Gaussian, with mean z_0 and variance V. The expected number to survive selection is $\mathbb{E}\left[e^{\beta z}\right] = e^{\beta z_0 + \beta^2 V/2}$. The relatedness between any two genes (sampled from either the same or distinct offspring) is $F_{ij} = 1/2$. While the population size is small, inbreeding rapidly reduces the genetic variance, and so if the population is to survive, individuals with sufficiently large z must be produced in the first few generations. The probability that this will happen depends only on the two dimensionless quantities $z_0/\sqrt{2V}$ and on $\beta\sqrt{2V}$; the latter is the standard deviation in log fitness (measured in the new habitat) of the source population. It is convenient to scale both the trait value and the fitness gradient relative to $\sqrt{2V}$ in this way and thus set the variance in the source population to be $2V = 1$.

Figure 1 shows one example of a successful establishment, where we define establishment to mean reaching population size $N = 100$. We start with a single migrant of value $z_0 = -2$, and fitness gradient $\beta = 0.25$; thus, recalling that $2V = 1$, the expected number of surviving offspring from this founder individual is $\mathbb{E}\left[e^{\beta z}\right] = e^{\beta z_0 + \beta^2/4} = 0.62$. The population mean increases rapidly in the first few generations, as does the population size. After 15 generations, the population mean becomes positive, after which population size rises more rapidly (Fig. 1, middle). The population increases for two reasons: first, the increase in trait mean, and hence fitness, and second, the stochastic acceleration - the expected numbers conditional on fixation must rise faster than the unconditional expectation. Because there are only a few individuals during the first few generations, the heterozygosity, $1 - \overline{F}$, decreases rapidly, to only ~ 0.1 by the time the population is large. The actual trait variance fluctuates below this underlying heterozygosity (compare lower dashed with solid curve in Fig. 1, right). In a neutral model, one expects the average heterozygosity to decrease by a factor $1 - \frac{1}{2N}$ in each generation (upper dotted curve in Fig. 1, right); in this example the actual heterozygosity is slightly lower than this prediction. This is to be expected as selection will distort the pedigree, as fitter individuals are more likely
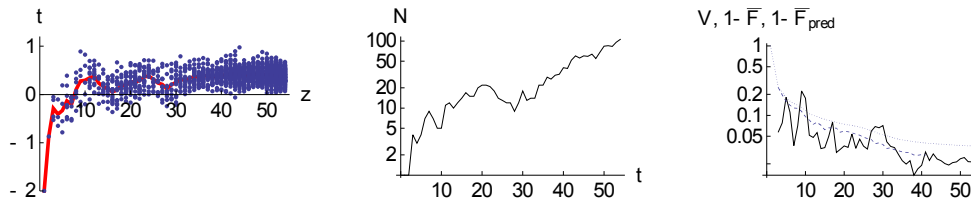
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Figure 1: An example of successful establishment, starting with a single migrant with $z_0 = -2$, $\beta = 0.25$. Left: Values of each individual though time; thick line shows the population mean. Middle: Population size, N. Right: The variance, $2V$, and heterozygosity, $1 - \overline{F}$ (solid, lower dashed), through time. The upper dashed curve shows the predicted heterozygosity, based on the population size: $\prod_t \left(1 - \frac{1}{2N_t}\right)$.

to reproduce, and so the probability of identity between surviving offspring should exceed the neutral prediction. Based on replicate trials (Fig. 3), the probability of establishment with $z_0 = -2$, $\beta = 0.25$ is 0.00012. Individual replicates are highly variable.

Figure 2 shows average features of 50 successful establishments, again with $z_0 = -2$, and for $\beta = 0.125$, 1 (left, right). When the population succesfully establishes, it increases rapidly, over the first ~ 20 generations for $\beta = 0.125$, and the first ~ 10 generations for $\beta = 1$ (top row). After this initial phase, the mean appears to settle to around 50; however, this is an artefact of the definition of establishment at $N \geq 100$. Once the population is above ~ 20, because of the variation in trait values across the population, it may rapidly fix, or it may fluctuate for 100 generations or more before taking off. As a result, the size of populations that have not yet reached $N = 100$, but will eventually do so, is roughly uniformly distributed between a small number and 100.

The middle row of Fig. 2 shows the trait mean; to make runs that reached $N \geq 100$ at different times more comparable, this is plotted against population size. Offspring of successful migrants tend to have substantially higher z than their parent (averaging ~ -1 for $\beta = 0.125$, and ~ 0 for $\beta = 1$, compared to an average over the source population of -2). On average, the trait mean increases to ~ 0.5 by the time the population is large, though this is highly variable: some populations establish with a trait mean that is close to zero. Once populations are large, the trait mean is almost always positive, so that there is a sharp lower bound to its distribution.

The bottom row of Fig. 2 shows the genetic variance, which decreases to an average of ~ 0.02 for $\beta = 0.125$, and ~ 0.1 for $\beta = 1$; more variance remains when the fitness gradient is steep, because then, establishment is

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faster. However, the variance remaining in large populations is highly variable between runs. We set the variance in the source population to be $2V = 1$ and compare the observed variance during establishment to $2V(1 - \overline{F})$. The mean heterozygosity, $1 - \overline{F}$, which determines the segregation variance, has a narrower distribution than the population variance, but almost the same mean. On average, the heterozygosity predicted from the population size, $\prod_t \left(1 - \frac{1}{2N_t}\right)$, is very close to that of the variance (compare dashed with solid lines).

The solid lines in Fig. 3 (left) show how the probability of establishment depends on the initial trait value, z_0, and on the fitness gradient, β. (Recall that both are scaled relative to the variance in the source population, $2V$, which is therefore set to 1 here, and that establishment is defined as reaching at least 100 individuals). As β becomes smaller, the dependence on the initial trait value becomes weaker, since fitness depends more weakly on the trait value. Indeed, in the limit $\beta = 0$, there would simply be a critical branching process, with each individual producing a Poisson number of offspring with mean 1; the probability of reaching $N = 100$ is then $\sim 1/100$, independent of z_0. However, even for the smallest fitness gradient ($\beta = 0.125$), selection still dominates in large populations.

A successful migrant will typically have trait value around one standard deviation from the mean $\bar{z}_s$ and so can be maladapted for $\bar{z}_s < 0$. But selection acting on the variance among the migrant's offspring means that the descendants of a maladapted migrant can still have a positive chance of becoming established.

The right plot of Fig. 3 shows the probability of establishment for $\beta = 0.125, 2$, as in the left plot (solid curves). The contribution of selection to establishment can be seen by comparison with the probability of establishment from a *homozygous* individual, whose offspring necessarily have the same trait value as the parent (lower dashed curve). This is just the establishment probability for a Galton-Watson branching process with Poisson offspring distribution of mean $e^{\beta z_0}$, which we approximate by the survival probability (recalling that establishment means reaching $N = 100$). It is zero for $z_0 < 0$, and increases steeply with βz_0 (dotted curves at far right). However, the solid and dotted curves converge as the initial value becomes more positive, showing that selection has little effect on establishment when the initial migrant is already well adapted.

We see that, even though genetic variance is rapidly lost during the first few generations, selection during this time greatly increases the chances of success. Indeed, even after the population has become large, some genetic variation remains, and so further adaptation will occur even without new
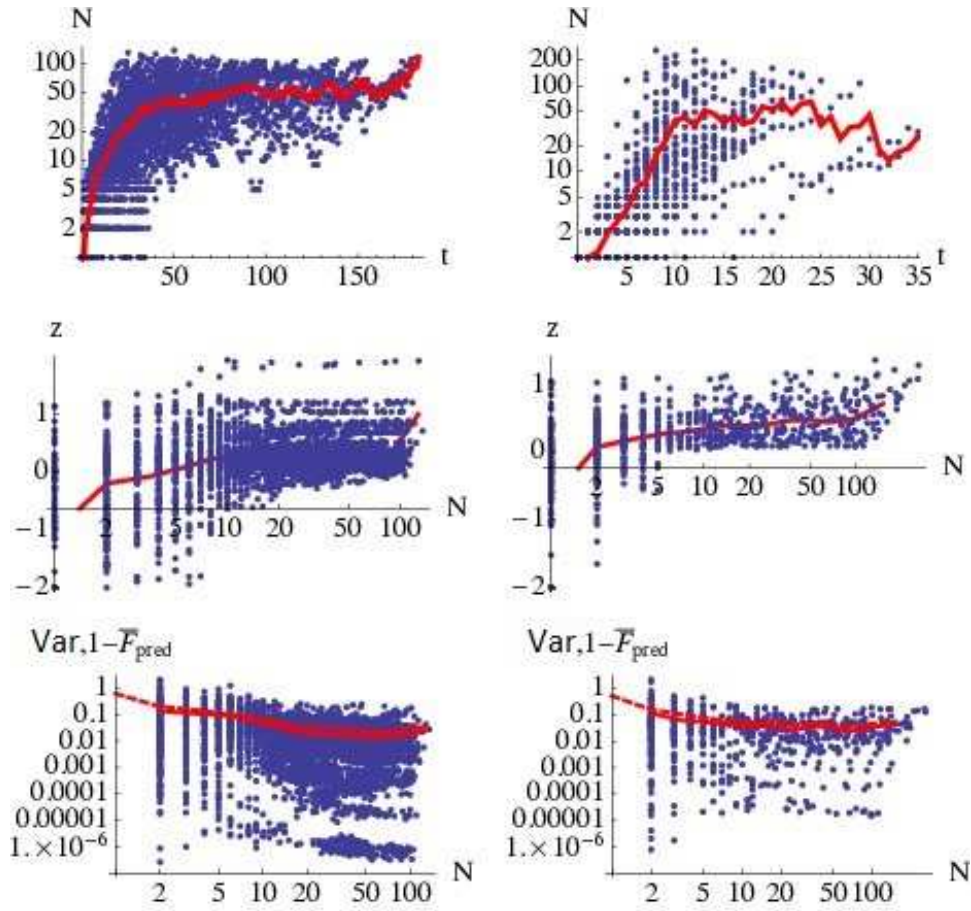
Figure 2: Population size, trait mean, and variance, for 50 successful establishments; $z_0 = -2$, $\beta = 0.125$ (left column), 1 (right column). (Results for $\beta = 2$ were not shown, since for those only 27 runs established within 10^5 trials). In each plot, the thick line shows the mean, whilst points show individual runs. Top: Population size, plotted against time. Middle: Trait mean, plotted against population size. Bottom: Trait variance, Var, plotted against population size. The mean of the variance across runs is shown by the thick line, and the mean heterozygosity predicted from population size, $1 - \overline{F}_{\mathrm{pred}}$, by the dashed line.
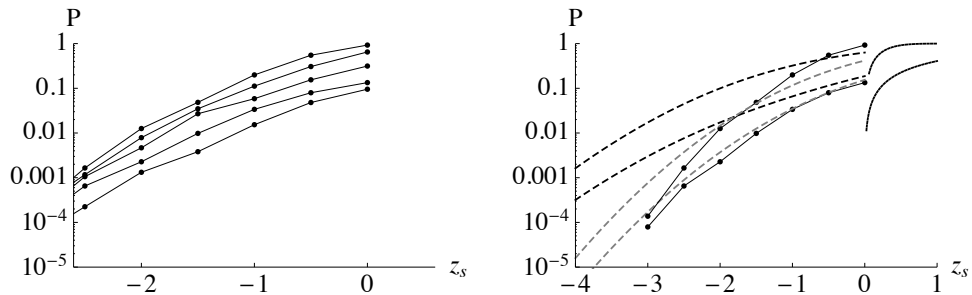
Figure 3: Left: Probability of reaching at least $N = 100$, starting from a single individual drawn from a population with mean trait value $\bar{z}_s$ and variance $2V = 1$; $\beta = 0.125$, 0.25, 0.5, 1, 2 (bottom to top). Right: For $\beta = 0.25$, 2, the solid curves show the probability of reaching at least $N = 100$ for a single migrant of trait value exactly $\bar{z}_s$. The dotted curves on the far right show the probability of establishment of a *homozygous* individual of value $\bar{z}_s$; this is the probability of establishment of a Galton-Watson branching process with Poisson offspring distribution with mean $e^{\beta \bar{z}_s}$ (which we have approximated by the survival probability). This is zero for $\bar{z}_s < 0$. The black dashed curves to the left show the probability of establishment of a migrant chosen randomly from a source population with mean $\bar{z}_s$ and variance $2V = 1$. Grey dashed curves show the same, but for a homozygous individual, so that the new population cannot evolve. The dashed curves are calculated by integration over the values shown by the solid curves; for $\bar{z}_s > 0.5$, the probability is approximated by these dotted curves. Estimates are based on the number of trials required to successfully establish 50 populations. Each of the 50 runs made a maximum of 10^5 trials; values here are maximum likelihood estimates of the establishment probability, assuming an exponential distribution for time to establishment, truncated at 10^5.

mutation. Random drift also contributes to some extent, but in two competing ways: random sampling may produce individuals with trait values well above the mean of the source population; on the other hand drift results in inbreeding, which reduces the variability of trait values. It is not clear how to separate this from the effect of selection, which systematically increases the trait mean.

Though selection and random drift make it possible for a single individual with expected fitness less than one to establish a population, this is unlikely when the initial value is more than a few genetic standard deviations below the critical threshold. The initial value, z_0, for which $P = 10^{-4}$, is $-2.01\sqrt{2V}$ for $\beta = 0.125$, and $-1.84\sqrt{2V}$ for $\beta = 1$: the probability of establishment is determined mainly by the initial trait value, relative to the genetic standard deviation, and is insensitive to the fitness gradient. We may also compare the fitness of the initial migrant, $e^{\beta z_0}$, which gives $P = 10^{-4}$; this is 0.78 for $\beta = 0.125$, but 0.16 for $\beta = 1$. Thus, an unfit migrant still has an appreciable chance to establish a population, provided that the fitness gradient is steep enough that its *descendants* can be fit.

The black dashed curves in Fig. 3 (right) show the probability of establishment by a migrant chosen randomly from the source population, for $\beta = 0.125, 2$, plotted against the mean trait value of the source population. For negative $\bar{z}_s$, these probabilities are much higher than for a migrant whose trait value is exactly $\bar{z}_s$, because the migrant may be a few standard deviations above the mean. Thus, establishment is feasible when the mean is 3 or 4 genetic standard deviations below the threshold, $z = 0$, and when an individual with trait value given by the mean in the source population would be extremely unfit in the new habitat. For $P = 10^{-4}$, the corresponding $\bar{z}_s$ is $-3.64, -3.92$ for $\beta = 0.125, 1$, respectively, and the corresponding fitnesses of the *mean* individual are $e^{\beta \bar{z}_s} = 0.63, 0.020$. With no evolution (i.e., assuming homozygous migrants), $P = 10^{-4}$ for $\bar{z}_s = -2.97, -3.55$, and $e^{\beta \bar{z}_s} = 0.69, 0.032$, respectively. Roughly speaking, the change in trait value required for the population to increase is contributed to a similar degree by the chance migration of an individual that is unusually well adapted to the new habitat, and by the subsequent evolution of the new population. This is illustrated further in Table 1.

3.2. Steady migration

Now, suppose that there is a steady influx of migrants from the source population. We still neglect density-dependence and stabilising selection, and so establishment is inevitable: eventually, a large enough population will be established, with sufficient genetic variation, to allow adaptation

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Table 1: Threshold values for establishment probabilities of 10^{-4}. (i) Top panel, z_0^c, the critical value of z_0 above which establishment probability is greater than 10^{-4}; (ii) Middle panel, $\bar{z}_s^c$, the critical value of $\bar{z}_s$ for which establishment from a migrant picked at random from the source population has probability 10^{-4}; (iii) Bottom panel, $\widetilde{z}_s^c$, the same as (ii) except that the migrant is taken to be *homozygous*. We have normalised so that $2V = 1$.

(i)

β	z_0^c	$\exp(\beta z_0^c)$
0.125	-2.00677	0.778142
0.25	-2.0357	0.601141
0.5	-1.99809	0.368231
1	-1.8381	0.159119
2	-1.62252	0.038967

(ii)

β	$\bar{z}_s^c$	$\exp(\beta \bar{z}_s^c)$
0.125	-3.63602	0.634763
0.25	-3.8175	0.385052
0.5	-3.90004	0.142271
1	-3.92306	0.0197804
2	-3.99407	0.000339465

(iii)

β	$\widetilde{z}_s^c$	$\exp(\beta \widetilde{z}_s^c)$
0.125	-2.97144	0.689748
0.25	-3.15104	0.454862
0.5	-3.31216	0.190886
1	-3.44909	0.0317746
2	-3.55486	0.00081712

and growth to indefinitely high numbers. When the influx is low, establishment depends on single migrants, and can be predicted from the results of the previous section (dashed lines at left of Fig. 4). However, as the migration rate increases, interactions between migrants become important, in two opposing ways. First, migrants introduce genetic variation, which can greatly increase the efficiency of selection. However, migration also pulls the trait mean back towards the value in the source population, which impedes adaptation. There is a strong positive feedback here, because small populations are especially liable to the swamping effects of gene flow, which impedes their adaptation to local conditions.

Figure 4 shows how the expected time to establishment (defined as reaching $N \geq 100$) depends on the number of migrants per generation, M, for $\beta\sqrt{2V} = 0.25$. Overall, we see that for $z_s/\sqrt{2V} > -0.5$ (lowest solid curve), the mean time to establishment decreases with immigration, and becomes very fast for large M. However, for higher levels of divergence ($z_s/\sqrt{2V} \leq -0.5$) there is an intermediate migration rate, M, which minimises the time to establishment; for large migration rates, establishment takes an extremely long time.

4. Approximating the dynamics of escape

While the population is rare in the new environment, we can neglect density dependent regulation. Conditional on the trait values, each possible pair of individuals in the population, independently, leaves behind a random number of offspring, with a distribution that depends on the parental traits. This is highly reminiscent of the nonlinear stochastic growth models introduced in a series of papers beginning with Kesten (1970); see Kesten (1971) for a review. Kesten's model is one of a diploid population and incorporates multiple types, and so in particular could be used to model multilocus traits. However, the only really satisfying analytic results currently available are when the type of an offspring is that of one of its parents. In our setting, in which the variance released by recombination plays a crucial role, these results do not apply. Here we shall satisfy ourselves with some simple caricatures of the joint evolution of population size and trait distribution, deferring a study of more sophisticated models to future work.

4.1. 'Deterministic' approximations

To understand why establishment becomes difficult at high migration rates when divergence is above a threshold value, we shall make the approximation that the trait distribution across the whole population is Gaussian.
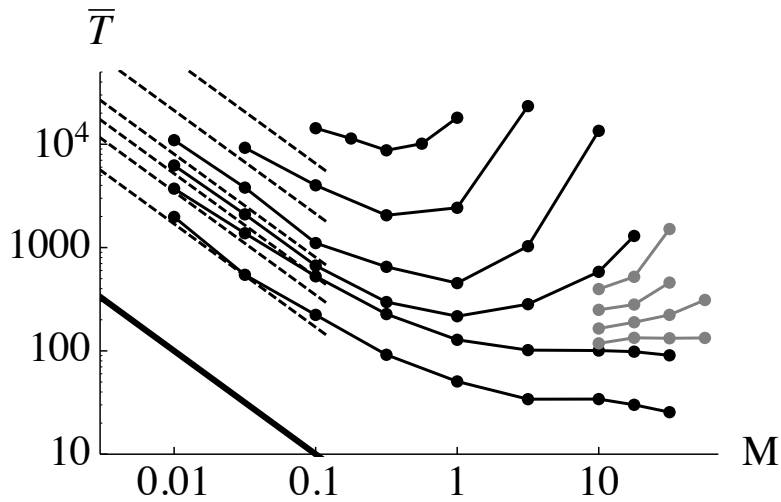
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Figure 4: Mean time to establishment, for $\beta = 0.25$, given migration at rate M from a source population with mean $\bar{z}_s$ and variance $2V = 1$; $\bar{z}_s = -1, -1.5, -2, -2.5, -3$ (bottom to top, black lines). Additional values, $\bar{z}_s = -1.55, -1.6, -1.65, -1.7$ are shown in grey, for large M (right of figure). The dashed lines at the left give the prediction, $\bar{T} = \frac{1}{MP}$, from the probability of establishment, P, of a single migrant, drawn randomly from the source population (Fig. 3, right, dashed curves). The thick line at lower left shows the lower bound, $\bar{T} = 1/M$, which would obtain if the first migrant to arrive immediately established a new population. Establishment is defined as a population of $N \geq 100$ for $M < 10$, and $N \geq 300$ for $M > 10$. Estimates of $\bar{T}$ are based on 100 replicates for each $\bar{z}_s, M$. Relatedness, F, is tracked between each pair of individuals up to $N = 50$, above which it is replaced by the mean relatedness.

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As a first approximation, we shall further suppose that the population size and the trait mean and variance evolve deterministically. We shall refer to this as the deterministic approximation. We emphasize that the Gaussian distribution across the population is not a consequence of using the infinitesimal model, which, in the presence of selection, only guarantees that within each family the trait distribution is normally distributed.

We expect this to be a reasonable approximation if migration rates are moderately high and the selection gradient is not too extreme. Under the infinitesimal model, each diploid migrant carries half of the genetic variance in the source population, and so modest rates of migration into a small 'sink' population can maintain high genetic variance, without causing large deviations from a Gaussian.

In Appendix A, we develop a recursion for the joint evolution of population size, trait mean, trait variance and average identity, which fits the dynamics well, and predicts a critical divergence, beyond which maladaptation becomes stable. Here, we develop a simpler recursion, by assuming that the variance remains approximately constant, despite selection and migration, and assuming that the identity is zero. In the more sophisticated models that follow, we shall routinely use the notation $V^* = V(1 - F_*)$ for the variance (before selection) among offspring of two individuals from the new population, where V is the segregation variance among offspring of two unrelated individuals and F_* is the average identity in the new population. We shall also use that notation here, even though we are assuming $F_* = 0$. Directional selection does not change the variance, and so if the variance across the population is approximately constant it will be $2V^*$.

Our aim is to write down deterministic equations which, under these assumptions, govern the joint evolution of the expected population size and the mean value of the trait across the population. With a slight abuse of notation, we denote these quantities by $N(t)$, $\bar{z}(t)$, respectively. Since the within family variance is V^*, the mean fitness, $\overline{W}$, among offspring is

$$\overline{W} = \mathbb{E}\left[\exp\left(\beta\frac{(Z_1 + Z_2)}{2} + \frac{\beta^2 V^*}{2}\right)\right],$$

where Z_1 and Z_2 are the traits of two parents sampled at random from the population. (Here we are using our assumption that identity is zero in both the new and the source populations, so that the within family variance is the same irrespective of whether one or both of the parents is a newly arrived migrant or not, but see Appendix A for the more general case.) The distribution of traits across the population is Gaussian with mean $\bar{z}$ and

variance $2V^*$, giving

$$\overline{W} = \exp\left(\beta\bar{z} + \beta^2 V^*\right),\tag{3}$$

and so after reproduction and the subsequent migration,

$$N(t+1) = M + N(t)\exp\left(\beta\bar{z}(t) + \beta^2 V^*\right).\tag{4}$$

The mean trait among these individuals is

$$\bar{z}(t+1) = \frac{1}{N(t+1)}\left(M\bar{z}_s + N(t)\mathbb{E}[ze^{\beta z}]\right),$$

where the expectation is with respect to the distribution of the trait among offspring (before selection) and can be calculated by differentiating $\overline{W}$ with respect to β. This yields

$$
\begin{aligned}
\bar{z}(t+1) &= \frac{1}{N(t+1)}\left(M\bar{z}_s + N(t)(\bar{z}(t) + 2\beta V^*)e^{\beta\bar{z}(t)+\beta^2 V^*}\right)\\
&= (\bar{z}(t) + 2\beta V^*)\left(1 - \frac{M}{N(t+1)}\right) + \bar{z}_s\frac{M}{N(t+1)}\\
&= \bar{z}(t) + 2\beta V^*\left(1 - \frac{M}{N(t+1)}\right) - \frac{M}{N(t+1)}\left(\bar{z}(t) - \bar{z}_s\right).\tag{5}
\end{aligned}
$$

It is convenient to rescale equations (4) and (5) by setting $n = N/M$, $\alpha = \beta\sqrt{2V^*}$ and $y = (\bar{z} - \bar{z}_s)/\sqrt{2V^*}$. Then the equations become

$$n(t+1) = 1 + n(t)W_s e^{\alpha y(t)}, \quad y(t+1) = (y(t) + \alpha)\left(1 - \frac{1}{n(t+1)}\right),\tag{6}$$

where

$$W_s = \exp\left(\beta\bar{z}_s + \beta^2 V^*\right)$$

is the mean growth rate of the source population in the new conditions.

If W_s is above some critical value, $W_{s,\text{crit}}$, population size and trait increase together even from low values, regardless of M. For smaller values of W_s, there are two equilibria, one stable and one unstable. In this case, the population may be unable to grow, regardless of how large is M; instead, it is maintained by migration as a poorly adapted 'sink'. Although an increase in M increases the population size, it also impedes adaptation, and therefore prevents indefinite growth.

To find the critical value, observe that at equilibrium $y(t) = y(t+1) = \alpha(n-1)$, i.e., $y_{\text{crit}} = \alpha(n_{\text{crit}} - 1)$ and writing $f(n) = 1 + nW_s e^{\alpha^2(n-1)}$ we

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must solve

$$n = f(n), \qquad 1 = f'(n).$$ (7)

This yields a quadratic in n whose positive solution is

$$n_{\text{crit}} = \frac{\alpha^2 + \sqrt{\alpha^4 + 4\alpha^2}}{2\alpha^2} = \frac{1}{2}\left(1 + \sqrt{1 + 4/\alpha^2}\right).$$ (8)

In our original variables, this becomes

$$N_{\text{crit}} = \frac{M}{2}\left(1 + \sqrt{1 + 2/(\beta^2 V^*)}\right),$$

and substituting in (7) to find $W_{s,\text{crit}}$ we find

$$W_{s,\text{crit}} = \frac{n_{\text{crit}} - 1}{n_{\text{crit}}} e^{-\alpha^2(n_{\text{crit}}-1)} = \left(1 - \frac{M}{N_{\text{crit}}}\right) e^{-\alpha^2(N_{\text{crit}}-M)/M},$$

and finally, since $W_{s,\text{crit}} = \exp(\beta\bar{z}_{s,\text{crit}} + \beta^2 V^*)$, we find

$$\beta\bar{z}_{s,\text{crit}} = -\frac{1}{2}\alpha\left(\sqrt{4 + \alpha^2}\right) - \log\left(\frac{\alpha + \sqrt{4 + \alpha^2}}{-\alpha + \sqrt{4 + \alpha^2}}\right).$$ (9)

For $\alpha = \beta\sqrt{2V^*} \ll 1$, $\beta\bar{z}_{s,\text{crit}} \sim -2\alpha$. For $\alpha \gg 1$, $\beta\bar{z}_{s,\text{crit}} \approx -\alpha^2/2 - 2\log\alpha$.

The solid line in Fig. 5 (top) shows the critical log fitness of an average migrant above which establishment is inevitable in this deterministic limit, $\beta\bar{z}_{s,\text{crit}}$, plotted against the standard deviation of log fitness in the source population, $\alpha = \beta\sqrt{2V^*}$. The dashed line shows the more sophisticated approximation of Appendix A, which takes into account the different within-family variance of offspring resulting from different combinations of native and migrant parents. The lower plot shows the corresponding critical fitness of the source population in the new environment, $W_{s,\text{crit}}$.

4.2. The diffusion approximation to the stochastic dynamics

In this section we shall continue to assume that the trait distribution across the population has a Gaussian distribution, but we extend the analysis of the last section to incorporate stochastic fluctuations in the population size and trait mean to capture demographic stochasticity and random sampling drift. We shall use a continuous time approximation.

The first step is to find the appropriate continuous time approximation to the discrete equations (4), (5). If $\beta\bar{z} + \beta^2 V^*$ is small, neglecting the second
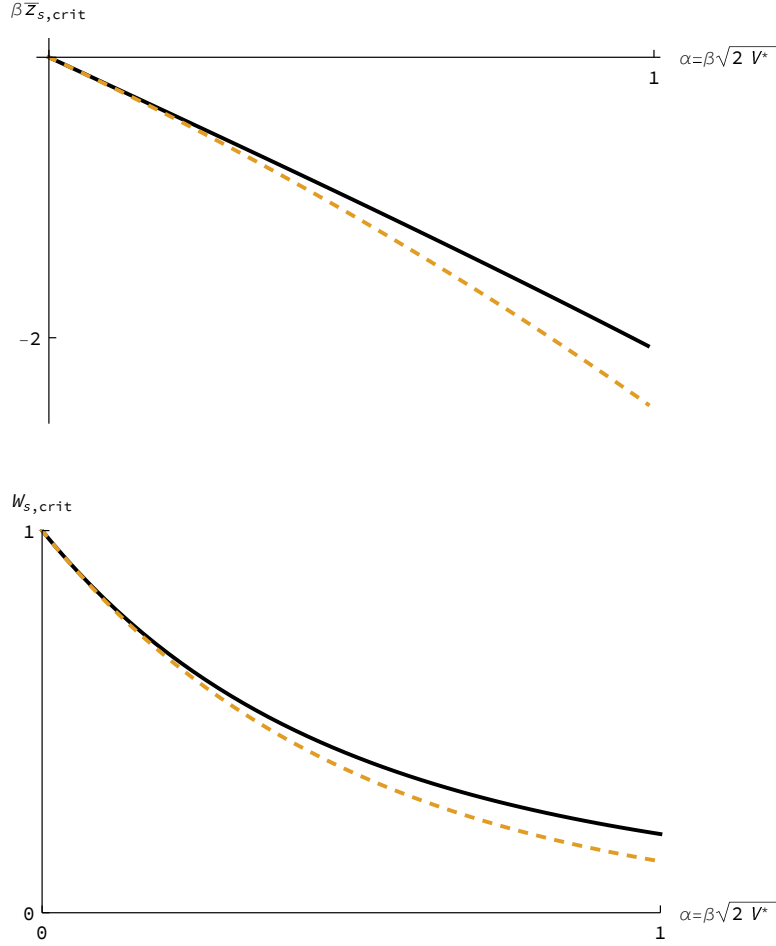
Figure 5: Top: The critical log fitness of an average migrant, $\beta\bar{z}_{s,\text{crit}}$, above which establishment is inevitable in the deterministic limit, plotted against the standard deviation of log fitness in the source population, $\beta\sqrt{2V^*}$. The solid line assumes constant variance $2V^*$ (Eq. 9). The dashed line allows variance to evolve (Appendix A). Bottom: The critical fitness of an average migrant in the new environment, $W_{s,\text{crit}} = \exp(\beta\bar{z}_{s,\text{crit}} + \beta^2 V^*)$.

order term $\beta^2 V^*$, we arrive at the pair of ordinary differential equations:

$$\frac{dN(t)}{dt} = M + \beta\bar{z}(t)N(t);$$

$$\frac{d\bar{z}(t)}{dt} = 2\beta V^* \left(1 - \frac{M}{2N(t)}\right) - \frac{M}{N(t)}(\bar{z}(t) - \bar{z}_s).$$

In fact, as we explain in Appendix B, if we wanted to accumulate an error of order at most $\beta^2(M+N)$ per generation in using this differential equation for population size in place of our discrete recursion, we should (at the expense of much more complex expressions in what follows) replace the immigration rate M in the first equation by $M(1 - \beta\bar{z}(t)/2)$. With this equation the error is order $\beta\bar{z}M + \beta^2(M + N)$. Since our model is in any case only a caricature, we take these simpler equations.

We now add random perturbations ζ_N, $\zeta_{\bar{z}}$ with the appropriate variances. Recall that the variance of the trait across the population was taken to be $2V^*$. The dynamics can then be described by a potential, U:

$$U = M \log N + \beta(N - \frac{M}{2})\bar{z} - \frac{M}{4V^*}(\bar{z} - \bar{z}_s)^2,$$

for which

$$\frac{dN}{dt} = N\frac{\partial U}{\partial N} + \zeta_N = M + \beta\bar{z}N + \zeta_N, \qquad\qquad <\zeta_N^2> = N;$$

$$\frac{d\bar{z}}{dt} = \frac{2V^*}{N}\frac{\partial U}{\partial \bar{z}} + \zeta_{\bar{z}} = 2\beta V^* \left(1 - \frac{M}{2N}\right) - \frac{M}{N}(\bar{z} - \bar{z}_s) + \zeta_{\bar{z}}, \quad <\zeta_{\bar{z}}^2> = \frac{2V^*}{N}.$$

If there were a stationary distribution, ψ, then, see e.g. Gardiner (2004), §5.3.3, it would satisfy

$$\psi \propto \frac{e^{2U}}{N} = N^{2M-1} \exp\left(\beta(2N - M)\bar{z} - \frac{M}{2V^*}(\bar{z} - \bar{z}_s)^2\right). \qquad (10)$$

This expression diverges for large N, $\bar{z}$, but it should approximate the density of the population while it is near to a stable 'sink' equilibrium, when that exists. In the next section, we extend it to include density regulation and stabilising selection.

Equation (10) has a simple form, with three terms that correspond to migration that increases population size (N^{2M-1}), directional selection on the trait ($e^{\beta(2N-M)\bar{z}}$), and gene flow that pulls the trait mean towards the
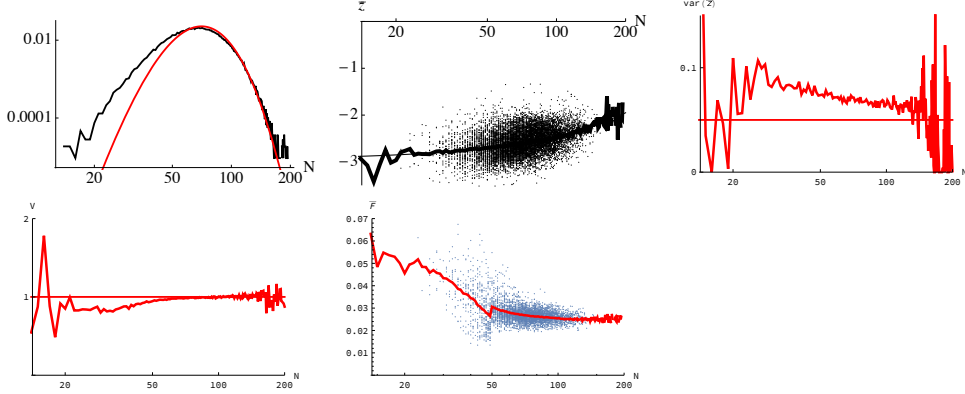
Figure 6: The distribution of N, $\bar{z}$ for a population trapped in a sink; $z_s = -3$, $\beta = 0.05$, $M = 10$. 11 replicate simulations were made with a total of 10^5 generations; the first 200 generations were discarded. Top left: the distribution of N, compared with that predicted by Eq. (11), $N^{2M-1}\exp\left((2N-M)\beta\bar{z}_s + (2N-M)^2\beta^2/4M\right)$ (red). Top middle: The trait mean, conditional on N compared with the predicted $\bar{z}_s + \beta V^*(2N-M)/M$, assuming $2V^* = 1$. Top right: The variance of the mean compared with the predicted var($\bar{z}$) = $1/2M$. Bottom left: The population variance, $2V^*$, conditional on N, compared with the assumed $2V^* = 1$. Bottom middle: Mean identity, $\bar{F}$, conditional on N.

source $\left(e^{-M(\bar{z}-z_s)^2/2V^*}\right)$.

For given N, the trait mean is normally distributed, with variance V^*/M, and mean $\mathbb{E}\left[\bar{z}\right] = \bar{z}_s + \beta V^*(2N-M)/M$; this is the deterministic equilibrium in which selection $2\beta V^*(1-M/2N)$ increases the trait mean, [...] is opposed by gene flow at rate M/N. Integrating over the trait mean, the distribution of N is proportional to

$$N^{2M-1}\exp\left(\beta^2(2N-M)^2\frac{V^*}{2M} + \beta(2N-M)\bar{z}_s\right). \tag{11}$$

If $M > 1/2$ (which is required for genetic variance, $2V^*$, to be high and approximately constant), and if $\bar{z}_s < -2\sqrt{V^*(1-1/(2M))} + \beta V^*/2 \sim -2\sqrt{V^*}$, then the distribution has a peak at low density, and with $\bar{z} < 0$, which represents a metastable 'sink', in which the population is maintained by gene flow despite its maladaptation. Figure 6 compares this approximation with the distribution of $\bar{z}$, N for $M = 10$.

5. Understanding the new equilibrium

5.1. Deterministic equilibrium

Once the new population is established, it will grow and adapt. Eventually, its size must be limited by some form of density dependence, and the trait will reach some equilibrium mean and variance. Despite inbreeding, there will be some residual genetic variance (the amount being highly variable), which will slowly be augmented by new mutation. We will first outline how trait evolution may be limited, and then develop a diffusion approximation for the full process. In the following section, we complete the analysis by using the deterministic approximation to estimate the degree to which the newly established population is reproductively isolated from its progenitor.

Suppose that fitness decreases linearly with density, at rate γ, giving a continuous-time approximation:

$$\frac{dN(t)}{dt} = M + N(t)\beta\bar{z}(t) - \gamma N(t)^2,$$

$$\frac{d\bar{z}(t)}{dt} = 2\beta V^* \left(1 - \frac{M}{2N(t)}\right) - \frac{M}{N(t)}\left(\bar{z}(t) - \bar{z}_s\right).$$

A homogeneous population with trait $\bar{z}$ would equilibrate at

$$N = \frac{1}{2\gamma}\left(\beta\bar{z} + \sqrt{\beta^2\bar{z}^2 + 4M\gamma}\right),$$

but the trait is also evolving. For the trait mean to be in equilibrium, we must have $\bar{z} = \bar{z}_s + \beta V^* \frac{2N-M}{M}$, which implies equilibria for population size at:

$$N = \frac{M}{2\left(2\beta^2 V^* - M\gamma\right)}\left(-\beta\bar{z}_s + \beta^2 V^* \pm \sqrt{\left(\beta\bar{z}_s - \beta^2 V^*\right)^2 - 8\beta^2 V^* + 4M\gamma}\right).$$

There are three distinct regimes. If $2\beta^2 V^* < \gamma M$, the trait cannot evolve fast enough to overcome migration and density regulation, and the population will be trapped in a unique 'sink' equilibrium. If

$$8\beta^2 V^* - \left(\beta\bar{z}_s - \beta^2 V^*\right)^2 < 4\gamma M < 8\beta^2 V^*,$$

then there is a stable 'sink', but the population can escape to indefinitely

high density if it can get beyond an unstable saddle point. Finally, if

$$4\gamma M < 8\beta^2 V^* - \left(\beta \bar{z}_s - \beta^2 V^*\right)^2,$$

the population will expand indefinitely, even when it starts at low density and is poorly adapted.

Simply adding linear density-dependence cannot maintain a stable equilibrium at high density, in addition to the stable 'sink' which exists for $8\beta^2 V^* - (\bar{z}_s - \beta^2 V^*)^2 < 4\gamma M$. However, there are (at least) three ways by which the indefinite adaptive increase of the population might be limited. First, density-dependence might be steeper than linear (e.g. $\sim -\gamma N^a$ for $a > 1$); then, population size would stabilise and the trait would be maintained in a migration-selection balance. Second, under purely directional selection, genetic variance would decrease, and mutation pressure would decrease the mean, as favourable alleles fix. Third, the trait might be under stabilising selection towards $z_{\text{opt}} > 0$, with log fitness $\frac{s}{2}\left(z_{\text{opt}}^2 - (\bar{z} - z_{\text{opt}})^2\right)$, preventing its indefinite increase. We have chosen this form of log fitness so that the threshold for positive growth is at $\bar{z} = 0$. Near that threshold, the trait would still be under approximately directional selection with $\beta \sim s\, z_{\text{opt}}$, provided $z_{\text{opt}} \gg \bar{z}_s, \sqrt{2V^*}$.

5.2. Diffusion approximation at a stationary state

We now extend the diffusion approximation to include density-dependence and stabilising selection; it is not immediately obvious how to include mutation or fixation of favourable alleles in the quantitative genetic model in a consistent way, and so we do not consider these cases. We shall use $2\hat{V}$ to denote the variance of the trait across the population. As we explain in Appendix C, under stabilising selection, negative linkage disequilibrium results in $2\hat{V} < 2V^*$ (although for small s, $\hat{V} \sim V^*$). The potential, U, is modified to allow density dependence $-\gamma N^a$, and arbitrary mean fitness $\bar{r}$:

$$U = M \log N + N\bar{r} - \frac{M}{4\hat{V}}\left(\bar{z} - \bar{z}_s\right)^2 - \frac{\gamma}{a}N^a$$

$$\frac{dN}{dt} = N\frac{\partial U}{\partial N} + \zeta_N = M + N\bar{r} - \gamma N^a + \zeta_N \qquad <\zeta_N^2> = N$$

$$\frac{d\bar{z}}{dt} = \frac{2\hat{V}}{N}\frac{\partial U}{\partial \bar{z}} + \zeta_{\bar{z}} = 2\hat{V}\frac{\partial \bar{r}}{\partial \bar{z}} - \frac{M}{N}\left(\bar{z} - \bar{z}_s\right) + \zeta_{\bar{z}} \qquad <\zeta_{\bar{z}}^2> = \frac{2\hat{V}}{N}$$

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Hence, the stationary density is proportional to:

$$\psi \propto \frac{e^{2U}}{N} = N^{2M-1} \exp\left(2N\bar{r} - \frac{M}{2\hat{V}}(\bar{z} - \bar{z}_s)^2 - \frac{2\gamma}{a}N^a\right) \qquad (12)$$

This is valid on the assumption that the genetic variance changes slowly, so that the population size and trait mean approach the stationary distribution conditional on the current genetic variance. Stabilising selection would be represented by:

$$\bar{r} = \frac{s}{2}\left(z_{\text{opt}}^2 - (\bar{z} - z_{\text{opt}})^2\right).$$

Then, for example, if $a = 2$ and we normalise so that $2\hat{V} = 1$, the stationary distribution $\psi[N, \bar{z}]$ satisfies

$$\psi[N, \bar{z}] \propto N^{2M-1}$$
$$\times \exp\left(-M(\bar{z} - \bar{z}_s)^2 - s\left(N - \frac{M}{2}\right)\left((\bar{z} - z_{\text{opt}})^2 - z_{\text{opt}}^2\right) - \gamma N^2\right).$$

Integrating over the trait we find that the density of the marginal distribution of the population size satisfies

$$\psi[N] \propto \frac{N^{2M-1}}{\sqrt{M + s\left(N - \frac{M}{2}\right)}}$$
$$\times \exp\left(\frac{-sM(N - M/2)(z_{\text{opt}} - \bar{z}_s)^2}{M + s\left(N - \frac{M}{2}\right)} + s\left(N - \frac{M}{2}\right)z_{\text{opt}}^2 - \gamma N^2\right).$$

On the other hand, if we condition on the population size, then the trait has mean and variance given by

$$\mathbb{E}[z|N] = \frac{M\bar{z}_s + sz_{\text{opt}}\left(N - \frac{M}{2}\right)}{M + s\left(N - \frac{M}{2}\right)}, \qquad \text{Var}(\bar{z}|N) = \frac{1}{2\left(M + s\left(N - \frac{M}{2}\right)\right)}.$$

Figure 7 shows the result of a simulation of a population subject to stabilising selection towards an optimum at $z_{\text{opt}} = 5$ with $s = 0.02$ and density regulation as above with $a = 2$ and $\gamma = 0.001$. There are two metastable states. Over a total of 55,000 generations, 8 of 11 replicate simulations, each started from a single migrant, jump from low density to high density, and none jump in the opposite direction. Thus jumps are too rare for it to be feasible to estimate the rates of transition in the two
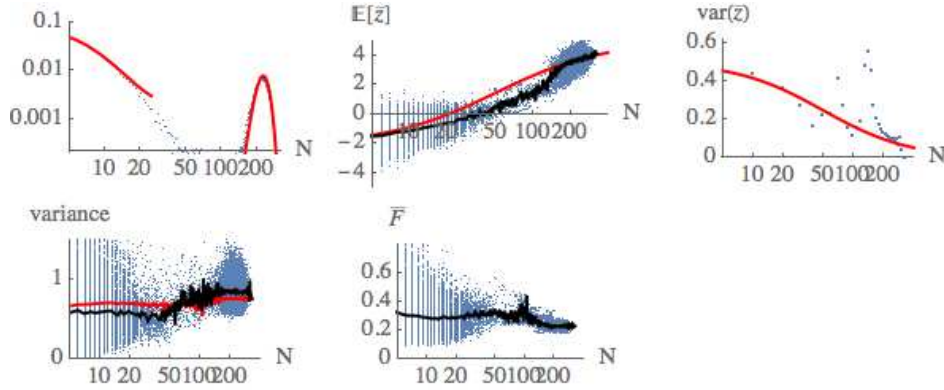
Figure 7: The distribution of $N, \bar{z}$ for a population subject to stabilising selection, $s = 0.02$, towards an optimum at $z_{\text{opt}} = 5$, and density regulation with $a = 2$, $\gamma=0.001$; migrants enter at rate M, and have mean $z_s = -2$. 11 replicate simulations were made, starting with a single migrant, and with a total of 55,000 generations. Over this time, 8 of the 11 replicates jumped to high density. Top left: The distribution of N, compared with the diffusion approximation (red), assuming $2V^* = 1$. Top middle: The trait mean, conditional on N. The black line shows the mean for each value of N, and is compared with the diffusion approximation (red curve). Top right: The variance of the mean, conditional on N, compared with the diffusion approximation (red curve). Dots show the variance, pooled into windows of width $\Delta N = 10$. Bottom left: within-population variance, conditional on N. The black line shows the mean for each value of N, and is compared with the diffusion approximation (red curve). Bottom right: Mean identity, $\overline{F}$, conditional on N; this is used to calculate the predicted variance, $2V^*$ (red line at bottom left).

directions, and therefore the relative weight of each metastable state, but the diffusion approximation does predict the joint distribution of $N, \bar{z}$, given that the population is in one or other of the two metastable states. This prediction is shown by the red curve at top left of Fig. 7. The predicted distribution has been separated into two peaks which are then weighted by the observed weights; thus the fit is to the shape of each peak separately, not to their relative weights. The population variance is assumed to be $2V^*$, the mean identity being calculated from pooled data at low and high densities (0.29, 0.23 respectively). The other four panels of Fig. 7 show the expected mean, the variance of the trait mean, the variance within populations, and the mean identity. The expectation and the variance of the trait mean match well, except in the transition region ($20 < N < 150$), where there is little data. The variance within populations is somewhat lower than the predicted $2V^*$ at low density, but somewhat higher at high density (bottom left).

6. Introgression into the new population

Once the new population is established with large numbers, and has adapted to its new environment, it will still receive migrants from its progenitor population. These will impede adaptation by pulling the trait mean back, but given that establishment was possible, the new population will be able to remain distinct unless conditions change. Moreover, introgression will be reduced both because the new population is larger, and because it is better adapted. Here, we calculate the reproductive value of an individual backcrossing into such a population - that is its expected long-term genetic contribution, normalised so that the mean contribution of native individuals is one. When averaged over the trait values and degree of relatedness of migrants, this gives the *gene flow factor*, which measures the reduction in gene flow due to selection against introgressing genes (Bengtsson, 1985). This determines the strength of reproductive isolation, and hence, whether the new population should be considered a biological species.

The new population will initially be highly inbred (Fig. 2), and gene flow may play an important role by introducing new genetic variation. Because individuals that migrate into a large population contribute additively to the decrease in the mean relatedness, $\overline{F}$, the rate of influx of trait variance due to migrants is proportional to their reproductive value, just as for allele frequencies or trait means. In the following, we describe how reproductive value depends on trait mean and on relatedness, assuming that the new population is at an equilibrium involving mutation and directional selection. We also outline the corresponding derivation for stabilising selection, but we are unable to provide an analytic expression for the reproductive value in this case. Derivations are in Appendix C.

Directional selection

Suppose that the newly established population is at equilibrium in a balance between directional selection and mutation. As before, we write V for the variance in the trait among offspring of two unrelated individuals, the within-family variance is $V(1 - F_*)$ where F_* is the average identity of two individuals chosen from the population, and under directional selection with fitness $e^{\beta z}$ the equilibrium genetic variance is $2V^*$.

In each generation, selection increases the mean by $2\beta V^*$, and this is counterbalanced by mutation. We assume that mutation only slowly increases the genetic variance, and that this is offset by weak random drift or stabilising selection; these effects are assumed to be negligible on the short timescale set by recombination and by selection on the trait mean.

We define $w[z, F_w, F_b]$ to be the reproductive value of an individual back-crossing into the population. Here z is the value of the trait of the individual, F_w is the probability of identity of two distinct copies of a gene sampled within the individual, and F_b is the mean identity between the individual and a randomly chosen individual from the established population.

First we consider a single generation. The *immediate fitness* of an individual is the expected number of its offspring, normalised by the average growth rate across the native population (given by Eq. 3). For an individual with trait value z, the immediate fitness is

$$\exp\left(-\beta\bar{z} - \beta^2 V^*\right) \mathbb{E}\left[\exp\left(\beta\frac{(z+Y)}{2} + \frac{\beta^2 V_b}{2}\right)\right]$$
$$= \exp\left(\beta\frac{(z-\bar{z})}{2} - \frac{\beta^2 V^*}{4} + \frac{\beta^2}{2}(V_b - V^*)\right),$$

where the expectation is over the trait value Y of a randomly chosen mate from the native population and V_b is the within-family variance among offspring:

$$V_b = V\left(1 - \frac{F_w + F_*}{2}\right). \tag{13}$$

For a native individual, $V_b = V^*$. For a migrant, we see two conflicting forces; we expect that for a new migrant $z < \bar{z}$, but if it brings extra variance ($V_b > V^*$), the offspring can nonetheless be successful.

After selection and mutation (which reduces the mean by $2\beta V^*$), the trait distribution of surviving offspring is normal with mean

$$\frac{z+\bar{z}}{2} + \beta V_b - \frac{3\beta V^*}{2}$$

and variance $V_b + V^*/2$. Writing $\mathcal{N}[x|\mu, \sigma^2]$ for the density function at x of a normally distributed random variable with mean μ and variance σ^2, we now have a recurrence for the reproductive value:

$$w[z, F_w, F_b] = \exp\left(\beta\frac{(z-\bar{z})}{2} - \frac{\beta^2 V^*}{4} + \frac{\beta^2}{2}(V_b - V^*)\right)$$
$$\times \int w\left[x, F_b, \frac{F_b + F_*}{2}\right] \mathcal{N}\left[x \,\middle|\, \frac{z+\bar{z}}{2} + \beta V_b - \frac{3\beta V^*}{2}, V_b + \frac{V^*}{2}\right] dx.$$

For a native individual, with trait value z, $F_w = F_b = F_*$ and the

reproductive value is

$$w_*[z] = e^{\beta(z-\bar{z})-\beta^2 V^*}. \tag{14}$$

(Notice that this averages to one across native individuals.) Equation (14) says that the reproductive value is proportional to the *square* of the immediate fitness. This can be understood using Robertson's (1960) argument, that with no linkage, an inherited increase in fitness halves across each generation, and so persists for, on average, two generations. The fixation probability of a favourable mutation has the same dependence on reproductive value (Barton, 2009).

The reproductive value of a migrant individual with trait z is:

$$w[z, F_w, F_b] = \exp\left(\beta(z - \bar{z}) + 4\beta^2(V_b - V^*) - \beta^2 V^*\right). \tag{15}$$

This decreases with F_w, F_b, because an inbred migrant has less variable offspring ($V_b < V^* = V(1 - F_*)$). The factor $\exp(z - \bar{z})$, which reduces the contribution of a less well-adapted migrant, is multiplied by a factor which increases the contribution if the migrant produces more variable offspring than the natives. When the new population is relatively outbred (right of Fig. 8), the effect of the trait mean dominates, and introgression is reduced. However, when it is highly inbred ($F_* \sim 1$; left of Fig. 8), the increased variance of hybrids can give them a strong advantage if there is a high genetic variance in the source population.

Stabilising selection

We now turn to the case of stabilising selection. We assume that the population is at equilibrium with constant relatedness F_* between all genomes; fitness is proportional to $\exp\left(-s(z - z_{\text{opt}})^2/2\right)$, and the mean is assumed to be at the optimum. The trait z is taken to be normally distributed with variance $2\hat{V}$. As before, $V^* = V(1 - F_*)$ denotes the within family variance *before selection*. Because stabilising selection causes negative linkage disequilibrium, $\hat{V} < V^*$ at equilibrium. In Appendix C we find an expression for $\hat{V}$ and show that for small s it is approximately equal to V^*.

Before the action of selection, the offspring of two individuals sampled at random from the population have mean z_{opt} and variance $\hat{V} + V^*$ and so an easy calculation (Appendix C) shows that the mean growth rate across the population is $1/\sqrt{1 + s(\hat{V} + V^*)}$. Now focus on an individual with trait value z. The variance across its offspring (before selection) when it reproduces with a randomly chosen member of the native population is $\hat{V}/2 + V_b$, with V_b given by (13). Normalising by the mean growth rate, an analogous
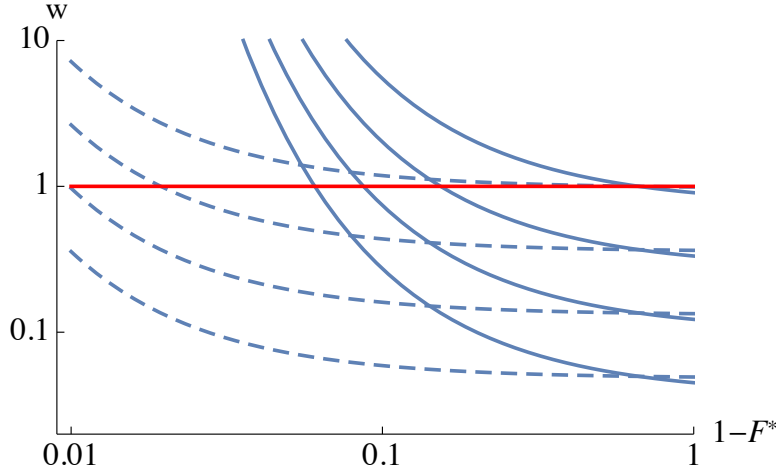
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Figure 8: Reproductive value of an unrelated and outbred individual ($F_w = F_b = 0$) that backcrosses into a population with inbreeding coefficient F_* under directional selection (Eq. 15). This population has genetic variance $2V^* = 2V(1 - F_*)$. The variance in log fitness is $2\beta^2 V_* = 0.02$ (dashed curves), 0.2 (solid curves); relative fitness of the migrant is $e^{\beta(z-\bar{z})} = 1, e^{-1}, e^{-2}, e^{-3} \ (= 1, 0.37, 0.135, 0.050)$ (top to bottom).

calculation shows that the immediate fitness of the individual is

$$\frac{\sqrt{1 + s(\hat{V} + V^*)}}{\sqrt{1 + s(\hat{V}/2 + V_b)}} \exp\left(-\frac{(z - z_{opt})^2}{4} \frac{s}{2(1 + s(\hat{V}/2 + V_b))}\right).$$

The distribution of surviving offspring of this individual is normal with mean

$$z_{\mathrm{opt}} + \frac{z - z_{\mathrm{opt}}}{2(1 + s(\hat{V}/2 + V_b))}$$

and variance

$$\frac{\hat{V}/2 + V_b}{1 + s(\hat{V}/2 + V_b)},$$

from which we deduce the recursion for the reproductive value. Using the

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same notation as for directional selection:

$$w[z, F_w, F_b] = \frac{\sqrt{1 + s(\hat{V} + V^*)}}{\sqrt{1 + s(\hat{V}/2 + V_b)}} \exp\left(-\frac{(z - z_{\mathrm{opt}})^2}{4} \frac{s}{2(1 + s(\hat{V}/2 + V_b))}\right)$$

$$\times \int \mathcal{N}\left[x \,\middle|\, z_{opt} + \frac{(z - z_{opt})}{2(1 + s(\hat{V}/2 + V_b))}, \frac{(\hat{V}/2 + V_b)}{(1 + s(\hat{V}/2 + V_b))}\right] w\left[x, F_b, \frac{F_b + F_*}{2}\right] dx.$$

(16)

In general, even for native individuals we have not been able to find a closed form solution for this recursion. However, for small s, for a native individual, an approximate solution to (16) is provided by

$$w(z) \propto \exp\left(-\theta \frac{s}{2}(z - z_{opt})^2\right),$$

where

$$\theta = \frac{-(2\alpha - 1) + \sqrt{4\alpha^2 + 4\alpha - 15}}{4(\hat{V} + 2V^*)},$$

and $\alpha = 2 + s(\hat{V} + 2V^*)$. Since for small s, at equilibrium, $\hat{V} \sim V^*$, substituting we find

$$\theta \sim \frac{s}{3} \qquad \text{as } s \downarrow 0,$$

so that for small s the reproductive value of a native individual is approximately proportional to the immediate fitness to the power 4/3.

More generally, the reproductive value of migrants, and hence their contribution to gene flow, depends on their degree of inbreeding (F_w), their relatedness to the new population (F_b), and on the product of the strength of stabilising selection and the genetic variance, $2sV$, which is a measure of the genetic load due to stabilising selection. The reproductive value, of an individual with the optimal trait value, $z = z_{\mathrm{opt}}$, is greater than 1 if it comes from the native population, so that $F_w = F_b = F_*$, and increases with $2sV$. Unrelated individuals that move into a highly inbred population have substantially lower reproductive value, because their offspring are highly variable, and hence tend to be further from the optimum.

7. Discussion

We analyse a simple, yet quite general, model for establishment in a new habitat, following the joint evolution of the numbers and fitness distribution

of individuals in the new environment. Although most of our results come from simulations, we obtain approximations for the limiting cases of low and high numbers of immigrants. More important, a thorough description is possible because there are just three parameters: the number of migrants per generation, M, and the mean and variance of log fitness of individuals from the source population, measured in the new environment. These quantities are, in principle, directly observable - though it has been very difficult to measure the genetic variance in fitness in any organism (Kruuk et al., 2014).

The probability that a single migrant will establish a new population depends primarily on how many genetic standard deviations the source lies below the threshold fitness needed for positive growth ($\bar{z}_s/\sqrt{2V}$). Roughly, establishment becomes feasible if the mean of the source population is less than ~ 4 standard deviations below the threshold growth rate; even though individuals that would have positive growth may be extremely rare, their offspring will be selected for faster growth, allowing establishment. A positive growth rate is achieved in roughly equal measure by the success of migrants that by chance are better adapted to the new environment, and by the subsequent adaptation of their offspring. Following intense inbreeding during establishment, some genetic variance remains, but the extent of inbreeding - and hence, of future adaptation - is highly variable (Fig. 2).

Steady immigration gives more opportunity for establishment, and maintains higher genetic variance in the new population. However, it also pulls the diverging population back towards the maladaptation of the source; if the divergence of the source is greater than some threshold number of standard deviations, then the expected time to establishment increases indefinitely with migration rate, M (Fig. 4, upper right). This threshold can be predicted by a simple deterministic approximation that ignores random fluctuations, and assumes a constant genetic variance (Fig. 5). Above this threshold level of divergence, establishment is still possible, provided that M is not too high, but relies on random fluctuations that allow escape from a metastable 'sink' state.

We introduce a simple diffusion approximation, which captures the qualitative behaviour of the model. The key assumptions are that the genetic variance is constant - reasonable for moderate to large numbers of migrants - and that changes are slow. This continuous time approximation is the main source of error, since the small initial population size and strong fitness differences necessarily set a short timescale. Nevertheless, the diffusion approximation is a powerful aid to intuition, and readily extends to give the joint distribution of population size and trait means or allele frequencies in a population that experiences density regulation and stabilising selection

(Eq. 12; see Banglawala, 2010).

We have used a very simple model of trait evolution, which depends primarily on a single parameter - the additive genetic variance. There is obvious scope for including greater realism - in particular, investigating the effects of the number of loci, and including dominance and inbreeding depression. The diffusion approach may be fruitful here, since it readily extends to discrete biallelic loci, with dominance (see Banglawala, 2010). Gomulkiewicz et al. (2010) argue that establishment is harder when more loci are involved. However, as they point out, this argument depends on which quantities are held fixed. If the additive variance is fixed, then there is a well-defined infinitesimal limit, which is insensitive to the number of loci and their distribution of effects.

Gomulkiewicz and Houle (2009) investigate the effects of genetic constraints on evolutionary rescue, using a model of stabilising selection on multiple traits. A large population will always reach the optimum, provided there is at least some genetic variance in every direction. However, when adaptation must occur rapidly if a small population is to survive, genetic constraints (represented by directions in trait space with low variance) may lead to extinction. Here, we only consider a single trait, which can be seen as the vector that connects the source population with the new optimum. Genetic constraints are represented by the variance along this direction. This will be a good approximation if the new optimum is far from the threshold for positive growth - a considerable simplification.

The rapid adaptation that is needed to establish a growing population in a new habitat is unlikely to depend on mutation: a heterozygote for a single mutation would need to increase growth rate to a positive value by itself. This may be plausible for specific environmental challenges - pesticides or plant toxins for example - but seems unlikely where multiple adaptations are needed for growth. However, a mutation of large effect could act together with polygenic adaptation. For a single migrant that carries such an allele in heterozygous form, it is trivial to extend our analysis. However, continued migration would tend to swamp the new allele. Indeed, the facilitating mutation might eventually be lost, even if its initial presence was crucial for establishment (c.f. Gomulkiewicz et al., 2010).

The strong dependence of establishment probability on the number of standard deviations that separate the source from the threshold for positive growth simply reflects the rapid decline of probability in the tails of a normal distribution. It implies that if the size of the gap, measured in standard deviations, fluctuates in space or time, then rare instances when the gap is small will be most likely to lead to establishment. Once a large population is

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established, it can increase and adapt further, until numbers are limited by competition, and the trait is limited by either stabilising selection, mutation pressure, or lack of variation that can further increase fitness.

Once a new population is established in large numbers, N, the rate of immigration will be low if $M \ll N$. Moreover, immigrants will have low fitness in the new habitat; under the infinitesimal model with initial fitness $e^{\beta z} < 1$, the rate of gene flow into the new population is given by Eq. (10). If gene flow is sufficiently reduced, then we have a model of speciation. Recalling the scenario in which demes in a metapopulation experience a fluctuating environment, whether the new population survives and remains distinct depends more on the distribution of suitable habitat than on genetic details.

Note that this mechanism is distinct from classical 'founder-effect' speciation, because it is impeded rather than assisted by inbreeding and the consequent loss of genetic variance during establishment (Barton and Charlesworth, 1984). Directional selection acts throughout establishment in the new environment, so that no fitness valley needs to be crossed. Nevertheless, a combination of genetic and demographic fluctuations are needed to establish large numbers of well-adapted individuals despite gene flow from populations that are already abundant in a different environment (or environments).

It is not immediately obvious whether the model analysed here should be classed as sympatric or parapatric. Microhabitats might be intimately mingled, and individuals from the source population might land randomly across habitats. However, individuals that do manage to survive in the new habitat are assumed to leave offspring there, and they must mate primarily with others born there. Provided that the original population is sufficiently many standard deviations from the threshold for growth in the new habitat, only a few individuals can immigrate for establishment to be feasible. So, this is a model of parapatric speciation. However, if the evolving trait itself induced habitat or mate preference, or a trait that determined premating isolation were added, we would have a model for sympatric speciation (c.f. Polechová and Barton, 2005; Barton, 2010). This could be seen as an extension of the infinitesimal models of Polechová and Barton (2005) and Barton (2010) to include local adaptation and random drift.

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Appendix A. Gaussian approximations

We develop a deterministic approximation which assumes that after migration, random mating, and selection, the population follows a Gaussian distribution. Otherwise, the derivation allows for strong selection, and for the excess variance generated by mixing populations. Our aim is to write down a recursion for the joint evolution of the population size, the mean trait value, and the variance within and between families.

Recall the order of events over a generation in our infinitesimal model. At the start of the generation, M migrants enter the population. Every pair of individuals (both native and migrant) produces a random number of offspring with mean trait value the average of the two parents and (within family) variance determined by the relatedness between the parents. Offspring

Table A.2: Contributions from the three classes of mated pair.

mating	fraction	mean	variance between families	variance within families
migrant × migrant	$\frac{M^2}{(M+N)^2}$	$\bar{z}_s$	V	V
migrant × native	$\frac{2MN}{(M+N)^2}$	$\frac{\bar{z}_s+\bar{z}}{2}$	$\frac{V+v}{2}$	V
native × native	$\frac{N^2}{(M+N)^2}$	$\bar{z}$	v	$V(1-F)$

mating	total variance	mean fitness
migrant × migrant	$2V$	$\exp\left[\beta\,z_s + \beta^2 V\right]$
migrant × native	$\frac{3V}{2} + \frac{v}{2}$	$\exp\left[\beta\frac{\bar{z}_s+\bar{z}}{2} + \frac{\beta^2}{2}\left(\frac{3V}{2}+\frac{v}{2}\right)\right]$
native × native	$v + V(1-F)$	$\exp\left[\beta\bar{z} + \frac{\beta^2}{2}\left(v + V(1-F)\right)\right]$

survive with a probability determined by their fitness. For our derivation it is convenient to follow the (equivalent) strategy of our simulations. Each pair of individuals in the population produces a Poisson number of offspring with mean w_{ij} given by (2). The traits of offspring are independent samples from a normal distribution with mean $\beta v_{ij} + (z_i + z_j)/2$, where z_i and z_j are the trait values of the parents and v_{ij} is the within family variance.

Assume that the distribution of individuals in the population, size N, is Gaussian, with mean $\bar{z}$ and variance $2v$. The average identity is F. At the start of the generation, M migrants enter, with mean $\bar{z}_s$ and variance $2V$; these make a fraction $m = \frac{M}{M+N}$ of the population. We now have three classes of mated pair (Table A.2).

The new population size, mean trait value among offspring *before* selec-

tion, and the average within family variance are:

$$N^* = \frac{M^2}{(M+N)} \exp\left(\beta \bar{z}_s + \beta^2 V\right)$$
$$+ \frac{2MN}{(M+N)} \exp\left(\beta \frac{\bar{z}_s + \bar{z}}{2} + \frac{\beta^2}{2}\left(\frac{3V}{2} + \frac{v}{2}\right)\right)$$
$$+ \frac{N^2}{(M+N)} \exp\left(\beta \bar{z} + \frac{\beta^2}{2}\left(v + V(1-F)\right)\right);$$

$$N^* \bar{z}^* = \frac{M^2}{(M+N)} \exp\left(\beta \bar{z}_s + \beta^2 V\right)$$
$$+ \frac{2MN}{(M+N)} \exp\left(\beta \frac{\bar{z}_s + \bar{z}}{2} + \frac{\beta^2}{2}\left(\frac{3V}{2} + \frac{v}{2}\right)\right)$$
$$+ \frac{N^2}{(M+N)} \exp\left(\beta \bar{z} + \frac{\beta^2}{2}\left(v + V(1-F)\right)\right);$$

$$N^* V_w^* = \frac{M^2}{(M+N)} V \exp\left(\beta \bar{z}_s + \beta^2 V\right)$$
$$+ \frac{2MN}{(M+N)} \left(\frac{3V}{2} + \frac{v}{2}\right) \exp\left(\beta \frac{\bar{z}_s + \bar{z}}{2} + \frac{\beta^2}{2}\left(\frac{3V}{2} + \frac{v}{2}\right)\right)$$
$$+ \frac{N^2}{(M+N)} \left(v + V(1-F)\right) \exp\left(\beta \bar{z} + \frac{\beta^2}{2}\left(v + V(1-F)\right)\right).$$

We shall add the between-class variance, and the change in mean trait value due to selection, later. Let $v = V + \delta v$, and $\tilde{M} = M \exp\left(-\beta(\bar{z} - \bar{z}_s)/2\right)$, $\tilde{N} = N \exp\left(\beta^2 \delta v/8\right)$. The expressions above become

$$N^* = \frac{\exp\left(\beta \bar{z} + \beta^2 V\right)}{(M+N)} \left(\left(\tilde{M} + \tilde{N}\right)^2 - \tilde{N}^2 \gamma\right);$$

$$(\bar{z}^* - \bar{z}_s) = \frac{\left(\left(\tilde{M} + \tilde{N}\right) - \tilde{N}\gamma\right)\tilde{N}}{\left(\left(\tilde{M} + \tilde{N}\right)^2 - \tilde{N}^2 \gamma\right)} (\bar{z} - \bar{z}_s);$$

and

$$2V_w^* = 2V + \frac{\tilde{N}\left(\tilde{M}\delta v + \tilde{N}(1-\gamma)\left(\delta v - VF\right)\right)}{\left(\left(\tilde{M}+\tilde{N}\right)^2 - \tilde{N}^2\gamma\right)};$$

where

$$\gamma = \left(1 - \exp\left(-\beta^2 VF/2\right)\right).$$

We also need to find the identity, F^*, within the offspring, after selection. More precisely, we require the identity between the two distinct genes in a diploid individual, since this determines the segregation variance released by meiosis. Individuals from crosses between migrants and natives cannot be inbred; those from crosses amongst the M migrants have identity $\frac{1}{2M}$; and those from crosses amongst the N natives have identity $\frac{(1-F)}{2N} + F$. Hence:

$$F^* = \frac{1}{2M}\phi_{M,M} + \phi_{N,N}\left(\frac{1}{2N}(1-F) + F\right) \tag{A.1}$$

where

$$\phi_{N,N} = \frac{\tilde{N}^2(1-\gamma)}{\left(\left(\tilde{M}+\tilde{N}\right)^2 - \tilde{N}^2\gamma\right)}, \qquad \phi_{M,M} = \frac{\tilde{M}^2}{\left(\left(\tilde{M}+\tilde{N}\right)^2 - \tilde{N}^2\gamma\right)}.$$

The mean trait value of offspring will shift by β times the within-family variance due to selection and so the shift in the mean trait value across the whole population due to selection is given by $2\beta V_w^*$, so that after selection we have

$$(\bar{z}^{**} - \bar{z}_s) = \frac{\left(\left(\tilde{M}+\tilde{N}\right) - \tilde{N}\gamma\right)}{\left(\left(\tilde{M}+\tilde{N}\right)^2 - \tilde{N}^2\gamma\right)}\tilde{N}\left(\bar{z} - \bar{z}_s\right) + 2\beta V_w^*.$$

Finally, we must add the variance generated by mixing the three classes. The three classes of mating are in the ratio $\alpha = \left\{\tilde{M}^2, 2\tilde{M}\tilde{N}, \tilde{N}^2(1-\gamma)\right\}$, and have means (after selection) of $m = \left\{0, \frac{\Delta}{2} + \beta\frac{\delta v}{2}, \Delta + \beta\delta v - F\beta V\right\}$, plus a constant; $\Delta = \bar{z} - z_s$. The variance generated by mixing the three classes is $\frac{1}{(\sum\alpha)^2}\left(\alpha.m^2(\sum\alpha) - (\alpha.m)^2\right)$, where we have abused notation and

written m^2 for the vector whose entries are the squares of those of m, giving:

$$V_b = \frac{\tilde{M}\tilde{N}}{4\left(\left(\tilde{M}+\tilde{N}\right)^2 - \tilde{N}^2\gamma\right)^2} \times \left\{ 2A^2\left(\left(\tilde{M}+\tilde{N}\right)^2(1-\gamma) + \gamma\tilde{M}^2\right) \right.$$

$$\left. - 4A\beta VF\tilde{N}(1-\gamma)\left(\tilde{M}+\tilde{N}\right) + 2\beta^2 V^2 F^2(1-\gamma)\tilde{N}\left(\tilde{M}+2\tilde{N}\right) \right\},$$

where $A = \beta\delta v + (\bar{z} - \bar{z}_s)$.

We can rewrite these expressions in a simpler dimensionless form by letting $y = (\bar{z} - \bar{z}_s)\sqrt{2V}$, $\alpha = \beta\sqrt{2V}$, $\delta = \delta v/V$, $\delta_b = V_b/V$, $n = N/M$, $\gamma = \left(1 - \exp(-\alpha^2 F/4)\right)$:

$$n^* = \frac{\exp\left(\beta\bar{z}_s + \frac{\alpha^2}{2}\right)}{(1+n)}\left((1+nC)^2 - n^2C^2\gamma\right),$$

$$\delta_w^* = \frac{nC\left(\frac{\delta}{2} + nC(1-\gamma)\left(\frac{\delta}{2} - \frac{F}{2}\right)\right)}{((1+nC)^2 - n^2C^2\gamma)},$$

$$y^{**} = \frac{(1 + nC(1-\gamma))}{((1+nC)^2 - n^2C^2\gamma)}nCy + \alpha\left(1 + \delta_w^*\right),$$

$$\delta_b = \frac{nC}{4\left((1+nC)^2 - n^2C^2\gamma\right)^2}\left\{ 2a^2\left((1+nC)^2(1-\gamma) + \gamma\right) \right.$$

$$\left. - 4a\alpha F(1-\gamma)nC(1+nC) + \alpha^2 F^2(1-\gamma)nC(1+2nC) \right\},$$

$$F^* = \frac{1}{2M}\phi_{M,M} + \phi_{N,N}F\left(1 - \frac{1}{2Mn}\right)$$

$$= \frac{1}{((1+nC)^2 - n^2C^2\gamma)}\left(\frac{1}{2M} + n^2C^2(1-\gamma)F\left(1 - \frac{1}{2Mn}\right)\right),$$

where

$$\phi_{M,M} = \frac{1}{((1+nC)^2 - n^2C^2\gamma)}, \qquad \phi_{N,N} = \frac{n^2C^2(1-\gamma)}{((1+nC)^2 - n^2C^2\gamma)},$$

$\tilde{N}/\tilde{M} = nC$ and $C = \exp(\alpha y/2 + \alpha^2\delta/8)$, $a = y + \alpha\delta/2$. If F reaches a

quasi-equilibrium, $n^* = n$, and:

$$F \sim \frac{1}{(2M(1 + 2nC) + nC^2(1 - \gamma))} \tag{A.2}$$

If F is negligible, as it will be for large M, we can set $F, \gamma = 0$, obtaining:

$$n^* = \frac{(1 + nC)^2}{(1 + n)} \exp\left(\beta\bar{z}_s + \frac{\alpha^2}{2}\right), \qquad y^{**} = \alpha + \frac{nC}{(1 + nC)}\left(y + \alpha\frac{\delta}{2}\right),$$

$$\delta^* = \delta_w^* + \delta_b^* = \frac{nC}{(1 + nC)}\frac{\delta}{2} + \frac{nC}{2(1 + nC)^2}\left(y + \alpha\frac{\delta}{2}\right)^2.$$

Figure A.9 compares this deterministic recursion with stochastic simulations of the full model. The mean of the source population is sufficiently negative that there is a 'sink' state that can trap the population. The panels show the outcome for different starting points. If the mean, $\bar{z}_s$, is initially low, the population remains small (top row, $\bar{z}_s = -2.5, -2, -1.5$), whilst if it is sufficiently high, it quickly escapes (bottom row, $\bar{z}_s = -1.0, -0.5, 0$). The full Gaussian approximation developed in this section (orange dots) fits closely to the mean of those populations that remain trapped (red line), whilst the cruder approximation outlined in the main text which assumes a constant variance fits less well (brown dots).

Next, we find the critical point above which escape is inevitable. Assuming that $y \gg \alpha\delta$, and that δ is rapidly pulled towards a quasi-equilibrium, we have for αy small

$$\delta \sim \frac{nCy^2}{((2 + nC)(1 + nC) - \alpha ynC)} \sim \frac{ny^2}{(2 + n)(1 + n)}.$$

If $y^2 \ll n$, then δ is small, and

$$n^* = \frac{(1 + nC)^2}{(1 + n)} \exp\left(\beta\bar{z}_s + \frac{\alpha^2}{2}\right), \qquad y^{**} = \alpha + \frac{nC}{(1 + nC)}y.$$

At equilibrium, $n = (y - \alpha)\exp(-\alpha y/2)/\alpha$. Hence:

$$\beta\bar{z}_s = \log\left(\frac{(y - \alpha)}{y^2}e^{-\alpha y/2}\left(\alpha + (y - \alpha)e^{-\alpha y/2}\right)\right) - \frac{\alpha^2}{2}. \tag{A.3}$$

This has a peak at some critical value of $\beta\bar{z}_s$, which determines the critical point below which a stable 'sink' state is possible.

The still simpler approximation developed in the main text assumes $C \sim$
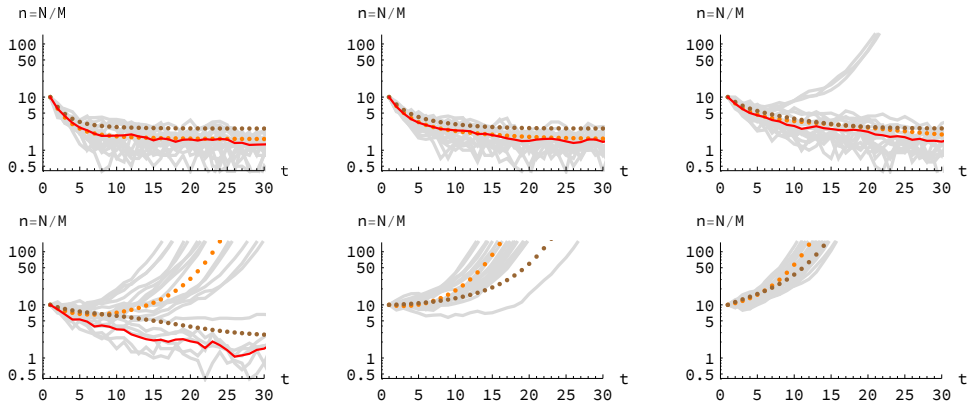
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Figure A.9: We compare the Gaussian approximation of Appendix A with simulations of the full model; $\beta = 0.25$, $M = 10$. Grey lines show 20 replicates, starting from $N = 100$, with the mean of the source population $\bar{z}_s = -2.5$. This is below the critical value of $\bar{z}_s = -2.0$ (from either Eq. 9 or Eq. A.3), and so there is an unstable point below which the population is trapped in a 'sink'. Each panel shows a different starting condition, $\bar{z}_s = -2.5, -2.0, \ldots, 0$ (from top left). Orange dots are the Gaussian approximation, with $F = 0$, whilst brown dots are the simpler approximation of Eqs. (4), (5), which assumes constant variance. The red line is the mean of those runs which did not escape by the end.

1, and approximates changes due to selection to be small, leading to Eqs. (8), (9). Figure A.10 shows that this is close to the Gaussian approximation of Eq. (A.3).

Appendix B. A note on diffusion approximations

In Section 4.2, we wrote down a system of differential equations to approximate the evolution of the population size and mean trait value, under the assumption that the trait value across the population has a Gaussian distribution with constant variance. If we wish the differential equations to mimic the discrete system given by equations (4) and (5), some care is needed in choosing the coefficients.

It is convenient to consider the recursions for N and $N\bar{z}$. These are:

$$N(t+1) = M + N(t)\exp\left(\beta\bar{z}(t) + \beta^2 V^*\right), \tag{B.1}$$

$$N(t+1)\bar{z}(t+1) = (N(t)\bar{z}(t) + 2\beta V^* N(t))\exp\left(\beta\bar{z}(t) + \beta^2 V^*\right) + M\bar{z}_s. \tag{B.2}$$
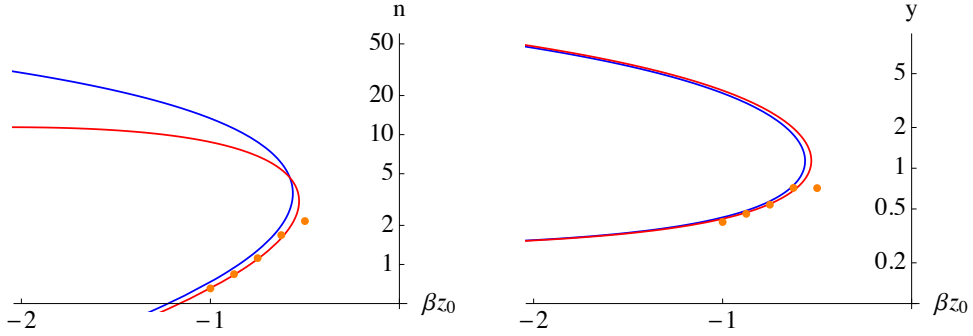
Figure A.10: This shows the equilibria for $n = \frac{N}{M}$, $y = (\bar{z} - \bar{z}_s)\sqrt{2V^*}$ (left, right), against $\beta\bar{z}_s$, for $\beta = 0.25$. The lower equilibrium is stable, the upper unstable; the critical value of βz_s where these equilibria merge. Blue: naive approximation; Red: Gaussian approximation. Orange points show means over simulations of the full model, run for 10^4 generations, or until escape, and dropping the last 50 generations. This procedure was repeated until a total of at least 5000 generations were accumulated.

We note that the solution to

$$\frac{df(t)}{dt} = g(t) + a(t)f(t)$$

satisfies

$$f(t + T) = \int_t^{t+T} g(u) \exp\left(\int_u^{t+T} a(r)dr\right) du + f(t) \exp\left(\int_t^{t+T} a(r)dr\right).$$
$$\text{(B.3)}$$

If we take the differential equations

$$\frac{dN}{dt} = M + \beta\bar{z}N \tag{B.4}$$

$$\frac{d\bar{z}}{dt} = 2\beta V^*\left(1 - \frac{M}{2N}\right) - \frac{M}{N}(\bar{z} - \bar{z}_s), \tag{B.5}$$

then

$$\frac{d(N\bar{z})}{dt} = M\bar{z}_s + 2\beta V^*\left(N - \frac{M}{2}\right) + \beta\bar{z}(N\bar{z}). \tag{B.6}$$

Solving for N using (B.3) with $T = 1$ yields:

$$N(t + 1) = \int_t^{t+1} M \exp\left(\int_u^{t+1} \beta\bar{z}(r)dr\right) du + N(t) \exp\left(\int_t^{t+1} \beta\bar{z}(r)dr\right).$$

Now we expect $\bar{z}$ to change by order β over a single generation (this will

be the order of its shift due to selection) and so for small β, expanding the exponential, we see that

$$N(t+1) = M + N(t)(1 + \beta\bar{z}(t)) + \frac{1}{2}\beta\bar{z}(t)M + \mathcal{O}\left(\beta^2(N(t)+M)\right).$$

Comparing with our discrete recursion (in which we also expand the exponential), the errors we are accumulating in using (B.4) in place of (B.1) are of order at most $\beta M + \beta^2 N$ per generation. If we wanted to reduce the error to order $\beta^2(M+N)$, we would need to replace M in (B.4) by $M(1-\beta\bar{z}/2)$. The point is that in contrast to the discrete world, in which all migrants arrive after reproduction, here migrants arrive throughout the time interval and once arrived, they produce offspring, thereby increasing the overall effect of migrants on the population size at the end of the generation. We chose not to make this adjustment to M. We expect $\beta\bar{z}M$ to be small relative to N; once $\bar{z}$ is large, the population grows rapidly.

Now consider the equation for $N\bar{z}$. Again we use (B.3):

$$(N\bar{z})(t+1) = \int_t^{t+1} \left(M\bar{z}_s + 2\beta V^* \left(N(u) - \frac{M}{2} \right) \right)$$
$$\times \exp\left(\int_u^{t+1} \beta\bar{z}(r)dr \right) du$$
$$+ (Nz)(t)\exp\left(\int_t^{t+1} \beta\bar{z}(r)dr \right).$$

Now again using (B.3), we see that for $u \in [t, t+1]$, up to an error of order β, $N(u) = N(t) + (u-t)M$. Substituting we find

$$(N\bar{z})(t+1) = \int_t^{t+1} \left(M\bar{z}_s + 2\beta V^* \left(N(t) + M(u-t) - \frac{M}{2} \right) \right)$$
$$\times \exp\left(\int_u^{t+1} \beta\bar{z}(r)dr \right) du + (Nz)(t)\exp\left(\int_t^{t+1} \beta\bar{z}(r)dr \right)$$
$$= M\bar{z}_s \left(1 + \frac{\beta\bar{z}}{2} \right) + 2\beta V^* N(t) + (NZ)(t)\left(1 + \beta\bar{z}(t) \right)$$
$$+ \quad \mathcal{O}\left(\beta^2(M+N)\right).$$

Taking a factor $(1 - M/(2N))$ in (B.5) in place of the $(1 - M/N)$ in the discrete equations, results in the cancellation of two terms $\beta V^* M$. Once again, we see that if we replace M by $M(1 - \beta\bar{z}/2)$ in equation (B.4), our approximation is accurate up to order $\beta^2(M+N)$.

Appendix C. Reproductive value of migrants

Directional selection

Here we set up and solve a recursion for the reproductive value of an individual backcrossing into a population that has established in the new environment. We denote the reproductive value of an individual of trait z by $w[z, F_w, F_b]$, where F_w is the probability of identity of two distinct copies of a gene sampled within the individual and F_b is the mean identity between the individual and a randomly chosen individual from the native population. In order to write down a recursion, we must keep track of not only the trait value, but also F_w and F_b for offspring of our chosen individual.

It is convenient to replicate the steps in our simulations. First we calculate the mean growth rate across the whole population. Then we calculate the contribution from our individual of trait z. Finally we write down the conditional distribution of the trait of a second individual sampled from the population, given that it produced an offspring with our chosen individual.

Since the population is assumed to be at equilibrium with mean $\bar{z}$ and variance $2V^*$, exactly as before (Eq. 3), the mean growth rate of the population is $\exp\left(\beta\bar{z} + \beta^2 V^*\right)$.

Suppose now that an individual has trait value z, and we calculate its expected number of offspring. Offspring could come from multiple partners in our model, but the mean number of offspring is

$$
w_z = \mathbb{E}\left[\exp\left(\beta\frac{(z+Y)}{2} + \frac{\beta^2 V_b}{2}\right)\right] = \exp\left(\beta\frac{(z+\bar{z})}{2} + \frac{\beta^2 V_b}{2} + \frac{\beta^2 V^*}{4}\right),
$$

where the expectation on the left is with respect to the choice of the mate Y from the population, and we have used V_b to denote the within-family variance of the offspring:

$$
V_b = V\left(1 - \frac{F_w + F_*}{2}\right). \tag{C.1}
$$

The immediate fitness of the individual, that is its relative weight in the whole population, is

$$
\exp\left(\beta\frac{(z-\bar{z})}{2} - \frac{\beta^2 V^*}{4} + \frac{\beta^2}{2}(V_b - V^*)\right).
$$

To find the distribution of the trait Y of the mate of our chosen individual, we must weight the random pick from the population by the relative

fitness of offspring of parents z and y compared to the quantity w_z that we just calculated. The resulting tilted distribution has density proportional to

$$\exp\left(\beta\frac{(y-\bar{z})}{2} - \frac{(y-\bar{z})^2}{4V^*}\right)$$

and so is a normal distribution with mean $\bar{z} + \beta V^*$ and variance $2V^*$. Given $Y = y$, the trait values among offspring will then be normal with mean $(z+y)/2 + \beta V_b - 2\beta V^*$, and variance V_b. The term $-2\beta V^*$ in the mean reflects mutation (which restores the population to equilibrium).

Combining the above, we can now write down the recursion for the reproductive value. We write $\mathcal{N}[x|\mu, \sigma^2]$ for the density function at x of a normally distributed random variable with mean μ and variance σ^2. Then

$$w\left[z, F_w, F_b\right] = \exp\left(\beta\frac{(z-\bar{z})}{2} - \frac{\beta^2 V^*}{4} + \frac{\beta^2}{2}(V_b - V^*)\right)$$
$$\times \int \int w\left[x, F_b, \frac{F_b + F_*}{2}\right] \mathcal{N}\left[x\left|\frac{y+z}{2} + \beta V_b - 2\beta V^*, V_b\right.\right]$$
$$\times \mathcal{N}\left[y\left|\bar{z} + \beta V^*, 2V^*\right.\right] dy dx \quad \text{(C.2)}$$

We can find the reproductive value of a native individual as a special case. Writing $w_*[z] = w\left[z, F_*, F_*\right]$,

$$w_*[z] = \exp\left(\beta\frac{(z-\bar{z})}{2} - \frac{\beta^2 V^*}{4}\right)$$
$$\times \int \int w_*[x]\mathcal{N}\left[x\left|\frac{y+z}{2} - \beta V^*, V^*\right.\right] \mathcal{N}\left[y\left|\bar{z} + \beta V^*, 2V^*\right.\right] dy dx. \quad \text{(C.3)}$$

To solve this, one can integrate out y on the right hand side to see that x has a normal distribution with mean $(z + \bar{z} - \beta V^*)/2$ and variance $3V^*/2$ and then postulating a solution of the form $\exp\left(\theta\beta(z - \bar{z}) - \theta^2\beta^2 V^*\right)$ and matching coefficients yields

$$w_*[z] = \exp\left(\beta(z - \bar{z}) - \beta^2 V^*\right). \quad \text{(C.4)}$$

(The second term in the exponent is needed in order for the mean reproductive value across the population to be one). That is the reproductive value is proportional to the *square* of the immediate fitness.

One can apply a similar technique to find the reproductive value of a migrant, but now we obtain a recursion. Again integrating out y in equa-

tion (C.2), we find that x is normally distributed with mean $(z + \bar{z})/2 + \beta V_b - 3\beta V^*/2$, and variance $V_b + V^*/2$. We make the ansatz that

$$w[z, F_w, F_b] = \exp\left(\delta(F_w, F_b)(z - \bar{z}) - \theta(F_w, F_b)\right).$$

Then equation (C.2) becomes

$$w[z, F_w, F_b] = \exp\left(\beta\frac{(z - \bar{z})}{2} - \frac{\beta^2 V^*}{4} + \frac{\beta^2}{2}(V_b - V^*)\right)$$
$$\times \exp\left(\delta\left(F_b, \frac{F_b + F_*}{2}\right)\left(\frac{z - \bar{z}}{2} + \beta V_b - \frac{3\beta V^*}{2}\right)\right.$$
$$\left.+ \delta\left(F_b, \frac{F_b + F_*}{2}\right)^2\frac{1}{2}\left(V_b + \frac{V^*}{2}\right) - \theta\left(F_b, \frac{F_b + F_*}{2}\right)\right). \quad \text{(C.5)}$$

Equating the exponents in (C.5) yields

$$\delta(F_w, F_b) = \frac{\beta}{2} + \frac{1}{2}\delta\left(F_b, \frac{F_b + F_*}{2}\right),$$

and iterating we see that
$$\delta(F_w, F_b) = \beta.$$

Substituting $\delta(F_w, F_b) = \delta(F_b, (F_b + F_*)/2 = \beta$ into the recursion for θ obtained by equating coefficients in (C.5) we obtain

$$-\left(\theta(F_w, F_b) - \theta\left(F_b, \frac{F_b + F_*}{2}\right)\right) = 2\beta^2(V_b - V_*) = \beta^2 V\left(F_* - F_w\right).$$

Again iterating, and using the solution we obtained before for a native individual, we find that,

$$\theta(F_w, F_b) = \beta^2 V^* - 4\beta^2(V_b - V^*).$$

Thus the reproductive value of a migrant individual with trait z is

$$w[z, F_w, F_b] = \exp\left(\beta(z - \bar{z}) + 4\beta^2(V_b - V^*) - \beta^2 V^*\right).$$

Stabilising selection

We assume that the fitness is proportional to $\exp(-s(z - z_{\text{opt}})^2/2)$ and the mean in the population is assumed to be at the optimum. Because stabilising selection causes negative linkage disequilibrium, the variance in

the trait across the population will no longer be $2V^*$ Let us write $2\hat{V}$ for the variance across the whole population. We retain the notation $V^* = V(1-F_*)$ for within family variance (before selection), where V is the variance (before selection) among offspring of two unrelated individuals.

Before the action of selection, the variance among offspring is $\widetilde{V} = \hat{V} + V^*$. The action of selection reduces this to $\widetilde{V}/(1+s\widetilde{V})$ and so at equilibrium

$$2\hat{V} = \frac{\widetilde{V}}{\left(1 + s\widetilde{V}\right)}, \tag{C.6}$$

leading to a quadratic in $\hat{V}$ whose positive solution is

$$\hat{V} = \frac{1}{4s}\left(\sqrt{1 + 12sV\left(1 - F_*\right) + \left(2sV\left(1 - F_*\right)\right)^2} - \left(1 + 2sV\left(1 - F_*\right)\right)\right) \tag{C.7}$$

which tends to V^* for small s. So for small s, the variance in trait values across the population is $\sim 2V^*$, as for the classical infinitesimal model.

To set up a recursion for the reproductive value, it is convenient to note that if Z is normally distributed with mean μ and variance σ^2, then

$$\mathbb{E}\left[\exp\left(-s\frac{Z^2}{2}\right)\right]$$
$$= \int \frac{1}{\sqrt{2\pi\sigma^2}}\exp\left(-\frac{s\sigma^2 + 1}{2\sigma^2}\left(z - \frac{\mu}{s\sigma^2 + 1}\right)^2 - \frac{\mu^2 s}{2(s\sigma^2 + 1)}\right)$$
$$= \frac{1}{\sqrt{1 + s\sigma^2}}\exp\left(-\frac{\mu^2 s}{2(1 + s\sigma^2)}\right). \tag{C.8}$$

First we calculate the mean growth rate in the population. Before selection, the distribution of the offspring of two individuals sampled at random from the population is Gaussian with mean z_{opt} and variance $\hat{V} + V^*$ and so using (C.8), the mean growth rate is $1/\sqrt{1 + s(\hat{V} + V^*)}$.

Now, define $w\left[z, F_w, F_b\right]$ to be the reproductive value of an individual with trait value z backcrossing into such a population. By analogy with our calculation for directional selection, our first task is to find its mean number of offspring. Before selection, the trait value of offspring is normal with mean $(z + z_{\text{opt}})/2$ and variance $\hat{V}/2 + V_b$ where, as before, V_b is the within family variance of the offspring and is defined by (C.1). Using (C.8) applied to the offspring trait value minus z_{opt} which has mean $(z - z_{\text{opt}})/2$

and variance $\hat{V}/2 + V^*$, and our expression for the growth rate across the population, the immediate fitness of the individual is

$$\frac{\sqrt{1 + s(\hat{V} + V^*)}}{\sqrt{1 + s(\hat{V}/2 + V_b)}} \exp\left(-\frac{(z - z_{\mathrm{opt}})^2}{4} \frac{s}{2(1 + s(\hat{V}/2 + V_b))}\right).$$

Now we can read off the distribution of the trait value of successful offspring from the calculation that led to (C.8). It is normal with mean

$$z_{\mathrm{opt}} + \frac{(z - z_{\mathrm{opt}})}{2(1 + s(\hat{V}/2 + V_b))}$$

and variance $(\hat{V}/2 + V_b)/(1 + s(\hat{V}/2 + V_b))$. The recursion for the reproductive value is therefore

$$w[z, F_w, F_b] = \frac{\sqrt{1 + s(\hat{V} + V^*)}}{\sqrt{1 + s(\hat{V}/2 + V_b)}} \exp\left(-\frac{(z - z_{\mathrm{opt}})^2}{4} \frac{s}{2(1 + s(\hat{V}/2 + V_b))}\right)$$

$$\times \int \mathcal{N}\left[x \,\middle|\, z_{\mathrm{opt}} + \frac{(z - z_{\mathrm{opt}})}{2(1 + s(\hat{V}/2 + V_b))}, \frac{(\hat{V}/2 + V_b)}{(1 + s(\hat{V}/2 + V_b))}\right] w\left[x, F_b, \frac{F_b + F_*}{2}\right] dx.$$

$$(C.9)$$

We have been unable to find a closed form solution to this equation, even for native individuals. However, when s is small, for a native individual it is close to Gaussian. To see why, try a solution of the form

$$w_* \propto \exp\left(-\theta \frac{s}{2}(z - z_{\mathrm{opt}})^2\right),$$

then substituting in (C.9) with $F_b = F_*$ and equating exponents, we find a quadratic in θ. Writing $\alpha = 2 + s(\hat{V} + 2V^*)$, the positive solution is

$$\theta = \frac{-(2\alpha - 1) + \sqrt{4\alpha^2 + 4\alpha - 15}}{4(\alpha - 2)}.$$

For small s, we saw above that at equilibrium $\hat{V} \sim V^*$ and substituting we find

$$\theta \sim \frac{1}{3} \qquad \text{as } s \downarrow 0.$$

Moreover, substituting back into the recursion, we see that with this value

of θ, as $s \downarrow 0$, we have an approximate solution. Thus, for small s, the reproductive value of a native individual is approximately proportional to the immediate fitness to the power $4/3$.

The reason that this approach does not work for larger values of s is that although the same expression for θ in terms of α ensures that when we substitute w_* of this form into (C.9), the exponents in the exponentials on both sides of the equations match, the constant terms multiplying those exponentials are not equal.