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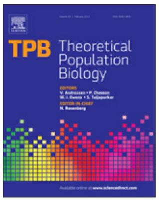

Establishment in a new habitat by polygenic adaptation

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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 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 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 (Gomulkiewicz and Holt, 1995; Kawecki, 2008).

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 (Holt and Gomulkiewicz, 1997). 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

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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. Tufto, 2001; Holt et al., 2003; Holt and Barfield, 2011) and along one-dimensional environmental gradients (Kirkpatrick and Barton, 1997; Polechova and Barton, 2015). Such analyses have almost all been based on simulations of discrete loci, or on deterministic models that assume a constant additive variance for one or more traits. Tufto (2000, 2001) applied the infinitesimal model to study establishment despite initial maladaptation. His approach allows the evolution of trait variance due to selection and migration. We develop this model, taking account of random drift and demographic stochasticity.

The infinitesimal model motivates a deterministic approximation for the evolution of population size and trait mean, similar to that considered by Tufto (2001). (In an appendix, we show that inbreeding can also be incorporated into the approximation in a relatively straightforward way.) We extend this deterministic approximation to a diffusion approximation that takes account of random sampling drift in the trait mean and demographic stochasticity.

The central result of our analyses of these models takes a remarkably simple form: establishment depends upon just two dimensionless parameters, the change in trait needed to make growth positive and the fitness of an average migrant, both being 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, measured through the reproductive value of an individual backcrossing into the population. We show that once again this depends on very few parameters: the divergence of the new population from its source and its degree of inbreeding.

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 we take to be under directional selection. As argued by Holt and Gomulkiewicz (1997), at low density it is the logarithm of the absolute fitness that will determine whether a population will increase. This fitness may be mediated via very many traits, but we absorb the genetic component of all of these into a single value, determined by the additive effect of many genes. This is less restrictive than it might seem. Even with strong underlying interactions at the level of genes, trait variance may be largely additive (Hill et al., 2008). There is little direct evidence on fitness variance, but indirect arguments suggest that there is substantial additive variance (Charlesworth, 2015).

Our 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 migration 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 (Kirkpatrick and Barton, 2006). 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 (Le Corre and Kremer, 2012; Yeaman, 2015). 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 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. This simple model has proven remarkably accurate in practical animal breeding (Lynch and Walsh, 1998), in describing artificial selection experiments, and in analysis of natural populations (Kruuk et al., 2014). 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. (2017).

Under the infinitesimal model, 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.

The rest of this paper is laid out as follows. 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. Below this threshold, establishment requires a rare fluctuation in which the migrant is unusually fit. In this regime we also see the swamping effects of gene flow; time to establishment is no longer a monotone function of the migration rate. Assuming that

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