The phenomenology of niche evolution via quantitative traits in a 'black-hole' sink

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Previous studies of adaptive evolution in sink habitats (in which isolated populations of a species cannot persist deterministically) have highlighted the importance of demographic constraints in slowing such evolution, and of immigration in facilitating adaptation. These studies have relied upon either single-locus models or deterministic quantitative genetic formulations. We use individual-based simulations to examine adaptive evolution in a 'black-hole' sink environment where fitness is governed by a polygenic character. The simulations track both the number of individuals and their multi-locus genotypes, and incorporate, in a natural manner, both demographic and genetic stochastic processes. In agreement with previous studies, our findings reveal the central parts played by demographic constraints and immigration in adaptation within a sink (adaptation is more difficult in environments with low absolute fitness, and higher immigration can accelerate adaptation). A novel finding is that there is a 'punctuational' pattern in adaptive evolution in sink environments. Populations typically stay maladapted for a long time, and then rapidly shift into a relatively adapted state, in which persistence no longer depends upon recurrent immigration.

Keywords: immigration; niche evolution; source–sink dynamics; punctuated evolution

1. INTRODUCTION

Most species live in environments that are heterogeneous in space and time. The evolutionary trajectory of a species should reflect comparable heterogeneities in the direction of selection and in local population dynamics. A striking form of spatial heterogeneity in demography that has received considerable recent attention is 'source–sink dynamics' (Pulliam 1988; Watkinson & Sutherland 1995; Dias 1996; With & King 2001). In the simplest case, a species occupies discrete habitats. In some habitats (sinks), conditions are so poor that the species declines towards extinction without immigration from higher-quality habitats (sources). If a species' niche is defined as that set of conditions (abiotic factors, resources, etc.) that permit the species to persist deterministically in a closed environment, then sink habitats have conditions outside of the species' niche, whereas source habitats are within the niche (Holt & Gaines 1992; Pulliam 2000).

A fundamental issue at the intersection of ecology and evolutionary biology is the evolution of species' niches. For instance, at the edge of a species' geographical range, immigration may sustain populations in sink habitats. Given appropriate genetic variation, a population may adapt to the sink environment and, once sufficiently adapted, it may be able to persist locally without immigration, allowing range expansion. In previous studies (Holt & Gaines 1992; Holt & Gomulkiewicz 1997*a*,*b*, 2002; Gomulkiewicz *et al.* 1999; Kawecki & Holt 2002), we have explored the evolutionary dynamics of adaptation in 'black-hole' sinks, where there is no back-migration to source habitats. Two general conclusions were, that

increases in the rate of immigration could facilitate the initial stages of adaptive evolution, and that the rate of niche evolution should be greater in more benign sink environments. We argued that immigration promotes adaptation because immigrants sample variation present in the source, providing a more potent pool of genetic variation than mutation in the sink population itself. The reason that adaptation is more likely in a mild sink environment is that a mutant or immigrant allele will spread when rare only if it has an absolute fitness exceeding unity, which is more likely if the environment is not too harsh, relative to the source.

These previous results highlight the importance of demographic constraints on evolution in sink environments. However, one limitation of our previous analyses is that we assumed variation at a single genetic locus. Yet, in natural populations, many traits of ecological importance are polygenic (Falconer & MacKay 1996). It is not clear whether straightforward extensions of standard polygenic selection theory to coupled source and sink populations are appropriate (Holt & Gomulkiewicz 1997*b*). Simple quantitative genetic models ignore potential departures from normality caused by immigration, the linkage disequilibrium that is constantly generated by immigration and the dynamics of genetic variance (Tufto 2000). Moreover, prior studies of evolution in sink habitats (e.g. the authors, *op. cit.*, and see also Kawecki 1995, 2000; Tufto 2001; Ronce & Kirkpatrick 2001) have only indirectly dealt with demographic stochasticity (including extinction), and many potentially important aspects of genetic stochasticity (for example, drift and mutation) have not been explicitly considered at all. It is difficult to deal with these realistic genetic and ecological complexities analytically using recursion equations.

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We examine the generality of our previous conclusions, using a more complex and realistic model of adaptive evolution in a sink environment. We assume that fitness is determined by a polygenic character, and use individual-based simulation studies to examine coupled evolutionary and population dynamics. The results provide a phenomenological portrayal of the conditions facilitating, or hampering, polygenic evolution in sink environments, and of the 'tempo' of adaptation to sinks. We find that, just as in the simpler models, immigration can facilitate the initial stages of local adaptation, and that adaptation is more likely in milder sink environments. One striking new feature of our results is that niche evolution may often be characterized by 'punctuated' episodes of rapid evolution. We examine the robustness of these qualitative features to various ecological assumptions, such as the nature of density dependence and the ordering of life-history events. We also compare the findings of our simulations with related deterministic models for coupled population dynamics and adaptive evolution.

2. MODEL DESCRIPTION

Our model builds upon an individual-based approach used by Burger & Lynch (1995; Burger *et al.* 1989) to examine the interplay of evolution and extinction in a temporally changing environment. Our genetic and life-history assumptions follow those of Burger & Lynch (1995), but we differ in our assumptions about the ecological arena within which adaptive evolution occurs. Burger & Lynch (1995) considered a spatially closed population facing a continually changing environment. By contrast, we assume that the environment is temporally constant but heterogeneous in space. The species occupies two habitats: a source, where the population persists, and a sink, where immigrants are maladapted. For simplicity, we focus on 'black-hole sinks', which receive immigrants but do not export emigrants back to the source. The source population reaches a mutation–selection–drift equilibrium, independent of the state of the sink habitat. The flow of life-history events described by the model is shown in figure 1.

(a) *Ecological assumptions*

Each habitat has a finite population with discrete generations and random mating. Individuals are hermaphroditic and mating pairs are monogamous. Initially, we assume that there are no individuals in the sink, and K parents in the source. We allow the source to reach a mutation–selection–drift equilibrium by simulating dynamics over 1000 generations, and then begin immigration into the sink. Each parental pair produces $2B$ offspring. Selection occurs during a phase of density-independent survival (see below) from birth to adulthood. Density dependence can occur after selection. For simplicity, in most simulations described below, we assume a 'ceiling' form of density dependence with a carrying capacity of K. With more than K survivors (the normal situation in the source, for the parameter choices that we use), K individuals are sampled randomly (without replacement) from the survivors. With fewer than K survivors, all become parents (except one chosen at random, if the number of adults is odd). Mating pairs are randomly chosen to complete a generation. We
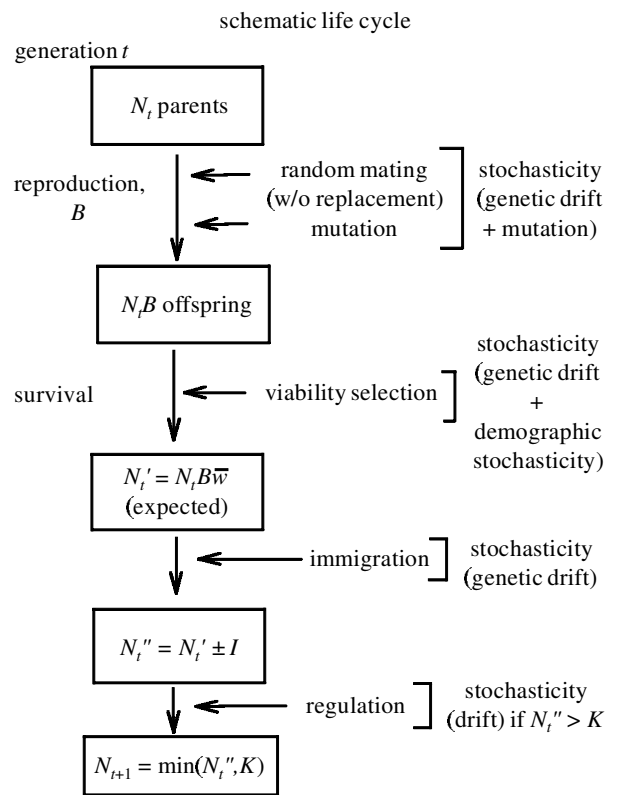

Figure 1. Flow of life-history events assumed in the individual-based simulation model. In § 3e, we reverse the order of immigration and selection.

also examined an alternative form of density dependence operating across the full range of densities, to gauge the robustness of our conclusions.

Once immigration begins, we assume that a constant number of immigrants (I) is randomly chosen from survivors of selection in the source each generation (before parents are chosen). In practice, for the parameter values that we use, this 'culling' does not affect the number of breeding adults in the source. These immigrants move to the sink habitat without mortality in transit. Immigrants join survivors of selection (if any) from the previous generation in the sink. As in the source, the total number of breeding adults is restricted to be no more than K (in our simulations, numbers in the sink are typically well below this ceiling, until adaptation occurs). Mating pairs in the sink are formed at random. Each pair produces $2B$ offspring. The 'sink' status of this habitat thus reflects low survivorship.

(b) *Selection*

Selection operates on the survival of offspring to adulthood, but with fitnesses determined by different phenotypic optima in source and sink; the greater the difference between the source and sink optima, the greater the maladaptation of immigrants into the sink. For simplicity, we assume that the optimal source phenotype is zero. The optimal sink phenotype then directly measures the probable degree of maladaptation of immigrants. In each habitat, selection is determined by a single polygenic character affecting offspring survival. The survival probability of an individual with phenotypic value z in habitat i is given by

$$W_i(z) = \exp\left[-\frac{(z - \theta_i)^2}{2\omega_i^2} \right],\qquad(2.1)$$

where θ_i is the optimal phenotype and ω_i^2 is inversely proportional to the strength of stabilizing selection in habitat i. We, for the most part, assume that ω_i^2 is unity in both habitats, corresponding to fairly strong selection.

(c) *Genetic assumptions*

The polygenic character z is determined by n freely recombining diploid loci, with additive allelic effects within and among loci (i.e. no dominance or epistasis). Each individual has a phenotypic value given by the sum of a genetic contribution and an environmental effect. The environmental effect is normally distributed, with a mean of zero and variance of unity. The phenotypic mean is the mean of the additive genetic values (thus when we discuss the average genotype below, this is also the expected average phenotype), and the phenotypic variance is the sum of the additive genetic variance and the environmental variance. As in Burger & Lynch (1995), the mutation rate per haplotype is $n\mu$, where μ is the mutation rate per locus. During the reproduction phase of the simulation, each haplotype was given either one mutation (with a probability of $n\mu$), or no mutations. Given a mutation, the locus at which it occurred was chosen randomly. The magnitude of the mutation was a zero-mean normal random value with variance α^2. This value was added to the previous value at that locus.

We examined the impact of the number of loci n. To standardize phenotypic and genetic variation across simulations that differed in n, the mutation rate per haplotype $n\mu$ and mutational variance α^2 were kept constant. (The basis for this standardization is the approximation of Burger *et al.* (1989) for the expected stochastic 'house-of-cards' (SHC) genetic variance at equilibrium, which shows that populations with the same haplotype mutation rate, mutational variance per locus and size have the same equilibrium genetic variance, regardless of n.) We found little quantitative difference among simulation results for $n \geqslant 5$ (see figure 6*b* for an example). For all other results reported here, $n = 10$.

(d) *Initial conditions*

At the start of each simulation, the genotypes of the original source parents were assigned, as follows: for each locus, five allelic values were chosen at random using a zero-mean normal distribution with a variance equal to the SHC genetic variance for that population (using eqn (14) in Burger & Lynch (1995), after Burger *et al.* (1989)). For each adult haplotype, at each locus, one out of the five values for that locus was chosen at random. Then, 1000 generations were run to allow the source to reach a mutation–selection–drift genetic equilibrium. Starting with this generation, I immigrants per generation were drawn at random from the source adults (survivors of selection) and introduced into the initially empty sink. Thereafter, the sink habitat contained a mix of immigrants and individuals who survived selection in the sink. Immigration into the sink was assumed to occur after selection, but before mating pairs were formed. The sink population was censused just before immigration.

3. RESULTS

The results of this study comprise the output of a large number of computer simulations. In the following paragraphs, we illustrate major trends in our results with representative runs, and figures summarizing patterns observed in a large number of runs.

The severity of the sink environment is determined by the difference between the optimal phenotypes in the source (set to zero) and sink. Using a standard deterministic quantitative genetic model with fixed heritabilities (stabilizing selection) and no immigration, given that the population persists its mean phenotype will converge geometrically to the sink optimum (Gomulkiewicz & Holt 1995). But without immigration, populations comprising discrete individuals ultimately become extinct, and extinction is rapid if average fitness is less than unity and there is no evolution. In the examples below, if the sink habitat has an optimum that differs from the source optimum by more than approximately twice the standard deviation ω of the individual fitness function (equation (2.1)), a propagule of immigrants would face almost certain extinction were it isolated; indeed, if the source populations were to experience abrupt environmental change of this magnitude, rapid extinction would be very likely for the parameters used here (Holt & Gomulkiewicz 2002).

Recurrent immigration prevents permanent extinction. With a fixed population size, deterministic quantitative genetic models with constant heritability predict gradual progression towards an equilibrium displaced from the local optimum (because of the regular admixture of locally maladapted genotypes) if immigrants are sufficiently maladapted to the local environment (Holt & Gomulkiewicz 1997*b*; Tufto 2000). If population size can change because of adaptations, multiple equilibria may emerge in deterministic formulations (Appendix A; Tufto 2001). In our individual-based simulations, heritabilities can evolve due to selection and drift, and population dynamics are inherently stochastic, including local extinction. The resulting temporal dynamics of adaptation are dramatically different from parallel deterministic quantitative genetic models.

(a) *Punctuated adaptive evolution in sinks*

Figure 2*a* shows characteristic examples of population abundance through time. For periods that can be short, but more often are very long, a population fluctuates at low levels maintained by immigration. In some generations (particularly in severe sinks), there may even be no survival of selection, so the population 'winks out' and then is re-established by immigration. As time proceeds, the population may quickly explode to levels at which it is limited by the intrinsic carrying capacity of the habitat. There is enormous variability among populations in the length of time that elapses before adaptation to the sink environment.

To examine the process of adaptation in more detail we monitored changes in the average genotype of each population (genotype here refers to the sum of the alleles for an individual, and these are averaged over the population). Figure 3 shows histograms describing the distribution of realized genotypes among replicate populations in the sink habitat, at different lengths of exposure to that environment. (The average genotype is measured
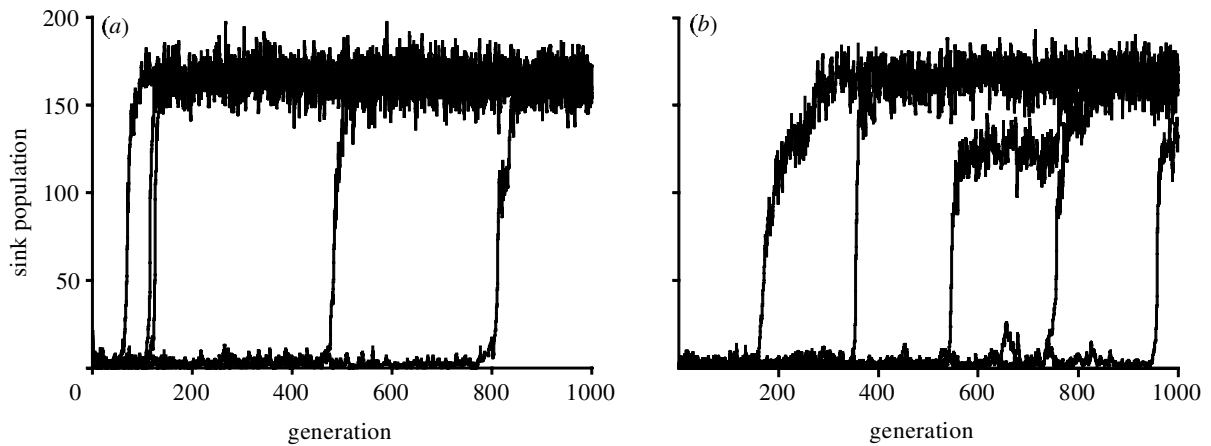
Figure 2. Characteristic examples of population dynamics for species adapting to sink habitats. For the five examples shown on each panel, $K = 64$, $2B = 8$, $n\mu = 0.01$, $n = 10$, $\alpha^2 = 0.05$, $I = 4$, $\omega^2 = 1$, $\theta_{source} = 0$, and $\theta_{sink} = 2.8$. The population sizes shown are numbers of adults, after selection and before immigration. (*a*) With sink mutation; (*b*) same as (*a*) except with no sink mutation.
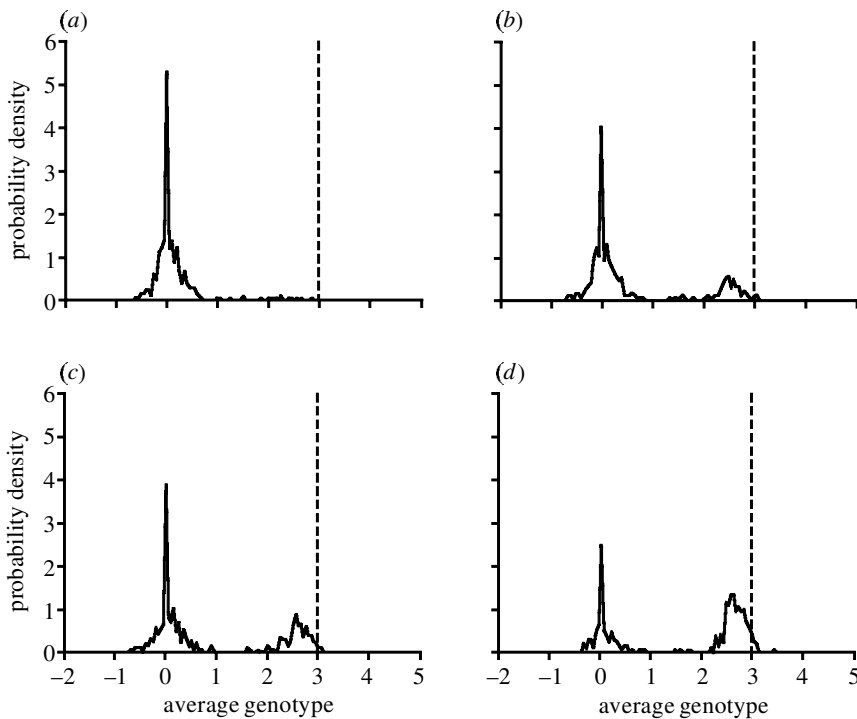

Figure 3. Frequency distributions of average genotypes in the sink habitat at different times after the start of immigration. Histograms are constructed from 400 replicate simulations with parameters as in figure 2*a* except $\theta_{sink} = 3.0$ (indicated by the vertical dashed line). (*a*) 100 generations of immigration; (*b*) 500 generations; (*c*) 1000 generations; (*d*) 2000 generations.

between selection and immigration.) The expected genotype of the immigrants is zero (the optimal phenotype in the source). In the example shown, there is moderately strong selection and the optimal sink phenotype is $\theta_{sink} = 3$. After a short period of exposure (100 generations; figure 3*a*), most populations remain close to the source optimum. As time progresses (500 generations; figure 3*b*), some populations achieve average genotypes much nearer the optimum in the sink habitat. As time continues to pass (figure 3*c,d*), a striking bimodal pattern emerges, in which populations are either locally maladapted and near to the source optimum, or near to the sink optimum, with very few populations found in between. This bimodality was observed under a variety of assump-

tions about parameter values (except for very high immigration rates, or weak selection; see § 3g).

The populations near the sink optimum are not perfectly adapted to the sink environment; the mean genotype is pulled slightly below the locally optimal state because of the recurrent immigration of maladapted individuals from the source. We return to this point below. For the moment, we can use the existence of this bimodality to characterize succinctly a large number of simulations. Namely, in simulations such as those shown in figure 3, populations exist in one of two states: (i) 'maladapted', with an average genotype closer to the source optimum (in this case, less than 1.5); and (ii) 'adapted' (with a value greater than 1.5). Few populations are found near the
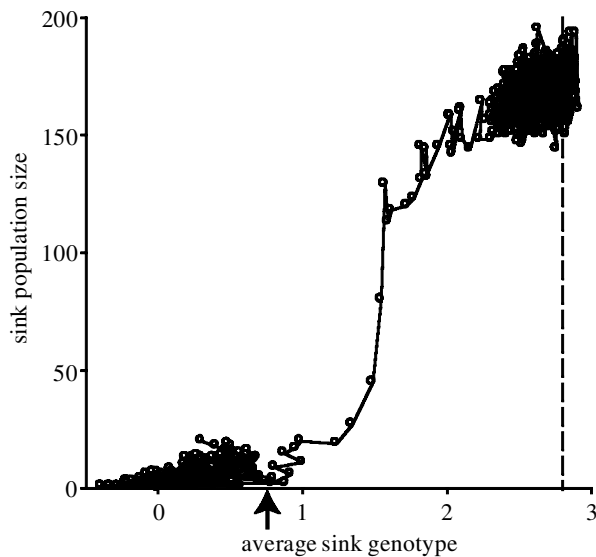
Figure 4. Joint population and evolutionary dynamics over 1000 generations of a representative population adapting to a sink habitat. The ordinate and abscissa indicate the size and average genotype, respectively, of the population censused just before immigration. Parameters are as in figure 2*a*. Open circles represent generations. Dashed line, sink optimum. Arrow, threshold at which mean absolute fitness exceeds unity.
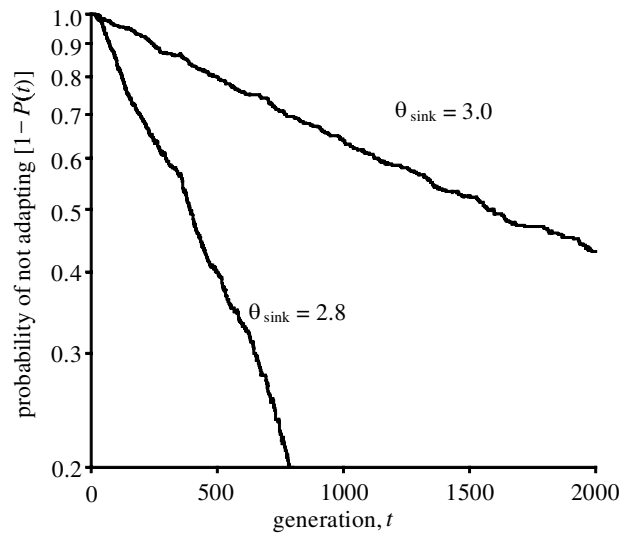

Figure 5. Semi-log plots of the probability of a population not being adapted to a sink as a function of time for two optimal phenotypes in the sink ($\theta_{sink} = 2.8$ and $\theta_{sink} = 3.0$). All other parameters are as in figure 2*a*, except $K = 32$.

threshold separating the maladapted and adapted classes. For almost all results reported here, this definition of 'adapted' corresponds closely with the ability of a population to survive after immigration ceases.

A more detailed study of evolutionary dynamics within each population reveals that transitions from the maladapted to adapted states typically occur just once, though a few populations do shift back and forth for a brief period across the midpoint separating 'maladapted' and 'adapted' states. Overall, there are few 'back-transitions', and these tend to be clustered in a brief period during the phase of adaptation. Figure 4 shows an example of joint population and evolutionary dynamics, represented in a phase plane with axes of population size and average genotype in the sink. In the initial phase of occupancy (lower left corner, figure 4), the population hovers around low abundances with an average genotype near that of the source, slightly displaced towards the sink optimum. In this phase, the average genotype fluctuates considerably, reflecting the combined effects of many processes (for example, genetic drift at low population sizes, random variation in immigrant genotypes, selection). During this phase, which can often be very long, if immigration were prevented then rapid extinction would almost always occur. This phase of local maladaptation is typically followed by a brief transition, during which there is a trend of rising average genotype for several generations, with a concomitant rapid increase in population size. The rate of population growth then slows, and the average genotype continues to climb toward the sink optimum. Finally, the population settles into a phase (upper right corner, figure 4) at which it experiences bounded fluctuations in both abundance and genotype. Once a population enters this adapted phase, it usually remains adapted, albeit displaced from the local

optimum by recurrent gene flow. In this adapted phase, if immigration is prevented, the population persists.

This 'punctuational' pattern of adaptation to the sink is quite striking in most of the simulations that we have carried out. This pattern provides a convenient tool for summarizing large numbers of simulation runs with a single number, because over a fixed number of generations, we can use the number of net transitions to estimate the probability of adaptation of a sink population. 'Adapted' populations have experienced a dramatic transition from initially being poorly adapted to the sink to being reasonably well adapted, and are able to persist without immigration.

(b) *Distribution of 'waiting times' to adaptation*

Figure 5 shows the distribution of times required for a population to achieve an adapted state in a sink (i.e. the time at which a population crosses the midpoint between source and sink optima). If $P(T)$ is the probability of becoming adapted by time T, $1 - P(T)$ is the probability of remaining maladapted at time T. The quantity $\log[1 - P(T)]$ is approximately linear, except at very low values of T. There appears to be a roughly constant probability of adaptation to the sink environment, per unit time, which is lower in more severe sink environments.

(c) *Effects of immigration and severity of sink environment upon adaptive evolution*

The likelihood of adaptation over any time-period depends upon each model parameter. Two particularly important parameters are the degree of maladaptation in the sink and the number of immigrants. Figure 6*a* shows how the probability of adaptation in a sink after 1000 generations of immigration depends on the expected degree of immigrant maladaptation (the distance between source and sink optima) for several immigration rates. When the degree of maladaptation is low (2.5 in figure 6*a*), local adaptation is very likely to occur by generation 1000. When the degree of maladaptation in the sink is severe (3.5 in figure 6*a*), the likelihood of adaptation at
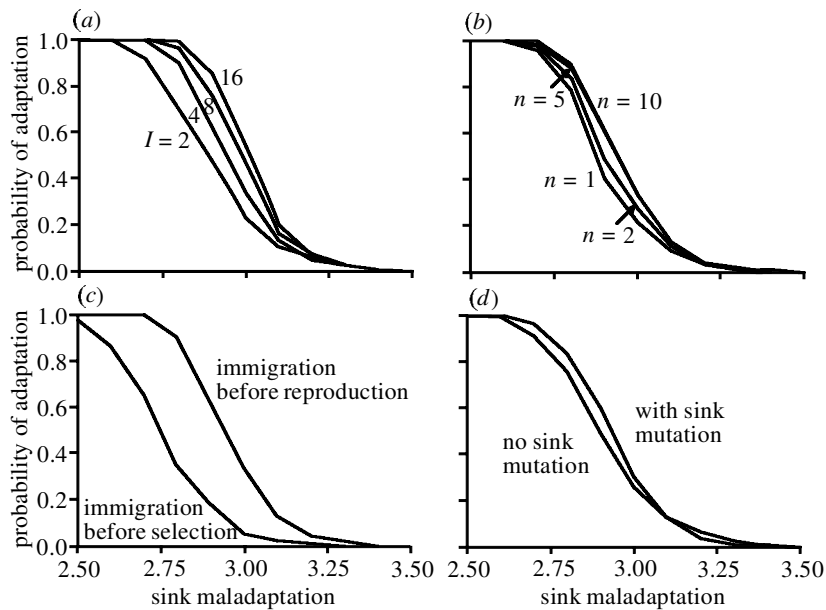
Figure 6. Probability of adaptation in a sink after 1000 generations of immigration as a function of expected immigrant maladaptation (θ_{sink}). Parameters not indicated are as in figure 2a. Probabilities were estimated from 400 replicate simulations for each set of parameters. (a) Effect of immigration rate I (immigrants/generation). (b) Effect of number of loci. The curves for $n = 5$ and $n = 10$ are almost completely congruent. (c) Effect of the life-history stage of immigration. For the upper curve, immigrants join the sink adult pool, from which parents are then chosen (as in (a), (b) and (d)). For the lower curve, immigrants arrive just before selection in the sink. (d) Effect of sink mutation. For the lower curve, the mutation rate in the sink is zero.

$T = 1000$ is, essentially, zero. The sigmoidal relationship between the probability of adaptation over a given time-period, and the degree of maladaptation faced by immigrants in the source, is a quite general feature of our simulations. As T increases, the sigmoidal curve shifts to the right.

At intermediate degrees of maladaptation, an increase in the number of immigrants per generation, from 2 to 16, substantially enhances the probability of adaptation to the sink habitat (figure 6a). Thus, immigration both prevents perfect adaptation (as in figure 3, where the mean genotype of adapted populations is displaced below the local optimum) and enhances the likelihood of the initial transition to a moderately adapted state.

(d) *Effect of number of loci*

Figure 6b illustrates how the probability of adaptation as a function of maladaptation depends on the number of loci underlying variation in the quantitative trait z. There is a moderately improved likelihood of adaptation in going from 1, to 2, to a greater number of loci. However, there is no practical difference between simulation results based on 5 and 10 loci. We thus used 10 loci for most simulations. Inspection of populations, post-adaptation, revealed that in some cases, adaptation reflected change mainly at a single locus, but in other cases, at multiple loci.

(e) *Effect of life-history*

For the above simulations, immigrants arrive after selection and are added to the sink adult pool, from which parents are chosen. We also performed simulations in which, alternatively, immigrants arrive just before selection. One might expect that adaptation would be more rapid when immigration precedes selection since the immigrants

would tend to increase genetic variation in the sink, thereby enhancing the effectiveness of selection. Indeed, this occurs in a deterministic model similar to that in Appendix A. We found, however, the opposite result in our simulations; the probability of adaptation was significantly lower when selection followed immigration, than the reverse (see figure 6c). We suspect that the explanation can be traced to factors not included in the deterministic model, in particular demographic stochasticity. If immigration precedes selection, then a single copy of a favourable allele in an immigrant must survive viability selection to be inherited subsequently. However, if immigration follows selection, then a favourable allele in an immigrant will, on average, be reproduced B times before it is subjected to viability selection (and chance extinction). The chance that at least one of B copies of the allele will survive to be inherited is greater than that of a single copy. The effect of demographic stochasticity is therefore likely to be larger when immigration precedes selection; our simulations suggest that this impedes the rate of adaptation. We intend to study this and other possible effects of different life-histories in more detail in the future.

(f) *Effect of sink mutation*

There are, potentially, two sources of genetic variation in the sink: infusion via immigration from the source, or *in situ* mutation (Gomulkiewicz *et al.* 1999). To assess the relative importance of *in situ* mutational variation for adaptation, we performed simulations in which the probability of mutation was set to zero in the sink. With 10 loci, this caused only a small reduction in the probability of initial adaptation (figure 6d). However, it did sometimes cause a significant slowing in the approach to 'complete' adaptation (figure 2b shows example runs). The

populations initially rose suddenly, as before, but only part (generally more than half) of the way to their final level; the populations then continued to increase more slowly toward their final values. This effect was particularly noticeable in the single-locus case (results not shown). These results suggest that variation from the source is most important in the initial stages of a sink population becoming adapted to its environment, with sink mutation mostly helping an already somewhat adapted population to become better adapted.

(g) *Strength of selection*

The above simulations assumed that stabilizing selection ($1/\omega^2$) was strong in both source and sink habitats. Reducing the strength of selection has a number of consequences. All else being equal, for a given degree of maladaptation θ_{sink}, weaker selection in the sink corresponds to a higher absolute fitness for new immigrants (see equation (2.1)), and slower convergence towards the sink optimum. We performed simulations with moderate selection ($\omega^2 = 9$) and weak selection ($\omega^2 = 99$), in both source and sink. Qualitatively, results with moderate selection were similar to those described above for strong selection, but the transition from high to low probability of adaptation occurred at much higher levels of maladaptation ($\theta_{sink} \approx 6$ instead of 3), and the transition to the adapted state was often less abrupt than with strong selection. With very weak selection, the transition occurred at even higher levels of maladaptation ($\theta_{sink} \approx 16$), but in this case, the threshold criterion for adaptation loses its utility, because many 'maladapted' populations can persist without further immigration.

4. DISCUSSION

Previous studies have shown that there are demographic constraints on evolution in sink environments (Holt 1996; Kawecki & Holt 2002) and that, in some circumstances, immigration has a positive influence on adaptation to sink conditions (Tufto 2001). The results presented here, based upon models with much genetic and demographic realism, support these general conclusions. In particular, adding demographic and genetic stochasticity (for example, drift, mutation and local extinction) does not alter these qualitative findings. Niche evolution and local adaptation seem to go hand-in-hand: if a population maintained by immigration can adapt to a sink, then it typically can also persist there in isolation.

As in earlier analyses of simpler one-locus models (Holt & Gomulkiewicz 1997a; Gomulkiewicz et al. 1999), the more severe the sink environment, the less likely is adaptive evolution (figure 6a). In our simulations, sink populations do eventually become adapted to the sink habitat, even for very severe sinks. However, this may require many thousands of generations, so that over shorter time-scales one would observe stasis, in which a species in the sink merely retains those traits that are adaptive in the source.

We have argued (Gomulkiewicz et al. 1999) that immigration can have disparate effects upon local adaptation. For instance, immigration boosts local population size, which may depress local fitnesses given density dependence, in turn making it harder for a locally superior

mutant to spread by selection. However, for the results of the individual-based model presented here, density dependence acts in a threshold fashion; at low rates of immigration there is no direct density dependence operating in the sink. There are some excellent empirical examples of sink populations with negligible density dependence at low densities (Keddy 1982). To assess the robustness of our results, we performed additional simulations without the ceiling on the number of parents, with a density-dependent viability factor of the form $1/(1 + N/k)$, where N is the number of offspring and k determines the strength of density dependence. The results were similar to those with ceiling density dependence, but gave lower probabilities of adaptation, especially for strong density dependence (low k). Increasing the strength of density dependence in general seems to hamper adaptation to a sink environment (Gomulkiewicz et al. 1999; Tufto 2001).

The main effect of immigration in our model is to permit exposure of variation, largely generated and maintained in the source population, to the sink environment. Most individuals in a sink population are unlikely to leave many descendants, so local evolutionary processes in sink populations may be undermined by demographic stochasticity. An increase in the number of immigrants both increases the genetic sample drawn from the source in each generation and improves the chances that a population will persist to evolve. Hence, our findings lend further support to the general conclusion that immigration can facilitate adaptive evolution to the sink environment (Holt & Gaines 1992; Holt & Gomulkiewicz 1997a,b, 2002; Gomulkiewicz et al. 1999; Kawecki & Holt 2002), at least when density dependence at low densities in the sink is weak.

Our results also reveal a striking, novel feature: the pattern of niche evolution in a sink is characterized by 'punctuated' episodes of rapid evolution, between long periods of relative stasis (figures 2a and 4). These dynamics are reminiscent of the saltational transitions expected between alternative stable equilibria of deterministic systems perturbed by stochastic 'noise' (as with the shifts between adaptive peaks caused by random genetic drift; Ludwig 1981; Lande 1985, 1986). The deterministic version of our individual-based simulations has alternative stable equilibria—corresponding to 'adapted' and 'maladapted' populations—for sufficiently high degrees of maladaptation (Appendix A). The noise in our simulations includes both genetic and demographic stochasticity (figure 1), both of which could lead to transitions between alternative stable equilibria. Tufto (2001) also observes alternative stable equilibria in a deterministic quantitative genetic model of sink evolution, and Ronce & Kirkpatrick (2001) likewise find alternative stable equilibria in a similar model that includes bi-directional migration between sources and sinks, and density dependence, but without individual-level stochasticity. This congruence among studies suggests that the existence of alternative evolutionary equilibria may be characteristic of adaptation in source–sink systems. (Note that classic population genetic models of gene flow and selection can also lead to alternative stable equilibria (Hedrick 2000). However, the mechanism for this effect in these classical models (genetic dominance) is quite different from our model.)

We observed regularity in the punctuational evolutionary patterns, with what appears to be an approximately exponential distribution of times-to-adaptation and niche evolution (figure 5). This regularity, along with the frequent episodes of (temporary) extinction that were commonly observed in our simulations, strongly suggests that the evolutionary transition does not depend on the slow buildup of local adaptation. The nearly exponential distribution of time to adaptation may reflect the appearance of pre-adapted genotypes amongst immigrants drawn at random from the source. Previous studies of single-locus models with mutation have shown that adaptation to a black-hole sink depends upon the appearance of genotypes with absolute fitnesses exceeding unity (Holt & Gomulkiewicz 1997*a*,*b*; Gomulkiewicz *et al.* 1999; LoFaro & Gomulkiewicz 1999). Given such genotypes, local population size should rise, reducing the deleterious impact of further gene flow from the source. Determining the extent to which these explanations hold for polygenic models will require further investigation.

Our results suggest that abrupt evolutionary patterns may occur in environments that are sufficiently heterogeneous in space to include both demographic sources and sinks. We hesitate to suggest, however, that our results explain patterns of punctuation in the fossil record (Eldredge & Gould 1972). Indeed, we have made a number of assumptions (for example, constant environments through time) that, while revealing much about the tempo and mode of adaptation in sink populations, may not be as relevant over the long time-scales pertinent to palaeobiology. An important area for future study of niche evolution will be the analysis of evolution in sink and source environments that are varying through time. At short time-scales, we suspect that examples of abrupt evolution in sink environments are likely to be found in the domain of applied ecology, for instance among exotic species introduced into heterogeneous landscapes, or pests impacted by chemical control measures.

APPENDIX A: A DETERMINISTIC QUANTITATIVE GENETIC BLACK-HOLE SINK MODEL

This appendix describes a simple deterministic counterpart to our individual-based simulations. Besides ignoring genetic and demographic stochasticity, this model relies on other simplifying assumptions that make it analytically tractable. For instance, it assumes that phenotypic and genetic distributions are always normal, and that the additive-genetic variance in the sink is fixed. These assumptions, in turn, imply that selection and immigration are relatively weak evolutionary forces compared with recombination. Tufto (2000; see also Holt & Gomulkiewicz 1997*b*) analysed a model similar to the one presented below, but without population dynamics, and showed that its evolutionary dynamics are similar to rela-

tively complex models that account for the dynamics of heritable variance. We expect the same congruence here since the population dynamics in our deterministic model affects evolution in any given generation only via the rate of gene flow (see equation (A 4)).

As in the simulations, we consider the evolution in a black-hole sink of an ecologically important, quantitative trait z. We likewise assume that all individuals have the same expected fecundity, B, and that the probability that an individual with phenotype z survives to adulthood in the sink is given by $W(z) = \exp[-(z - \theta)^2/(2\omega^2)]$, where θ is the optimal phenotype. We ignore emigration to the source. In the source, we assume that z has a fixed mean 0 and variance σ^2. Thus, the magnitude of θ measures expected maladaptation among newly arrived sink immigrants.

Before selection and immigration in generation t, z follows a normal distribution in the sink with mean $\bar{z}_t$ and fixed variance P. The magnitude of the dimensionless variable $d_t = (\theta - \bar{z}_t)/\theta$ characterizes the extent to which a population is maladapted to the sink environment in generation t. On this scale, immigrants have a constant expected maladaptation of $d = 1$. We also define the dimensionless parameters $\tilde{P} = P/\theta^2$ and $\tilde{\omega}^2 = \omega^2/\theta^2$. Mean viability at the start of generation t is

$$\bar{W}_t = v_{max}\exp\left[\frac{-d_t^2}{2(\tilde{\omega}^2 + \tilde{P})}\right], \tag{A 1}$$

where $v_{max} = \sqrt{\tilde{\omega}^2/(\tilde{\omega}^2 + \tilde{P})} = \sqrt{\omega^2/(\omega^2 + P)}$ is the maximum probability of survival in the sink. Assuming that the environment is initially a sink requires that the initial per capita production of surviving offspring, $B\bar{W}_0$, be less than one. We also assume $B > 1/v_{max}$ to ensure that a population with the optimal mean phenotype (i.e. with $d = 0$) would grow in the local environment.

After viability selection, the maladaptation and population size are, respectively,

$$d_t^* = \frac{\theta - \bar{z}_t^*}{\theta} = v_{max}^2 d_t, \tag{A 2}$$

$$N_t^* = \bar{W}_t N_t, \tag{A 3}$$

where $\bar{z}_t^*$ is the phenotypic mean after selection and $\bar{W}_t$ is given by equation (A 1). Note that equations (A 2) and (A 3) ignore the demographic and genetic stochasticity present in our individual-based simulations (figure 1). Following viability selection, I immigrants arrive from the source population. The maladaptation and population size become

$$d_t^{**} = (1 - m_t)d_t^* + m_t, \tag{A 4}$$

$$N_t^{**} = N_t^* + I, \tag{A 5}$$

respectively, where $m_t = I/(N_t^* + I)$ is the (variable) gene flow rate at time t. At this stage, the ceiling form of density regulation could be incorporated by replacing the right-hand side of equation (A 5) with $\min(K, N_t^* + I)$, where K is the carrying capacity. We will, however, ignore density dependence in this appendix since it complicates analyses considerably but does not add significant insight for our present purposes. Finally, we assume random mating after immigration, which leads to

$$d_{t+1} = d_t + h^2(d_t^{**} - d_t), \tag{A 6}$$

$$N_{t+1} = BN_t^{**}, \tag{A 7}$$

where h^2 is the (fixed) heritability of z—and of d. Equations (A 2)–(A 7) together form a coupled system of deterministic recursions describing joint evolutionary and population dynamics of the population in the sink.

(a) Equilibria

With the simplified dynamics of the system (A 2)–(A 7), one can analytically determine asymptotic states that a population might approach. Without density regulation, it turns out that either $d \rightarrow 0$ and $N \rightarrow \infty$ (indicating successful adaptation to the sink environment), or the local population approaches a joint demographic and evolutionary equilibrium at which $N_t = N_{t+1} = \hat{N}$ and $d_t = d_{t+1} = \hat{d} \neq 0$. At the second equilibrium

$$\hat{N} = \frac{BI}{1 - B\hat{\tilde{W}}} \tag{A 8}$$

and

$$\hat{d} = \frac{1 - B\hat{\tilde{W}}}{1 - v_{\max}^2 B\hat{\tilde{W}}}, \tag{A 9}$$

where $\hat{\tilde{W}}$ is the mean viability (equation (A 1)) when $d = \hat{d}$. Equations (A 8) and (A 9) are independent of h^2. Equation (A 9) is also independent of I but defines $\hat{d}$ implicitly since $\hat{\tilde{W}}$ depends on $\hat{d}$. Such 'maladapted' equilibria are biologically feasible provided $B\hat{\tilde{W}}$, the expected per capita number of offspring surviving until immigration, is less than unity. Moreover, since $v_{\max}^2 < 1$, the equilibrium population can never be more maladapted in the sink than new immigrants from the source, i.e., $\hat{d} < 1$ (see equation (A 9)). However, $B\hat{\tilde{W}} < 1$ means that were immigration prevented and evolution precluded, the population would decline; the sink remains a sink. With evolution, the population would eventually adapt and persist without immigration because the model is deterministic. By contrast, the stochastic simulations in the text permit actual extinctions. Numerical analysis of equations (A 8) and (A 9) shows that two maladapted equilibria are possible for sufficiently large values of the dimensionless measure of immigrant maladaptation, $\tilde{\omega}^{-2} = \theta^2/\omega^2$ (figure 7).

We simulated the recursions (A 2)–(A 7) to assess stability of the equilibria. Given an initial degree of maladaptation, d_0, sufficiently close to zero, the population can escape the effects of migration with the phenotype converging on the local optimum ($d \rightarrow 0$) and population size increasing without bound. When two maladaptive equilibria exist for a particular value of θ^2/ω^2 (see equations (A 8) and (A 9) and figure 7), one is unstable while the other is locally stable and represents a population that closely resembles the mean immigrant phenotype ($d = 1$). Which asymptotic state is approached depends on d_0; the set of unstable equilibria appears to be a separatrix (see figure 7). In this deterministic model, a sink population may remain maladapted because of immigration, but the magnitude of maladaptation at equilibrium is independent of the number of immigrants. (This particular conclusion depends on our assumption of no density dependence; see Gomulkiewicz *et al.* (1999); Tufto (2001)).

It is useful to consider a special initial condition that parallels our individual-based simulations, namely, an
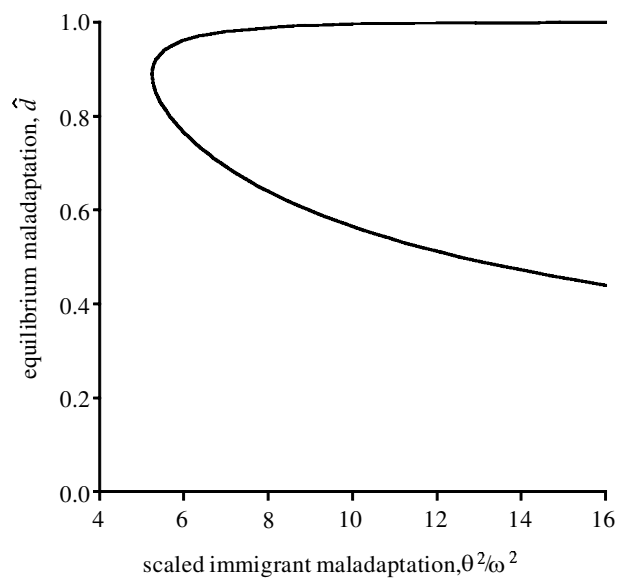

Figure 7. Equilibrium scaled maladaptation ($\hat{d}$), as a function of scaled immigrant maladaptation (θ^2/ω^2). Figure computed using equations (A 8) and (A 9) assuming $P = 0.1\omega^2$, and $B = 4$. Upper branch: stable equilibria; lower branch: unstable equilibria.

initial population consisting of I immigrants with maladaptation $d_0 = 1$. Numerical simulations of equations (A 2)–(A 7) from this initial condition reveal a remarkable feature of the system: there exists a threshold level of initial maladaptation, $(\theta^2/\omega^2)^*$, below which local adaptation is ensured and above which the sink remains perpetually a sink. This threshold is set by the local selective regime and quantitative genetic parameters, but is independent of the rate of immigration, I. Note that in the above model, if N and I were fixed, fixing m, then the system defined by equations (A 2), (A 4) and (A 6) would have a single equilibrium ($\hat{d} = m/[1 - (1 - m)v_{\max}^2]$). The bistability illustrated in figure 7 thus arises because the migration rate is a dependent variable of the system, setting up a positive feedback between population size and adaptation. This, in turn, leads to two stable deterministic equilibria for sufficiently maladapted initial conditions (see Tufto 2001; Ronce & Kirkpatrick 2001). The stochasticity contained in the simulations in effect permits the system to be 'kicked' from a maladapted equilibrium at low abundance, to an adapted equilibrium at high abundance. As pointed out by a reviewer, another form of positive feedback may arise via reciprocal effects of population size and genetic variance (see Tufto 2000).

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