

Temporal Variation Can Facilitate Niche Evolution in Harsh Sink Environments

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ABSTRACT: We examine the impact of temporal variation on adaptive evolution in “sink” environments, where a species encounters conditions outside its niche. Sink populations persist because of recurrent immigration from sources. Prior studies have highlighted the importance of demographic constraints on adaptive evolution in sinks and revealed that adaptation is less likely in harsher sinks. We examine two complementary models of population and evolutionary dynamics in sinks: a continuous-state quantitative-genetics model and an individual-based model. In the former, genetic variance is fixed; in the latter, genetic variance varies because of mutation, drift, and sampling. In both models, a population in a constant harsh sink environment can exist in alternative states: local maladaptation (phenotype comparable to immigrants from the source) or adaptation (phenotype near the local optimum). Temporal variation permits transitions between these states. We show that moderate amounts of temporal variation can facilitate adaptive evolution in sinks, permitting niche evolution, particularly for slow or autocorrelated variation. Such patterns of temporal variation may particularly pertain to sinks caused by biotic interactions (e.g., predation). Our results are relevant to the evolutionary dynamics of species’ ranges, the fate of exotic invasive species, and the evolutionary emergence of infectious diseases into novel hosts.

Keywords: niche evolution, immigration, source-sink, temporal variation, gene flow.

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A classic problem in evolutionary biology is to understand the factors that govern the tempo of evolutionary change (Simpson 1944). Many controversies have swirled around the issue of whether intrinsic factors (e.g., developmental constraints) or extrinsic factors (e.g., coevolving species, climatic variation) are most important in determining the pace of evolution. A pervasive extrinsic factor that could influence evolution is temporal variability in the environment (e.g., Smith et al. 1995). In this article, we consider the influence of temporal variability on the evolution of species’ niches—those sets of environmental requirements that characterize where a population is expected to persist without immigration (Hutchinson 1978; Holt and Gaines 1992). The empirical record shows examples of both niche conservatism over long timescales (Bradshaw 1991; Merila et al. 2001) and niche evolution over short timescales (Mongold et al. 1999; Thomas et al. 2001). A significant challenge is thus to elucidate the genetic, organismal, demographic, and ecological factors that can lead either to stasis in species’ niches, or instead to niche evolution, including rapid evolution.

In a closed population, the environment may change, so that the environment is no longer within the species’ niche, and then adaptive evolution may reshape the niche so that the species can persist in the changed environment. However, such populations are automatically exposed to heightened extinction risks, which may prevent such evolution (Lynch and Lande 1993; Gomulkiewicz and Holt 1995). The niche can evolve while avoiding this extinction risk if the species occupies a set of habitat patches, some of which have conditions within the niche, and some without. Immigration from the former “source” habitats to the latter “sink” habitats can maintain populations in the latter (Holt 1985; Pulliam 1988; Dias 1996). This provides an opportunity for adaptation leading to niche evolution in the sink, without risking global extinction (Kawecki 1995; Holt and Gomulkiewicz 1997*a*; Kawecki and Holt 2002). There is now a considerable literature on adaptive evolution in temporally constant sink habitats (e.g., Holt and Gaines 1992; Kawecki 1995, 2003; Holt 1996*a*, 1996*b*; Holt and Gomulkiewicz 1997*a*, 1997*b*; Proulx 1999, 2002;

Ronce and Kirkpatrick 2001; Tufto 2001; Kawecki and Holt 2002; Holt et al. 2003). One robust rule of thumb that emerges from this body of work is that the harsher the sink is (namely, the lower the absolute fitness in that environment), the less likely is adaptive evolution. There are several mechanistic reasons for this constraint on adaptation (Holt and Gomulkiewicz 1997a). For instance, a population in a harsh sink tends to have low abundance and so may be relatively vulnerable to “swamping” by gene flow (Kirkpatrick and Barton 1997; Ronce and Kirkpatrick 2001; Tufto 2001) and may also be less able to maintain adaptive genetic variation.

These prior analyses of adaptive evolution in sinks have assumed that the sink environment is constant. Yet severe environments may also be unstable environments. This is more likely for some environmental causes of harshness (e.g., climatic extremes, impacts of predators and parasites with temporally fluctuating abundances) than for others (e.g., concentrations of heavy metals in soil). What is the impact of temporal variability on niche evolution? Here, we demonstrate that in some circumstances a moderate amount of temporal instability can facilitate evolution of local adaptation and species’ niches in unfavorable environments. We will show that this is particularly likely if temporal variation is serially autocorrelated (as is often true for natural temporal variation; Ripa and Lundberg 1997).

The specific scenario we consider has two habitats coupled by one-way dispersal. One is a source where conditions fit the niche requirements of a species; in this habitat, the species persists at an evolutionary equilibrium. Individuals from this habitat migrate to a sink habitat, with conditions outside the niche (e.g., as may be found at the edge of a species’ geographical range). The initial condition of the system is such that without recurrent immigration or evolution, the species would go extinct in the sink habitat. The broad question we address is how temporal variation influences the likelihood of adaptation and niche evolution, potentially permitting the population in the sink to persist without immigration.

We explore two complementary models that illuminate how temporal variation in the sink influences evolution in species’ niches. We first describe the pattern of evolution observed in constant sink environments. We then use these results as a yardstick for assessing the impact of temporal variation. (This is the theoreticians’ analogue of carrying out an experiment, contrasting evolution in constant and variable environments.) The first model is a continuous-state quantitative-genetics model in which gene flow from a source can prevent adaptation in the sink in a constant environment. We show that with moderate, autocorrelated temporal variation in the sink, an initially maladapted population can overcome gene flow, adapting to a state in

which it can persist without further immigration. To assess the generality of this positive effect of temporal variation on niche evolution, we also examine coupled evolutionary and demographic dynamics in an individual-based model, which relaxes many assumptions of the continuous-state model (e.g., by incorporating mutation, drift, and demographic stochasticity). We again find that moderate temporal variation can facilitate adaptation to the sink and suggest that several distinct mechanisms contribute to the observed effect. The broad concordance of results from these two models suggests that a robust phenomenological conclusion is that temporal variation can at times facilitate evolution in harsh sink environments.

Models for Niche Evolution in a Constant Sink

Continuous-State Deterministic Model

Our first model (modified from Holt et al. 2003) describes the evolution of a single quantitative trait for a population with discrete generations in a “black hole” sink (a sink that receives immigrants from, but sends no emigrants back to, the source; see Holt and Gomulkiewicz 1997b). The population size of newborns in generation t is N_t . We assume that heritability is fixed and that offspring phenotypes are normally distributed. (These imply that selection and immigration are relatively weak evolutionary forces compared with recombination [Tufto 2000]; the individual-based model presented below relaxes these assumptions.) The probability that an individual with phenotype z survives to adulthood in the sink is $W(z) = \exp[-(z - \theta)^2 / (2\omega^2)]$, where θ is the optimal phenotype and $1/\omega^2$ determines the strength of selection in the sink. Rather than model dynamics in the source habitat directly, we assume genotypes there have a fixed mean of 0, so the magnitude of θ measures the expected maladaptation of newly arrived immigrants in the sink.

The phenotype z is assumed to be the sum of an additive-genetic part g and an independent, normally distributed environmental (plus nonadditive-genetic) component with mean 0 and variance E . At the start of generation t (after reproduction), the phenotype z has a normal distribution in the sink habitat with mean \bar{z}_t (equal to the mean genotypic value \bar{g}_t) and constant phenotypic variance P ; P is the sum of the additive-genetic variance G (the variance of g for the population) and the environmental variance E . Mean viability at the start of generation t is

$$\bar{W}_t = v_{\max} \exp\left[\frac{-(\bar{g}_t - \theta)^2}{2(\omega^2 + P)}\right], \quad (1)$$

where $v_{\max} = [\omega^2/(\omega^2 + P)]^{1/2}$ is the average probability of

survival in the sink for a perfectly adapted population. After viability selection, the mean genotype (Bulmer 1985, p. 181) and population size are, respectively,

$$\bar{g}_t^* = \bar{g}_t + \frac{G}{\omega^2 + P}(\theta - \bar{g}_t), \quad (2a)$$

$$N_t^* = \bar{W}_t N_p, \quad (2b)$$

where \bar{W}_t is given by equation (1). Following viability selection, I immigrants arrive from the source population, and the mean genotype and population size become

$$\bar{g}_t^{**} = (1 - m_t)\bar{g}_t^*, \quad (3a)$$

$$N_t^{**} = N_t^* + I, \quad (3b)$$

where $m_t = I/(N_t^* + I)$ is the gene flow rate at time t . Note that gene flow is not a parameter but a variable because population size itself varies with fitness and immigration rate (Holt and Gomulkiewicz 1997b; Tufto 2001). Finally, assuming random mating after immigration, the mean genotype and population size at the start of the next generation are

$$\bar{g}_{t+1} = \bar{g}_t^{**}, \quad (4a)$$

$$N_{t+1} = B N_t^{**}, \quad (4b)$$

where B is the birth rate (per parent). If a perfectly adapted population can persist, we must have $Bv_{\max} > 1$; we assume this to be true. Equations (2)–(4) together form a complete coupled system of deterministic recursions describing the interplay of gene flow, selection, and population dynamics in the sink.

The above model assumes no density dependence in the sink. If numbers remain low, this assumption may be reasonable, but it is usually not when populations expand to high numbers. Moreover, in some species, density dependence may be strong even in rare populations. We consider two forms of density dependence. The first acts continuously across all densities, in that mean viability declines with increasing density (incorporated by dividing the right-hand side of eq. [1] by $1 + cN_t$; $c = 0$ corresponds to no density dependence). The other form is ceiling density dependence, in which the number of breeding adults cannot exceed a carrying capacity, K . This is implemented by replacing the right-hand side of equation (3b) with $\min(K, N_t^* + I)$. In both cases, density dependence does not affect selection directly (eq. [2a]) but instead influences the effective gene flow rate (density dependence lowers fitness, which depresses population size, which in turn increases the fraction of the population comprised of immigrants each generation).

Models (2)–(4) are sufficiently tractable that the asymptotic states a population might approach can be expressed analytically. Without density regulation, either $\bar{g} \rightarrow \theta$ and $N \rightarrow \infty$ (indicating successful adaptation to the sink habitat; thick line in fig. 1A), or the local population approaches a joint demographic and evolutionary equilibrium at which $N_t = N_{t+1} = \hat{N} < \infty$ and $\bar{g}_t = \bar{g}_{t+1} = \hat{g} < \theta$. For a sufficiently harsh sink (i.e., θ above a critical value θ_c), there are two finite equilibria, labeled $c = 0$ in figure 1A. With either form of density dependence, all equilibria are finite (see appendix in the online edition of the *American Naturalist*; fig. 1). If density dependence is continuous and weak (fig. 1A, curve labeled $c = 0.001$) there is a single (adapted) equilibrium at low θ , a single maladapted equilibrium at high θ , and three equilibria for intermediate θ . If continuous density dependence is sufficiently strong (curve labeled $c = 0.002$), there is only a single equilibrium for each θ . With ceiling density dependence (fig. 1B), the finite-population equilibria are unchanged from the density-independent case (labeled $c = 0$ in fig. 1A) if the equilibrium population size (at mating) lies below the ceiling K . If equilibrium size reaches K , the genotypic equilibria depart from the density-independent curve, leading to the upper branch of figure 1B (the part above and to the left of the bar). There is an upper value of θ , denoted as θ' , above which only maladapted equilibria exist.

Maladapted equilibria in the sink exist when adaptation is prevented by recurrent gene flow from the source. We simulated recursions (2)–(4) to assess stability. Where only a single equilibrium exists, it is stable. Where three equilibria (including the infinite-population asymptotic state) exist, the one with the middle \hat{g} is unstable (dashed lines in fig. 1). The other equilibria are stable; the higher one is adapted, and the lower one is maladapted (and closely resembles the mean immigrant phenotype, $\hat{g} \approx 0$). The arrows in figure 1B illustrate alternative stable equilibria for one value of sink maladaptation. In cases with two stable equilibria, the outcome depends on the initial condition \bar{g}_0 (the set of unstable equilibria approximates a separatrix). If we begin with an empty sink, the initial population consists of I immigrants with average genotype $\bar{g}_0 = 0$. Iteration of equations (2)–(4) from this initial condition reveals a threshold level of maladaptation in the sink, θ_c (the same critical value noted above, at which we first obtain multiple equilibria), below which local adaptation is ensured and above which the sink population remains maladapted. Starting from the immigrant state of $\bar{g}_0 = 0$, the population always evolves to the maladapted equilibrium, if one exists. Alternative stable equilibria (one adapted, and one not) arise in this model if density dependence is weak or absent at low densities. A number of other authors (e.g., Tufto 2001) have also noted that the

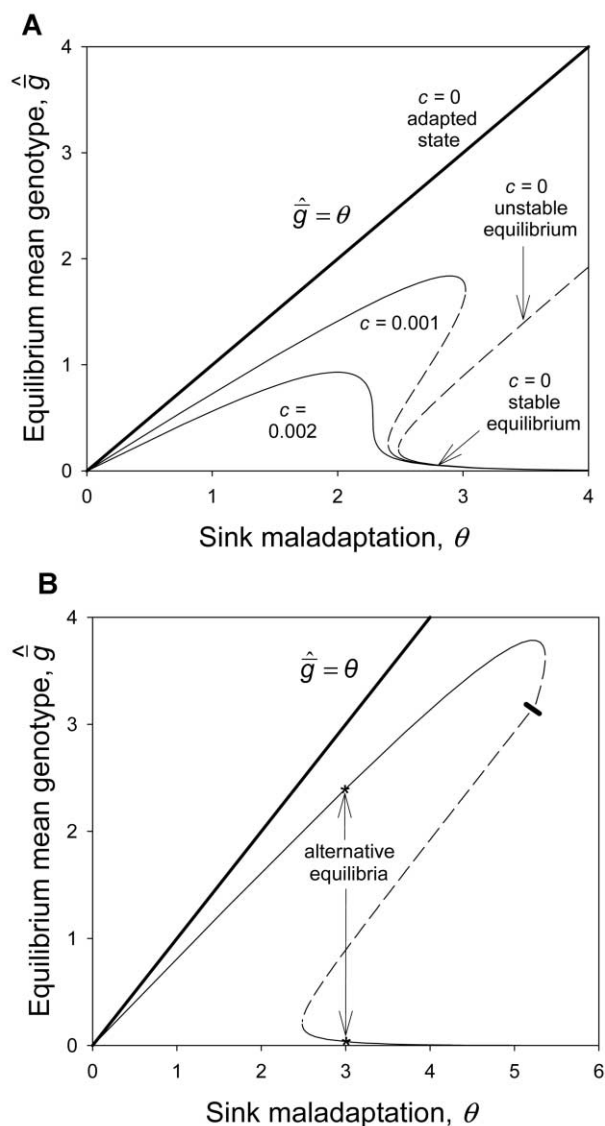


Figure 1: Alternative equilibrational states of a temporally constant sink with recurrent immigration for continuous-state model of coupled population change and evolution in a quantitative character (eqq. [2]–[4]). The mean genotypes at an evolutionary equilibrium between gene flow and selection (as evaluated from eq. [A2] in the appendix in the online edition of the *American Naturalist*) are shown as a function of sink maladaptation for several different strengths of density dependence. Genotypic equilibria represented by solid lines are stable, while those indicated by dashed lines are unstable. The heavy dark lines show the mean genotype equal to the sink phenotypic optimum, which is an asymptotic state of the population without density dependence when it becomes adapted and growing exponentially. A, Equilibria for continuous density dependence ($c > 0$) and no density dependence ($c = 0$). For $c = 0.002$, there is only one stable equilibrium, while for other sinks with weaker density dependence for sufficiently high θ , there are two. B, An example of alternative evolutionary equilibria for ceiling density dependence ($K = 256$). Other parameters used to generate the figures are $\omega^2 = 1$, $P = 1.05$, $I = 4$, $B = 4$, $G = 0.05$.

interplay of gene flow and selection can generate alternative stable states in populations.

Niche Evolution in a Constant Sink: Individual-Based Model

The above model makes many assumptions that are unlikely to hold when population sizes are very low (e.g., constant heritabilities). To assess the robustness of our conclusions, we consider a second model relaxing these assumptions. This model incorporates mechanisms constraining niche evolution other than gene flow (e.g., loss of genetic variation) and permits evaluation of immigration as a process sampling genetic variation from the source. This individual-based model with discrete generations extends a model earlier developed by Bürger and Lynch (1995; Bürger et al. 1989); it is fully described in a previous article (Holt et al. 2003).

The basic features of the individual-based model are as follows. As in the continuous-state model, the source and sink have different optimum phenotypes, with a one-way flow of immigrants from source to sink. The genotypic value of an individual is the sum of allelic values at 10 additive, independently segregating loci (varying the number of loci has only minor effects on the results). Each phenotypic value is the sum of this genotypic value and an independent standard normal random variable. Selection occurs during survival from offspring to adult. For phenotype z in habitat i , the probability of survival is $W_i(z) = \exp[-(z - \theta_i)^2 / (2\omega_i^2)]$, where θ_i is the optimal phenotype and $1/\omega_i^2$ is the strength of stabilizing selection in habitat i . We let $\theta_{\text{source}} = 0$, so the magnitude of θ_{sink} measures the expected degree of maladaptation experienced by immigrants from the source. We thus often refer to the sink optimum, hereafter denoted by θ , as the sink maladaptation. The strength of selection parameter, ω_i^2 , is set to unity in both habitats. This corresponds to moderately strong selection.

Individuals are assumed to be diploid, hermaphroditic, and monogamous. Mating pairs are formed randomly from all adults, with a maximum of K individuals reproducing (ceiling density dependence). The number of offspring per pair is binomially distributed, with a trial parameter of 16 and a probability parameter of 0.5 (giving a mean of 8). After each offspring haplotype is determined by simulating independent segregation, a mutation occurs on that haplotype with probability 0.01. When a mutation occurs, a zero-mean normal random value with variance 0.05 is added to the value of a randomly chosen allele on that haplotype. After both haplotypes are generated for an individual, its phenotype is determined by adding an environmental component to the (additive) genotypic value. Immigration occurs after selection and before mating. The

source is initialized with K individuals and followed for 1,000 generations before emigration begins to allow the source to reach mutation-selection-drift equilibrium (Bürger et al. 1989). The sink is initially empty. Once immigration starts, each generation four adults (randomly chosen from the source) are moved to the sink without mortality in transit. Parents for the next generation in the source are chosen from the remaining adults, and parents in the sink are chosen from all adults, including immigrants and any survivors of selection from the prior generation.

This individual-based model is far more complex than the continuous-state model and can feasibly be analyzed only by intensive computer simulation. It nonetheless provides a useful check on our results because the model contains many realistic evolutionary factors not present in the continuous-state model. For example, there is a distribution of genotypic values in the source in the individual-based model, and immigrants are sampled randomly from this distribution. In contrast, the continuous-state model assumes that the genetic makeup of the source and the immigrant pool are fixed.

Population sizes and genotypic distributions constantly fluctuate in the individual-based model, so deciding whether a sink population is “adapted” is not as straightforward as for the continuous-state model. In a previous article (Holt et al. 2003), it was found that with moderately strong selection, the distribution of average genotypic values in the sink tends to be strongly bimodal, with one peak near the source optimum and the other shifted slightly below the sink optimum; the former populations fluctuate at low numbers, whereas the latter are near carrying capacity. At any given time, the few populations found near the midpoint are in a brief transient phase of moving toward the sink optimum. We can thus use as a criterion for adaptation of a population that its mean genotype be closer to the sink than to the source optimum (i.e., genotypic value $> \theta/2$). The probability that a population becomes adapted in this sense increases with time. It was found for constant environments that the probability of adaptation over a given time horizon declines with the degree of sink maladaptation (Holt et al. 2003).

An alternative measure of adaptation comes from considering persistence following the cessation of immigration. We considered a sink population adapted if it persisted for at least 200 generations after immigration was discontinued. This criterion more directly corresponds to an assessment of niche evolution. For moderately strong selection, the two criteria produce virtually identical results (see below). Thus, local adaptation in the sense of a population matching the sink optimum amounts to niche evolution. For the results reported below, 400 populations were simulated for each combination of parameters to

determine the probability of adaptation per population after 1,000 generations of immigration and selection.

Niche Evolution in a Temporally Variable Sink

The above results for evolution in constant sink environments provide a baseline for understanding how temporal variability affects niche evolution and adaptation in the sink. Our basic protocol is to compare evolution in a constant sink environment, with evolution in a sink environment that is varying but with the same mean environmental conditions. We first consider a limiting case of the continuous-state model to demonstrate that moderate temporal variation can permit a sink population to escape a “trap” of maladaptation caused by gene flow.

Slow Variation in the Continuous-State Model

Consider the following simple thought experiment: imagine the sink habitat changes slowly, as compared to a population’s ability to respond to those changes. The population should then approximately track its genetic and demographic equilibria. We assume ceiling density dependence (as in fig. 1B) and that in the constant sink, $\theta > \theta_c$ by a moderate amount, so that alternative equilibria exist. As noted above, if the environment is constant, starting with immigrants with a mean genotype of 0, the population should approach the maladapted equilibrium. Now suppose that the degree of sink maladaptation, θ , varies slowly. If the environmental state falls below θ_c , there is no longer a maladapted equilibrium. If the degree of maladaptation stays below θ_c for a sufficient time, the population will evolve toward a state of adaptation near the local optimum. It will also increase in abundance. This leads to positive feedback between demography and evolution: increased local abundance weakens the effect of gene flow and so increases the effectiveness of local selection (Tufto 2001). Once adapted and near K , because of this reduction in gene flow, the population can continue to remain adapted, even if θ again increases slowly to well above θ_c (Lynch and Lande 1993)

Thus, slow temporal variation in θ that straddles θ_c can lead to adaptation in a population that would not adapt in an environment with constant θ , particularly given little or no density dependence at low densities in the sink. With strong negative density dependence in the sink at low densities in this model, there is only a single equilibrium for any θ (see fig. 1A; appendix), and so temporal variation will not provide an escape from gene flow. The positive effect of temporal variation upon local adaptation is thus more likely to be seen if negative density dependence is weak or absent in the sink habitat, permitting the existence of alternative evolutionary states (and the effect is likely

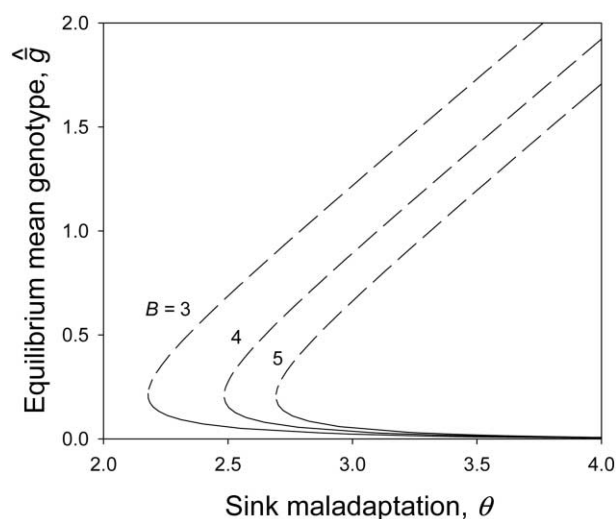


Figure 2: Mean equilibril genotype of a sink with recurrent immigration for different degrees of maladaptation and birth rates and no density dependence. Again, $\omega^2 = 1$, $P = 1.05$, $G = 0.05$, $I = 4$. B varies from 3 to 5. For visual clarity, the asymptotic states of adapted populations (heavy lines in fig. 1) are not shown. Increasing birth rates facilitates the likelihood of adaptation to the sink. A transient increase in births can permit a population to escape a trap of local maladaptation, and the adapted state may be retained after the environment returns to its initial state.

to be further enhanced if there is positive density dependence, i.e., Allee effects; Holt et al. 2004; R. D. Holt and M. Barfield, unpublished results).

This thought experiment shows that temporal variation can sometimes facilitate adaptation. However, the existence and magnitude of the effect depend on the amplitude of variation and the average state of the environment. Consider again figure 1B and imagine that θ varies slowly and continuously in a range $(\theta_{\min}, \theta_{\max})$ and that the population starts out in a maladapted state. The figure includes ceiling density dependence (similar forms arise with weak density dependence, as in fig. 1A). There is a value of θ , which we call θ' , above which the only equilibrium is the maladapted one and below which there is a zone with alternative equilibria. If $\theta_{\max} < \theta'$, then the population is expected to remain adapted. If instead $\theta_c < \theta_{\min}$, an initially maladapted population will stay maladapted. If $\theta_{\min} < \theta_c < \theta_{\max} < \theta'$, then temporal variation permits an escape from the maladapted state. Finally, if $\theta_{\min} < \theta_c < \theta' < \theta_{\max}$, then a population may alternate between adapted and maladapted states. Temporal variation thus may facilitate local adaptation but is likely to do so only for moderate variation in the local environment.

Adaptation can also be facilitated by slow temporal variation in parameters other than the degree of maladapt-

tation. Even if θ is constant, the system can shift from two to one stable equilibrium if variation in other parameters alters θ_c (which is determined by multiple parameters; see appendix). For example, curves of maladapted equilibria for several values of fecundity B (and no density dependence) are shown in figure 2. Increases in B shift the curve rightward. If B varies slowly, then when fecundity is high, the population can become locally adapted, which makes it more likely to maintain adaptation when fecundity is then reduced.

Sinusoidal Variation in the Continuous-State Model

If variation is more rapid, populations will not stay near equilibria. Numerical studies show that temporal variation may still permit adaptation to occur when it would not in a constant environment. An example is shown in figure 3, for which we assume that the population is initially at the maladapted equilibrium for $\theta = 2.7$ (solid dot in fig.

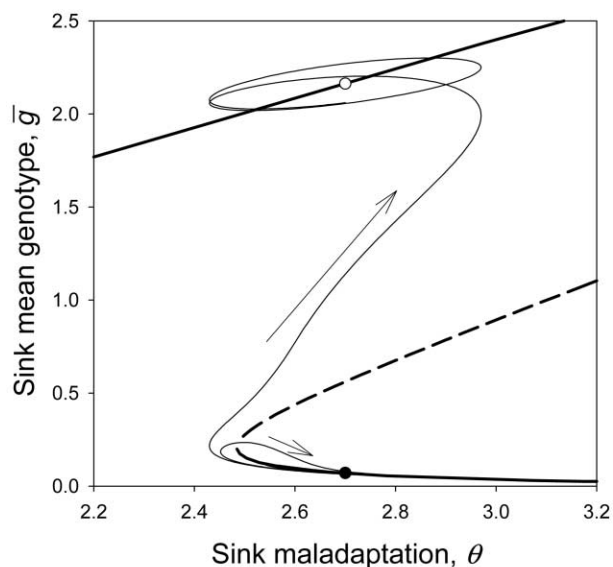


Figure 3: Phase plot of the dynamics of mean genotype of a sink with recurrent immigration in response to temporal variation in sink maladaptation. We assume that maladaptation in the sink is initially constant (and the population is at its evolutionary and demographic equilibrium) and then begins to vary in an oscillatory fashion, with waves of increasing amplitude but a fixed average. The amplitude remains constant after it reaches one-tenth the average. The particular form used to generate the figure is $\theta = 2.7(1 + a \sin 2\pi t/200)$, where t is the generation and $a = t/6,000$ until $t = 600$ and $a = 0.1$ thereafter. As in earlier figures, $\omega^2 = 1$, $P = 1.05$, $I = 4$, $B = 4$, $G = 0.05$; we here assume ceiling density dependence with $K = 256$. The dark lines indicate equilibria (solid for stable; dashed for unstable), as in figure 1B. Temporal variation permits the initially maladapted population to escape maladaptation and adapt to the sink environment.

3). Sinusoidal variation in θ is gradually introduced, with the cycle amplitude increasing linearly with time until it plateaus at 0.27 (after which it remains constant). The figure shows the trajectory of the population's average genotype, superimposed on the corresponding equilibria of the temporally constant system (from fig. 1B). Initially, the average genotype fluctuates but stays near the maladapted equilibrium. However, as the amplitude of variation grows, θ reaches values for which there is no maladapted equilibrium ($\theta < \theta_c$), and the population starts to adapt. In this example, there is not sufficient time to adapt during the first cycle for which θ drops below θ_c , but the following cycle is larger and allows adaptation to proceed further and population size to increase (not shown). When θ then returns again to values for which there are two stable equilibria (i.e., $\theta > \theta_c$), the population does not return to the maladapted state but instead approximately tracks the local adapted equilibrium. If the environment then returned to and stayed constant at its initial value of $\theta = 2.7$, the population would persist at its new, adapted equilibrium (open dot in fig. 3).

This evolutionary transition reflects a transient escape from gene flow, mediated by increases in population size when the environment is temporarily more favorable. If we take this example and assume that the gene flow parameter (m_i in eq. [3a]) is fixed at its initial value instead of varying with N and then iterate equations (2a) and (3a), we find that the genotypic state merely fluctuates between 0.062 and 0.075. In this case, no adaptation occurs because we have eliminated the feedback effect of population size on gene flow.

Sinusoidal variation may reflect seasonal or multiannual cycles in abiotic (e.g., climate) or biotic factors (e.g., predator-prey cycles). Whether or not local adaptation occurs in the sink depends on the mean, amplitude, and frequency of variation in θ . As noted for slow variation, there tends to be a nonmonotonic relationship between the magnitude of temporal variation and the likelihood of adaptation; adaptation increases with moderate variation and then decreases at high variation. For a given amplitude of variation, the effect tends to be reduced at higher frequencies of variation (results not shown).

Random Variation in the Continuous-State Model

Temporal variation is often random. We carried out numerical studies of the continuous-state models (2)–(4), incorporating stochastic variation in model parameters comparable to those used in the individual-based model (see below). The selection strength parameter ω^2 was set to 1, the additive-genetic variance G was 0.05, and the nonadditive variance was 1. This gives a heritability (G/P) of 0.0476. Simulations were run for the models (2)–

(4) with ceiling density dependence using $K = 256$. At the end of 1,000 generations of immigration, a population was considered adapted if its average genotype was closer to the mean sink optimum than to the source optimum.

We first introduced random temporal variation in the degree of sink maladaptation, drawing θ from a normal distribution with mean $\bar{\theta}$ each generation. In figure 4A, consecutive values of θ were drawn independently. The graph shows the probability of adaptation at generation 1,000 as a function of $\bar{\theta}$ for four levels of variation in θ (indicated by the coefficient of variation [CV], the standard deviation of θ divided by $\bar{\theta}$). With no variation (heavy line in fig. 4A), adaptation is always attained for means < 2.485 but never occurs for higher values. This agrees with the threshold value $\theta_c = 2.485$ calculated for the constant environment model above. As before, the likelihood of adapting varies nonmonotonically with the magnitude of temporal variation. For small to moderate CVs (0.1 and 0.2), the probability of adaptation increases for $\bar{\theta}$ slightly above the threshold. For higher variation (CV = 0.4), the probability of adaptation can decline, so that even populations encountering environments with $\theta < \theta_c$ can fail to adapt. Thus, moderate levels of uncorrelated temporal variation can foster adaptation, while higher levels tend to inhibit adaptation. However, the effect appears rather modest.

Figure 4B is the same as figure 4A except that consecutive values of θ are now strongly, positively correlated (with correlation coefficient of 0.9). Small to moderate amounts of variation once again increase the probability of adaptation when mean maladaptation is above the threshold θ_c . The effect is quantitatively much more pronounced than observed with uncorrelated variation. With $\bar{\theta}$ above the threshold, there is a stable maladapted equilibrium in a constant sink. Temporal variation can produce transient phases when the sink maladaptation is below the threshold. As with slow or low-frequency sinusoidal variation, at these times the system can adapt sufficiently so that it can continue to remain adapted even when the environment deteriorates again.

Autocorrelation does not influence the overall probability of the environment being below the threshold for local adaptation. However, following environmental change, there is always an evolutionary lag as the population shifts toward the new optimum (Lynch and Lande 1993). With uncorrelated variation, there will usually be little evolution before the environment changes again. With correlated variation, the population may have time to overcome much of the evolutionary lag and thus track changes in the environment (see Lande and Shannon 1996 for a similar result).

With large magnitudes of environmental variation, the probability of adaptation may be substantially lower than

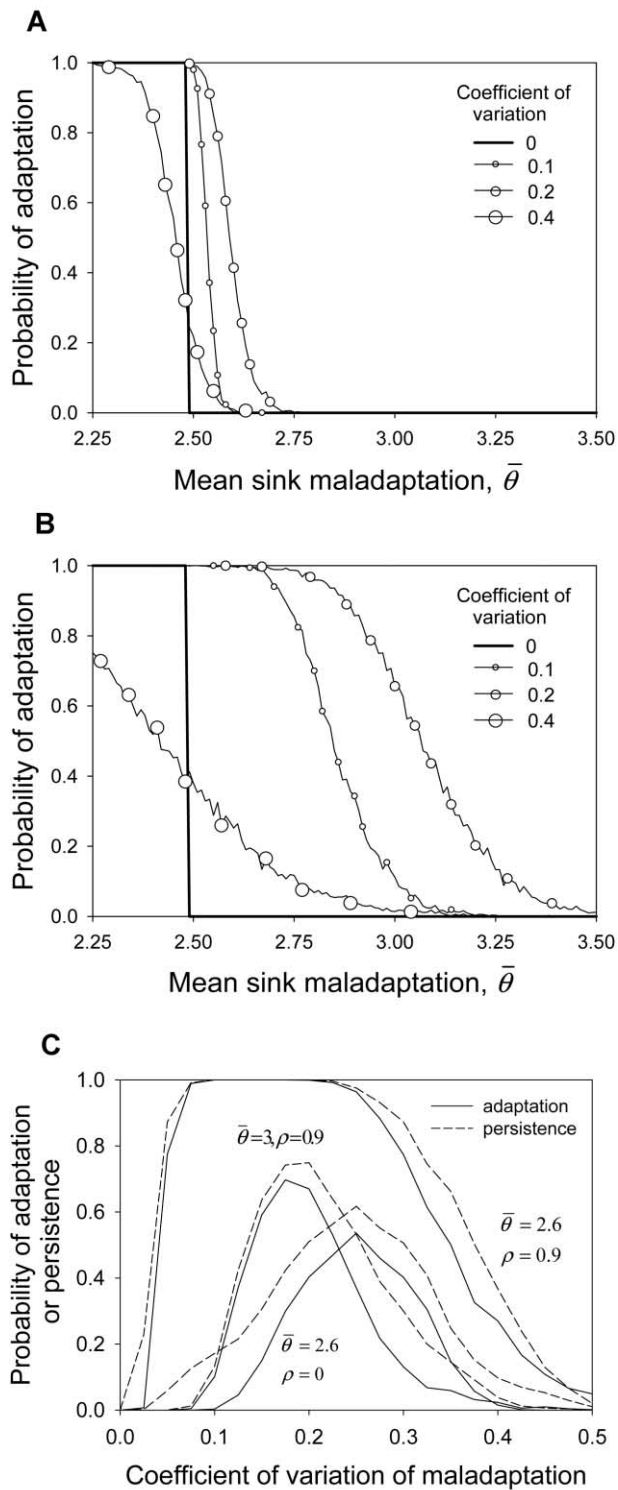


Figure 4: Probability of adaptation after 1,000 generations as a function of mean sink maladaptation for different coefficients of variation of sink maladaptation for the continuous-state model with ceiling density dependence (parameters as in fig. 3). *A*, The degree of sink maladaptation

in a constant environment for values of $\bar{\theta}$ below the threshold value describing adaptation in a constant environment (fig. 4*B*). One reason for the inhibition of adaptation by large-magnitude variation is that θ can change so strongly that the population lags well behind the environment. Thus, there are phases when the population dives to very low sizes and becomes maladapted due to relatively high gene flow from the source. This is more likely with larger amplitude variation. Consistent with this suggestion, we found that the probability that a population is at carrying capacity at the end of a simulation follows the same pattern as figure 4*A* and 4*B* but that the probability that the population reaches carrying capacity at any point in the 1,000 generations continues to increase as variation increases. This suggests that populations are indeed becoming adapted when environmental variation is high but do not remain adapted. In a strongly fluctuating sink environment, one might thus observe a pattern of alternating phases of local adaptation and local maladaptation.

In figure 4*C*, we show the probability of adaptation (*solid lines*) as a function of the magnitude of variation. The probability of adaptation is maximized for moderate variation. We also examined whether populations are able to persist if immigration is discontinued (as in the individual-based model above). Because strict extinction is precluded in the continuous-state model and evolution eventually rescues declining populations, we tested for niche evolution by assigning a threshold density below which the population would likely be on the brink of extinction in a more realistic model (e.g., with demographic stochasticity). Immigration was discontinued after 1,000 generations, and any population that dropped below a threshold of two individuals after that was considered effectively extinct. Results based on this persistence criterion (fig. 4*C*, *dashed lines*) were similar to those using our criterion for local adaptation. This supports our suggestion that adaptive evolution leads to a permanent expansion in the niche, so that a species can persist where it originally faced extinction without evolution.

θ is an uncorrelated normal random process with mean equal to the abscissa and standard deviation equal to the product of the indicated coefficient of variation and the mean. *B*, Same as *A*, except the variation has an exponential autocorrelation function with a correlation coefficient of 0.9 between sink maladaptation in consecutive generations. The magnitude of the effect of temporal variation is enhanced, compared with uncorrelated environments. *C*, The probability of adaptation and persistence (defined as a population that does not drop below two when immigration is discontinued) for different coefficients of variation in the degree of sink maladaptation; $\bar{\theta}$ indicates the average sink maladaptation and ρ the autocorrelation. The likelihood of adaptation and persistence is influenced by the average degree of maladaptation, the magnitude of variation, and the degree of autocorrelation.

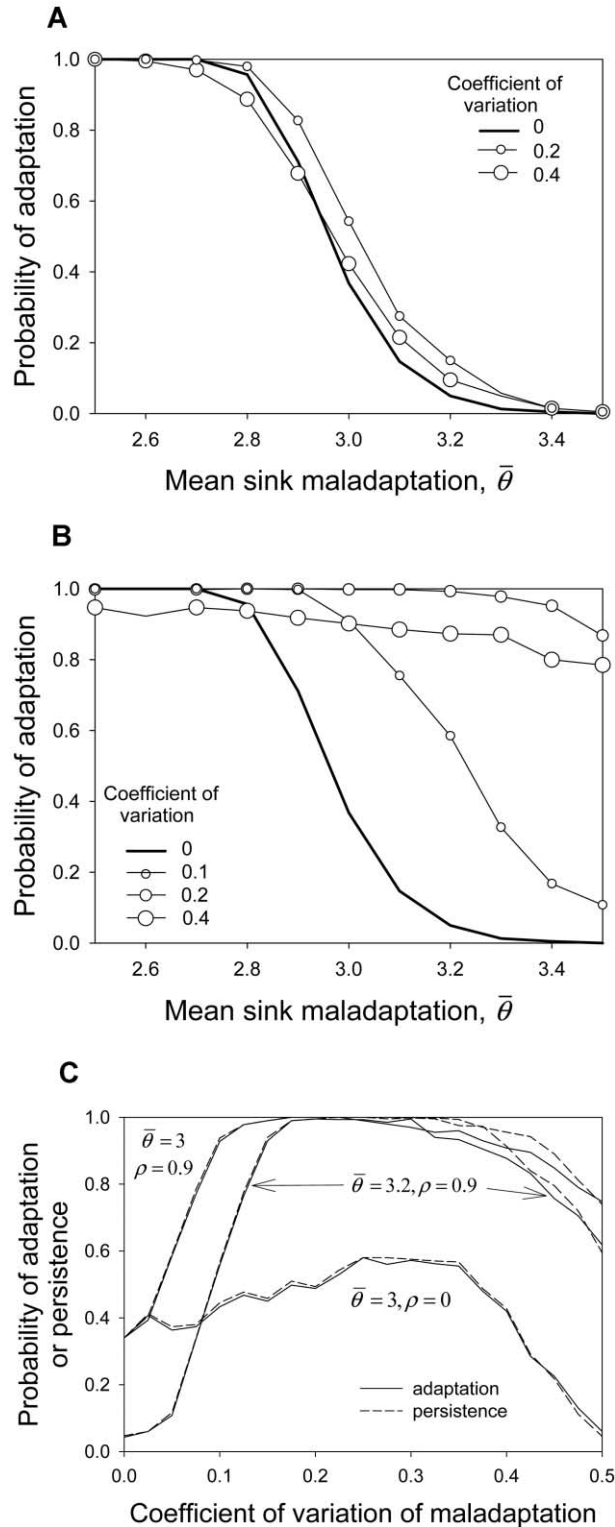


Figure 5: Probability of adaptation after 1,000 generations for temporal variation of sink maladaptation in the individual-based model. **A**, The sink maladaptation was an uncorrelated, normal random process with mean given by the graph's abscissa and standard deviation equal to the

Finally, we considered variation in parameters of the model other than θ (e.g., birth rates). We do not present these results in detail, because quite comparable patterns emerge: an intermediate magnitude of autocorrelated variation can facilitate adaptation to the sink, whereas large-magnitude variation can make adaptation more difficult.

Temporal Variation in the Individual-Based Model

All the patterns of temporal variation examined in the continuous-state model were also examined in the individual-based model, and comparable effects were observed. For brevity, we confine discussion to the effects of random normal variation of θ on probability of adaptation. With uncorrelated variation, moderate levels of variation of θ produce a slight positive effect that is lost at higher coefficients of variation (fig. 5A). With positively autocorrelated values of θ , the probability of adaptation increases more substantially with the coefficient of variation up to 0.2 (fig. 5B). Above this, the probability decreases slightly with increasing variation. The decrease in probability of adaptation with high variation is seen even at low $\bar{\theta}$ (for which there is a high probability of adaptation without temporal variation). We also directly tested for niche evolution by discontinuing immigration (after 1,000 generations) and assessing the probability of persistence of the sink population over 200 more generations. Figure 5C depicts the probabilities of adaptation and of persistence as functions of the coefficient of variation of θ . Both criteria give essentially identical results: intermediate levels of variation enhance adaptation and persistence, particularly with high serial autocorrelation in the environment.

Results for the individual-based model thus closely parallel those found in the continuous-state model. However, the negative effect of high levels of variation on adaptation and niche evolution appears more pronounced with the continuous-state model than with the individual-based

product of the indicated coefficient of variation and the mean maladaptation. Parameters used were carrying capacity $K = 256$, number of loci $n = 10$, mutational input per haplotype $\eta\mu = 0.01$, mutational variance $\alpha^2 = 0.05$, strength of selection $\omega^2 = 1$, and immigration rate $I = 4$; births per pair were binomial with parameters 16 and 0.5. **B**, Same as **A**, except the variation has an exponential autocorrelation function with a correlation coefficient of 0.9 between sink maladaptation in consecutive generations. Autocorrelation facilitates adaptation to the sink. **C**, The probability of adaptation and persistence (characterized as a population that survives for 200 generations after immigration is discontinued) for different coefficients of variation in sink maladaptation; $\bar{\theta}$ indicates the average sink maladaptation and ρ the autocorrelation. Adaptation to the sink and ability to persist in the absence of immigration (i.e., niche evolution) have essentially identical patterns.

model (cf. figs. 4, 5). There are likely to be several reasons for this difference, which we address in the "Discussion."

For the results presented above, we compared a variable environment with an environment that is constant at the average value of the varying parameter. Since survival of a closed population with discrete generations depends on its geometric mean fitness, we might instead have used for comparison an environment fixed at the parameter value that gave the same geometric mean fitness as in the varying environment. For varying sink maladaptation (figs. 4, 5), it can be shown that the constant parameter giving the same geometric mean fitness is $\bar{\theta}(1 + CV^2)^{1/2}$, which is greater than $\bar{\theta}$. For all the comparisons made above between constant and variable environments, the variable environments have lower geometric mean fitnesses. Nonetheless, we have shown that adaptation can sometimes occur more rapidly in the variable environments. This contrasts with comparisons of populations with differing degrees of constant maladaptation, where adaptation is harder when initial fitness is lower (Holt et al. 2003; e.g., thick solid lines in fig. 5A).

Discussion and Conclusions

The basic idea we have explored can be stated quite simply: if a sink habitat is variable, there may be times when it is temporarily a milder sink, or even not a sink at all, for immigrants from the source. With positive temporal autocorrelation, this provides a window of opportunity for adaptation by natural selection, which in turn permits an increase in population size. This then enhances the likelihood that the population can persist and remain adapted (e.g., in the face of gene flow), even when the environment shifts back to its original state. Temporal variation in some circumstances may permit a species to bootstrap through niche space (Holt and Gaines 1992) and to successfully occupy habitats from which it initially tended to be excluded.

We have shown here using two distinct but complementary models that temporal variation in sink environments can provide an "escape valve" for populations trapped in maladaptive states, permitting adaptation that would not be expected in constant but otherwise similar sinks. We suggest that temporal variation will tend to enhance local adaptation and niche evolution in a sink with recurrent immigration from a source, if the magnitude of such variation is moderate, if such variation is strongly, positively autocorrelated (leading to runs of "good" years, permitting a population to increase in abundance while it is honing its local adaptation), and if density dependence is negligible at low densities. The effect of positive autocorrelation is similar to a result in Lande and Shannon (1996), who showed for closed populations that evolu-

tionary loads can be reduced by environmental variation with a long autocorrelation time.

The results we have reported assume that genetic variance and heritability are low. This is reasonable for some traits that determine performance (e.g., metabolic traits; Bacigalupe et al. 2004). In the continuous-state model (eqq. [2]–[4]), increasing heritability makes it more likely that there will be alternative stable equilibria (one maladapted, one adapted), even with stronger density dependence, amplifying the potential impact of temporal variation upon adaptation in the sink (results not shown). In the individual-based model, an increase in mutation rate or weakening of selection in the source and sink can increase the standing crop of variation, increasing the overall rate of adaptation to the sink (Holt et al. 2003; R. D. Holt and M. Barfield, unpublished results).

The results from our two models are broadly similar, in that moderate temporal variation can facilitate niche evolution, while larger variation can hamper evolution, in both cases particularly when such variation is autocorrelated. This congruence makes sense, given that the individual-based model also includes the opposing forces of gene flow and selection. The major qualitative difference between the models is that the negative effect of large-scale variation appears to be somewhat weaker in the individual-based model. We believe there are several mechanisms at play in the individual-based model that contribute to this difference. One is that the inhibitory effect of gene flow from the source on the average sink genotype is likely to be larger in the continuous-state model, which uses the usual quantitative genetics assumption of a normal distribution of genotypes (with constant variance) after reproduction. In essence, immigration in the deterministic model pulls the entire genotypic distribution toward that of the source (with its mean of 0). However, the individual-based model can generate nonnormal genotypic distributions. Immigrants in that model tend to fatten the lower tail of the genotypic distribution after reproduction (due to the contribution of offspring of new immigrants) without affecting the main support of the distribution (the result of mating among sink residents). This distribution likely leads to a higher average fitness than does a normal distribution, which in turn makes the population more resistant to gene inflows and so more likely to adapt.

Differences between the two models may also trace to sources of variation exclusive to the individual-based model. In that model, the source population is in a selection-mutation-drift balance, but the mean genotype fluctuates around the (fixed) source optimum over time and produces corresponding fluctuations in the mean immigrant genotype. Moreover, immigrants are a random sample from this population; sampling variation can create fluctuations in the immigrant distribution. Adaptive evo-

lution in the sink may reflect drawing by chance immigrants relatively closer to the sink optimum than the source mean used in the continuous-state model. This effect can explain the observation that increasing the number of immigrants per generation can facilitate adaptive evolution in constant sink environments (as in the single-locus model considered in Gomulkiewicz et al. 1999). A similar positive effect of immigration on adaptation was found using the individual-based model (Holt et al. 2003), but in this case the increase in adaptation with increased immigration could also be partially caused by the small Allee effect introduced by our assumption of monogamous mating (see Holt et al. 2004).

A reviewer has made the interesting suggestion that temporal variation in this model may facilitate niche evolution because episodes of very harsh conditions clear out maladapted individuals from the sink, making it easier for immigrants who by chance have better-adapted genotypes to increase. We have analyzed the individual-based model with a pulse of one-time, rather than recurrent, immigration. In this case, immigrants always invade an empty sink, there are no residents to clear out, and gene flow obviously cannot swamp local selection (since immigration occurs in single pulses). Yet the probability of persistence is again a decreasing sigmoidal function of sink maladaptation, and a moderate degree of autocorrelated temporal variation appears to facilitate adaptive evolution in harsh sink environments. We will present these results elsewhere (R. D. Holt, M. Barfield, and R. Gomulkiewicz, unpublished manuscript) in the context of examining the evolutionary dynamics of exotic invasive species. In short, if a nonlinear function $P(\theta)$ describes the probability of adaptation given a fixed degree of sink maladaptation and if θ fluctuates around a mean $\bar{\theta}$, nonlinear averaging leads to a systematic deviation of the expected probability from $P(\bar{\theta})$. In harsh environments, in the models we have considered, $P(\theta)$ is concave upward, so by using an argument based on Jensen's inequality one can show that strongly autocorrelated temporal variation can be expected to enhance the probability of adaptation. For this reason (coupled with the argument presented above on how increases in fitness indirectly reduce the swamping effect of gene flow through an effect on population size), it appears that the evolutionary boost the population seems to get during transient periods that are better than average outweigh the negative effect of periods that are worse than average.

Finally, in the individual-based model, genetic variation is not fixed but instead emerges from the interplay of mutation, selection, and drift (in both source and sink) and immigration (in the sink). Immigration can facilitate local adaptation in the sink via the infusion of genetic variation from the source (for alternative models leading to this conclusion, see Gomulkiewicz et al. 1999; Barton

2001). In a constant environment, we have shown that the maladapted state in this model is only quasi-stable (Holt et al. 2003); eventually, even in a harsh sink, given recurrent immigration from the shifting genetic milieu of the source, along with in situ mutation and recombination, the sink population hits the jackpot in the genetic sweepstakes, and adaptation occurs sufficiently to permit population persistence in the absence of immigration. If temporal variation permits the sink population to increase in abundance for a period, this then permits it to more effectively retain genetic variation during that period, and therefore it should be able to respond more effectively to local selection pressures in the sink. A task for future work will be to assess the relative importance of each of the mechanisms sketched above, all of which can influence adaptive evolution in varying sink environments.

We have focused on the evolutionary consequences of persistent temporal variation in a sink, given a source with a constant environment. It is useful to consider briefly some alternative scenarios. For instance, the source, rather than the sink, may be variable. If variation is sufficiently slow and not too extreme, the source population should be able to track the local moving optimum. By chance, in some years this optimum will be closer to the optimum in the sink, and there is an increased likelihood of observing adaptation in the sink. To explore the magnitude of this predicted effect, we performed simulations using the above individual-based model in which the phenotypic optimum of the source rather than the sink varied as a correlated normal random process. We obtained results very similar to those shown in figure 5B for low-to-moderate magnitudes of variation (up to a coefficient of variation of 0.2). For higher levels of variation in the source, however, the probability of adaptation in the sink continues to increase. This monotonic influence of temporal variation in the source on adaptation to the sink contrasts with the pattern of effects arising from variation in the sink, where intermediate levels of variation provide the best conditions for adaptation to the sink environment.

The differential impacts of variation in the source and sink on the potential for adaptation to the sink reflect the importance of demographic constraints on evolution. If variation is present in the sink habitat, the sink population must track the continually changing local phenotypic optimum. With higher magnitudes of variation, the absolute rate of change of the local optimum can increase to a point at which the population can no longer track this optimum (Lynch and Lande 1993). The sink population becomes maladapted again because the average fitness drops below 1, the population size declines, and gene flow (among other factors such as loss of variation, not to mention local extinction) corrodes local adaptation. With temporal variation located in the source (but not sink) optimum, how-

ever, once the sink population becomes adapted and increases in numbers, it can remain adapted. A large magnitude of temporal variation in the source, correlated with evolutionary shifts in the population there, can lead to periods in which immigrants are less maladapted to the sink habitat, which thus facilitates niche evolution there.

We performed simulations in which both source and sink phenotypic optima varied independently with equal variance and autocorrelation. The increase in adaptation probability of the sink at small magnitudes of variation is greater than with either source or sink variation alone. At higher levels of variation, there was a tendency for the probability of adaptation to decline, and the global population could go extinct. Finally, one can imagine scenarios in which environments that are normally stable go through a transient phase of instability. Figure 3 provides an example showing how a pulse in instability can facilitate evolutionary transitions in a species' niche.

It is instructive to contrast our results for open sink populations to those of earlier authors examining adaptation to changing environments for closed populations. Bürger and Lynch (1995) used a very similar individual-based model (indeed, ours is based on theirs) to examine the time to extinction in isolated single populations with fixed or linearly changing local optima. When random variation was added to both environmental scenarios, increased variation resulted in earlier extinction. These authors considered only uncorrelated variation. Here, we likewise found that uncorrelated changes have little effect at low variances and generally negative effects on adaptation at high variances. Lande and Shannon (1996) analyzed a continuous-state and continuous-time model and derived expressions for genetic load (loss in fitness due to genetic and evolutionary factors). They considered directional, sinusoidal, uncorrelated random, and positively autocorrelated random variation in optimum phenotypes. In general, an increase in the rate of directional environmental change or in the magnitude of environmental variability increased the genetic load of the population, which will make it harder for a population to persist. Moreover, populations that evolve in response to transient environmental changes could be exposed to increased extinction risk.

In short, it appears that temporal variation in closed environments may make it more difficult for populations to adapt so as to facilitate persistence. This contrasts with our results, which show that temporal variation can at times facilitate adaptive evolution to the sink, permitting a population to persist in a habitat in which it originally could not. The reason for this difference, we suggest, is that the spatial coupling between a stable source and a sink provides both an ecological and evolutionary rescue, permitting a lineage to be exposed to novel conditions

without necessarily endangering its continued persistence and without expunging the genetic variation needed for adaptive evolution to occur. An open question then is how weak the coupling can be before its role in rescuing a variable sink is irrelevant.

It is likely that the effect we have explored pertains to some niche dimensions more than to others. A given habitat can be a sink for many reasons. For instance, if the habitat of a plant species is a sink because of unfavorable edaphic factors (e.g., soil chemistry), it is likely that this unfavorable feature of the environment changes very slowly, if at all, over timescales relevant to local adaptation. By contrast, if the species in question is a vulnerable prey species that is consumed by a resident generalist predator (whose presence creates a demographic sink for the prey, for which mortality exceeds local births), the intensity of such predation will vary temporally depending on the population dynamics of the predator itself and the temporal pattern of availability of alternative prey (e.g., spikes in the abundance of alternative prey may lead to switching and fewer predator attacks on a rare prey species present in a sink). Many populations show dramatic fluctuations, typically with short-term positive autocorrelation or periodic cycles (Turchin 2003). Thus, if a sink exists because of a shortage of a biotic resource or because of predation pressure, our results suggest that population dynamics in the resource or predator can make local adaptation in the sink habitat, and hence niche evolution, more likely. Evolutionary lability in traits related to interspecific interactions may thus be more likely in communities with unstable than with stable dynamics. Reznick and Ghalambor (2001), in a recent review of empirical studies of rapid evolution, found that evolution is often associated with periods of population growth. This is consistent with the theoretical scenarios we have explored here; increases in local fitness increase population size, particularly if density dependence is weak in the sink habitat, and thus can facilitate adaptive evolution.

As a concluding thought, we note that these theoretical studies potentially bear on a number of broad topics in evolutionary biology. There has been considerable recent interest in developing a theoretical understanding of the combined ecological and evolutionary dynamics of species' range limits (e.g., Kirkpatrick and Barton 1997; Case and Taper 2000; Holt 2003). If populations at the edges of ranges are maintained as demographic sinks (Keitt et al. 2001), evolution permitting local adaptation and an ultimate shift in the range limit is more likely if there is temporal variation in those sinks than if the sinks experience a chronic poor environment. Moreover, if one considers parasites, pathogens, and small-bodied herbivores, their hosts are in many ways akin to "habitats." We suggest that a fruitful arena for application of the growing body

of theory on niche conservatism and theoretical evolution will be the topic of host range expansion and shifts, including the public health issue of characterizing the evolutionary dimension of emerging diseases. These models may also provide insight into the evolutionary dynamics of potentially invasive species introduced into novel environments, particularly when invasion occurs into a heterogeneous landscapes, including sites within as well as outside the initial niche of the introduced species (R. D. Holt, M. Barfield, and R. Gomulkiewicz, unpublished manuscript).

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