

Allee Effects, Immigration, and the Evolution of Species' Niches

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ABSTRACT: Theoretical studies of adaptation to sink environments (with conditions outside the niche requirements of a species) have shown that immigration from source habitats can either facilitate or inhibit local adaptation. Here, we examine the influence of immigration on the evolution of local adaptation, given an Allee effect (i.e., at low densities, absolute fitness increases with population density). We consider a deterministic model for evolution at a haploid locus, and a stochastic individual-based model for evolution of a quantitative trait, and several kinds of Allee effects. We demonstrate that increased immigration can greatly facilitate adaptive evolution in the sink; with greater immigration, local population sizes rise, and because of the Allee effect, there is a positive indirect effect of immigration on local fitness. This makes it easier for alleles of modest effect to be captured by natural selection, transforming the sink into a locally adapted population that can persist without immigration.

Keywords: niche evolution, source-sink, Allee effect, local adaptation, sex ratio, individual-based model.

To a first approximation, the edge of a species' range is governed by its niche requirements (Brown and Lomolino 1998). A species' niche is an abstract characterization of those environmental factors that permit that species' populations to persist (Hutchinson 1957). Given dispersal, however, populations can be sustained in habitats with conditions outside the niche—"sink" habitats (Holt 1985; Pulliam 1988). Without immigration, sink populations face extinction because deaths exceed births (e.g., because of unfavorable abiotic conditions, scant resources, or intense predation). With immigration, sink population size

reflects the immigration rate, the average rate of population decline, and temporal variation in local growth rates (Gonzalez and Holt 2002; Holt et al. 2003a).

Over evolutionary timescales, a sink habitat will remain a sink for a species only if natural selection does not sculpt adaptations that permit it to utilize that habitat. How does the rate of immigration into the sink influence the likelihood of such adaptation? Theoretical studies in recent years have clarified the diverse ecological and genetic influences of dispersal on local adaptation and the evolution of species' niches, including to sink habitats (Holt and Gaines 1992; Hedrick 1995; Kawecki 1995, 2000; Holt and Gomulkiewicz 1997b; Kirkpatrick and Barton 1997; Gomulkiewicz et al. 1999; Case and Taper 2000; Ronce and Kirkpatrick 2001; Tufto 2001; Kawecki and Holt 2002; LeNormand 2002; Holt et al. 2003b). In this note, we examine how Allee effects—positive relationships between individual fitness and density (Courchamp et al. 1999; Stephens and Sutherland 1999)—influence adaptation to sink environments. The existence of Allee effects can blur what constitutes the "niche" of a species, since a population may persist in a habitat at high but not at low densities. Here, we focus on situations in which an Allee effect exists, but nonetheless, without local adaptation to the habitat, the population will not persist at any density if closed to immigration.

Immigration can have both positive and negative effects on local adaptation to sink habitats (Gomulkiewicz et al. 1999; LeNormand 2002). Without immigration from the source, a species will not experience the sink conditions at all, and so there will be no direct selection for adaptation to the sink. Gene flow potentially provides a potent source of genetic variation on which local selection can act (Hedrick 1995; Gomulkiewicz et al. 1999). Conversely, immigration can prevent local adaptation if gene flow swamps local selection (Mayr 1963; Antonovics 1976). Finally, immigration indirectly influences the likelihood of adaptation, because immigration typically increases population size (Holt 1983a, 1983b), which in turn changes local fitness if there is density dependence. Even if selection is density independent (i.e., relative fitnesses are density in-

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dependent), changes in fitness due to density dependence alter the potential for locally favored alleles to increase because of selection (Gomulkiewicz et al. 1999; Kawecki and Holt 2002).

Prior studies of the interaction between gene flow and selection (including those focused on sink populations) have assumed negative density dependence (e.g., logistic growth in Kirkpatrick and Barton 1997; Case and Taper 2000; nonlogistic negative density dependence in Gomulkiewicz et al. 1999; Kawecki and Holt 2002). However, in many species, populations at low density experience Allee effects, where death rates decline (or birth rates increase) with increasing abundance. A large and growing list of mechanisms are known to generate Allee effects (see "Discussion"). There has been a recent explosion of interest in the ecological importance of Allee effects (e.g., Courchamp et al. 1999; Stephens and Sutherland 1999). For instance, Allee effects can increase the probability of extinction in single populations (Dennis 1989, 2002; McCarthy 1997; Lande 1998; Poggiale 1998; Courchamp et al. 1999; Berec et al. 2001) and in metapopulations (Amarasekare 1998; Lande et al. 1998; Brassil 2001; Etienne et al. 2002), slow the rate of expansion of introduced species into new territory (Shigesada et al. 1995), cause range expansion to stop entirely if suitable habitat is patchy (Keitt et al. 2001), and even create alternative community states (e.g., Holt 1977, pp. 211–212; Amarasekare 2000).

By contrast, little attention has been given to the potential evolutionary significance of Allee effects. Morris (2002) notes that Allee effects in sink populations imply that immigration boosts local fitness. We suggest that because of this demographic impact, Allee effects make it more likely that moderate rates of immigration will facilitate, rather than hamper, the initial stages of local adaptation in unfavorable habitats. To support this suggestion, we present results from theoretical studies of adaptation in sink environments, explicitly incorporating Allee effects into dynamic models that track changes in both population size and genetic composition.

Previously (Holt and Gomulkiewicz 1997a, 1997b; Gomulkiewicz et al. 1999), we have shown that an absolute fitness criterion describes the condition for the initial increase in frequency of a rare allele in a sink. The basic idea can be explained without mathematical formalism. A sink habitat by definition is one in which immigrants have expected fitness less than unity, so individuals in the sink on average leave less than one offspring behind. For simplicity, assume genetic variation arises at a single haploid locus in the sink population (considering diploid variation complicates the algebra without changing the conclusions; Gomulkiewicz et al. 1999). Assume the mutant has higher relative fitness than does the immigrant type. If the absolute fitness of the mutant is less than unity, then each

generation one expects fewer copies of that allele than in the previous generation. Turning this around, for selection to increase the frequency of this locally favored type, absolute fitness of the novel mutation has to exceed unity so that copies of the allele will be able to increase in numbers over time. If most mutants have a small effect on fitness (measured against the fitness of the immigrant type), most will have absolute fitnesses <1 , and hence evolution of adaptation to the sink will be very slow (Gomulkiewicz et al. 1999; Holt et al. 2003b).

We have previously argued that given density dependence, a rare allele with high relative fitness in the sink population is most likely to establish when the immigration from the source to sink is at an intermediate rate (Gomulkiewicz et al. 1999). If immigration is very low, evolution in the sink population is hampered by a low rate of sampling of the genetic diversity of the source. If immigration is too high, migrants reduce both the frequency of the rare allele in the sink and the absolute fitness of the entire sink population (thereby making it less likely that any given mutation will have an absolute fitness exceeding 1). However, in Gomulkiewicz et al. (1999), we assumed negative density dependence, even at low density. Here, we show that Allee effects can substantially magnify the positive effect of immigration on local adaptation. We use two models to illustrate this effect. The first is a simple deterministic model for evolution at a haploid locus, which provides an analytic criterion for the increase of an allele when rare. The second is an individual-based model that describes evolution of a single quantitative trait; this model incorporates mutation, drift, and demographic stochasticity and so permits an evaluation of the rate of evolution in a sink. We consider a simple landscape with two habitats, one a sink, the other a source. For simplicity, we assume that if there is emigration from the sink, those emigrants (or their descendents) do not reenter the source habitat and so, in effect, are lost from the system. We also assume that the source habitat is at an evolutionary equilibrium.

Haploid Genetic Variation

Consider first a population with discrete generations and haploid variation. Assume the source is fixed for one type and that $R_i(N)$ is the absolute fitness of immigrants of this type in the sink (N is total sink population density, summed over genotypes). Likewise, $R_r(N)$ is absolute fitness of the alternative type. Fitness is assumed to be density dependent (for summed density over both types) with Allee effects at sufficiently low N . Because the habitat is a sink for the immigrant, $R_i(N) < 1$ for all N . We further assume a constant number of immigrants per generation, I . When considering the immigrant type alone, its nu-

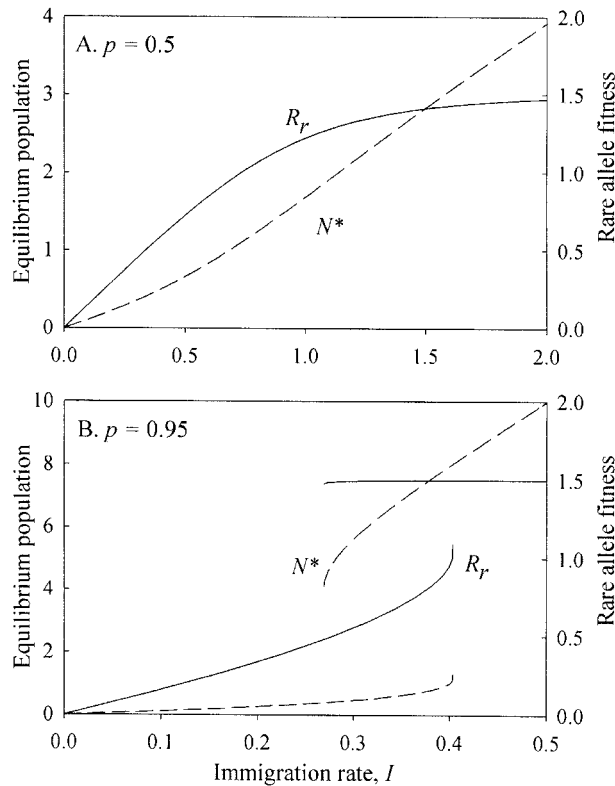


Figure 1: Relationship between equilibrium sink population density, N^* , the absolute fitness of the rare allele, R_r , and the rate of immigration from the source to the sink, I , when the relative fitness of the immigrant allele, p , is (A) 0.5 and (B) 0.95. Other parameters are $\mu = 1$ and $q = 1.5$.

merical dynamics are described by $N_{t+1} = R_t N_t + I$. The equilibrium population, N^* , is found by solving $N^*[1 - R_r(N^*)] = I$.

When the novel type is introduced at low density, its initial dynamics are defined by $N'_{t+1} = R_r(N^*)N'_t$, so it will increase in abundance (and frequency) if and only if $R_r(N^*) > 1$. By the chain rule, $dR_r/dI = (dR_r/dN^*)(dN^*/dI)$. In general, $dN^*/dI > 0$ (Holt 1983a, 1983b). At low densities, $dR_r/dN^* > 0$ because of Allee effects. Hence, at sufficiently low densities, $dR_r/dI > 0$, so increasing immigration enhances the initial fitness of the novel genotype. All else being equal, this makes it more likely that a given allele with higher relative fitness will increase in frequency in the sink environment (because it is more likely to have an absolute fitness exceeding 1).

To provide a concrete example, assume that over the range of densities exhibiting an Allee effect, $R_i = p(1 - e^{-\mu N})$ and $R_r = q(1 - e^{-\mu N})$, so relative fitness is density independent but absolute fitness increases with N . For the habitat to remain a sink for the immigrant type at all

densities, $p < 1$. The novel type is selectively favored in the sink if $q > p$. Because of the absolute fitness criterion, this inequality is necessary, but not sufficient, for evolution to capture this locally favored allele.

As expected, when the immigrant is alone, increasing immigration increases the equilibrium sink population density (fig. 1A, dashed line). (We use $\mu = 1$ for figs. 1 and 2. Using a different μ gives identical figures with the N^* and I axes rescaled by a factor of $1/\mu$.) Absolute fitness of the rare allele, R_r , increases asymptotically (toward q) with increasing I (fig. 1A, solid line). At rates of immigration such that $R_r > 1$, the rare allele increases in the sink. For each I , there is a single equilibrium population size and absolute fitness of the rare allele for most values of p . However, when p exceeds $e^2/(e^2 + 1)$ (about 0.88), there are three equilibria for some values of I (fig. 1B; the upper and lower equilibria are stable, whereas the middle equilibrium is unstable and not shown). Figure 2 depicts the maximum fitness of the locally favored type (q) needed for it to increase when rare as a function of immigration rate (for $p = 0.5$ or 0.95). The locally favored allele increases for q above the boundary line (given two stable equilibria for the immigrant, the lower q boundary shown in the figure applies when the immigrant is at its higher equilibrium density).

As I increases, N^* for the immigrant increases, in turn increasing the fitness of the locally favored type (because of the Allee effect). This reduces the selective advantage needed for invasion. If mutations of small effect arise more

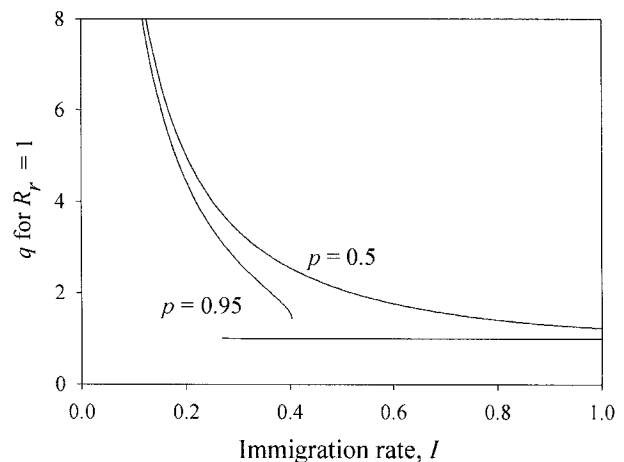


Figure 2: Lines show the fitness (q) necessary for a rare allele to have an absolute fitness (R_r) of 1 when the maximum fitness of the immigrant allele (p) is 0.5 and 0.95. In both cases, $\mu = 1$. For values of q exceeding the boundary for a given p , the allele can increase when rare. (For some values of I in the $p = 0.95$ case, there are two stable equilibria and therefore two boundaries, with the lower limit applying if the system is at the higher N^* .)

frequently than do mutations of large effect, the probability that a mutant arises with sufficient effect on fitness to increase when rare should be higher at higher immigration rates.

Eventually, of course, as density increases, negative density dependence becomes important, and continued immigration of maladapted alleles from the source lowers the frequency of the adapted allele. In simple haploid models, total population size equilibrates at the carrying capacity of the locally fitter type, independent of immigration rate (Holt 1983*b*; Tufto 2001), and immigration depresses both the frequency and absolute abundance of the locally fitter type.

Quantitative Genetic Model

A full analysis of the evolution of adaptation in a sink requires consideration of the stochastic processes of mutation, drift, and demographic stochasticity. Gomulkiewicz et al. (1999) examined in detail the interplay of selection and these stochastic processes for the case of a single diploid locus, assuming negative density dependence, and observed that the most rapid rate of establishment of favored alleles occurs at intermediate levels of immigration. To complement analytic studies of single-locus models, we have carried out individual-based simulations of adaptive evolution in sink habitats, assuming quantitative genetic variation influenced by multiple loci. The model structure includes mutation, drift, and demographic stochasticity; its basic structure is sketched in the appendix.

In the individual-based simulations reported here, we utilized two kinds of Allee effects. First, we used a function for offspring survival including positive density dependence so that expected fitness increased with population size (comparable in spirit to the haploid model presented above). Second, we assumed that there were two distinct sexes, leading to Allee effects arising from stochastic variation in adult sex ratios at low population size (we assume that mating is monogamous). Because the probability of individual mating success decreases with decreasing population size (fig. 3), this consequence of demographic stochasticity is considered a mechanism producing Allee effects (Stephens et al. 1999). (In fig. 3, given monogamous mating, the number of mating pairs [M] is the number of individuals of the rarer sex. Given N , the number of [e.g.] females has a binomial distribution, which was used to calculate the expected value of M . The mean probability that an adult will mate is twice the mean value of M divided by N . This probability is

$$1 - \left(\frac{N'}{N/2} \right) 0.5^{N'},$$

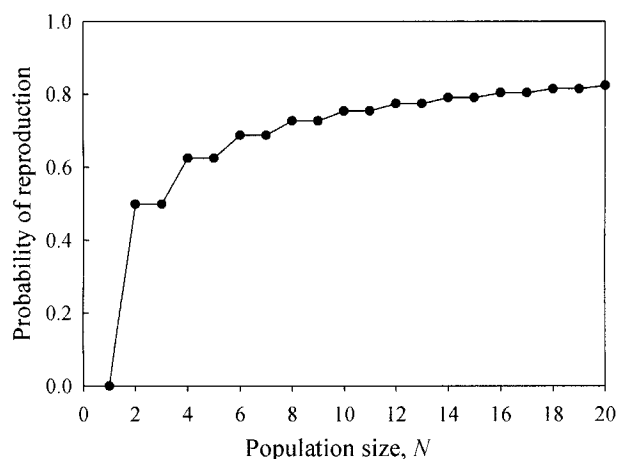


Figure 3: Mean probability that an adult will mate as a function of adult population size (N) for two-sex model.

where N' is the largest even integer $\leq N$. The mean number of offspring given N is this probability multiplied by $4N$ [since we assumed eight offspring per mating pair]. Demographic stochasticity thus generates an Allee effect in reproduction.) We compare the course of adaptive evolution in populations with an Allee effect with populations in which individuals are hermaphrodites and survival is density independent (for the latter, see also Holt et al. 2003*b*).

Results from these simulations are shown in figure 4. The figure depicts the probability of adaptation over 1,000 generations—as a function of the sink optimum phenotype (a measure of the maladaptation of immigrants in the sink habitat)—and the number of immigrants introduced per generation. Given the assumptions of our simulations, typically a population is either maladapted to the sink, with a mean phenotype similar to that of the source, or well adapted (with only a modest displacement of mean phenotype from the optimum because of recurrent gene flow from the source). Given strong selection, there usually is a rapid transition between these two adaptive states, and sink populations spend little time at intermediate stages of adaptation (Holt et al. 2003*b*). Thus, we can treat “adaptation” as a binary state of the population and summarize thousands of simulations compactly in terms of the probability of a transition from maladaptation to an adapted state over a given time horizon.

Without an explicit Allee effect, there is a modest increase in the probability of adaptation with increasing immigration (fig. 4*A*). With an explicit Allee effect on survival, an increase in immigration has a dramatic impact on the probability of adaptation (fig. 4*B*), especially at low immigration rates; the stronger the Allee effect is, the more pronounced the impact of immigration becomes (cf. fig.

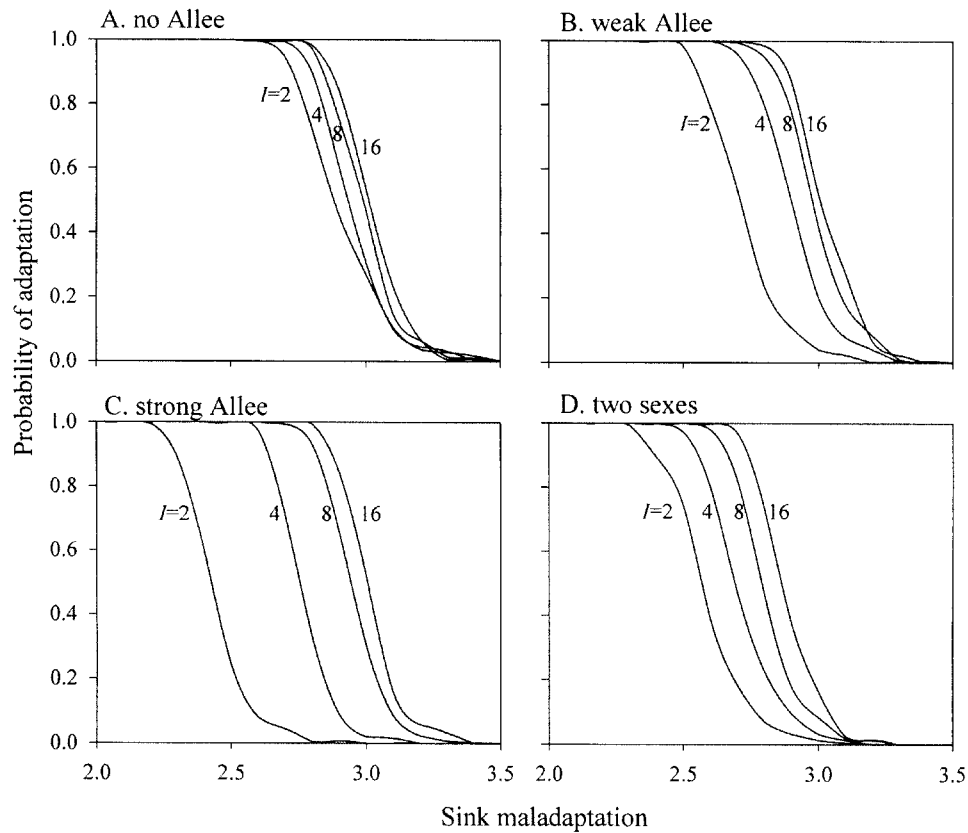


Figure 4: Relationship between the probability of adaptation after 1,000 generations of immigration and the degree of maladaptation of the sink population (θ_{sink}) for immigration rates of 2, 4, 8, and 16 per generation and assuming the following: (A) individuals are hermaphrodites, and survival is not density dependent; (B) individuals are hermaphrodites, and survival is positively density dependent (weak Allee effect, $a = 1$, $c = 0.1$); (C) same as B but with stronger positive density dependence ($a = 1$, $c = 0.05$); (D) there are two sexes, leading to positive density dependence in expected reproductive success (see fig. 3). Other parameters used are $K = 64$, $n = 10$, $n\mu = 0.01$, $\alpha^2 = 0.05$, $\omega = 1$, 8 offspring/pair. See appendix for details on individual-based models.

4B, 4C). Given a two-sex mating system, which leads to an Allee effect in expected fecundity (fig. 3), an increase in immigration also gives a large increase in the likelihood of adaptation (cf. fig. 4A, 4D). Moreover, figure 3 shows that a two-sex mating system has a lower expected fecundity even at relatively high population size, and so increased immigration seems to facilitate adaptation over a larger range of immigration rates than with a hermaphroditic mating system.

Discussion

While there has been considerable recent attention given to how Allee effects may increase the probability of population extinction (Dennis 1989, 2002; McCarthy 1997; Lande 1998; Poggiale 1998; Courchamp et al. 1999; Berec et al. 2001), there has been much less emphasis on how Allee effects may affect the probability that populations

adapt via natural selection to novel, harsh environments. Here, we have examined the role of immigration from a source population on the adaptation process of a sink population and have shown that Allee effects can magnify the positive influence of immigration on local adaptation. Gomulkiewicz et al. (1999) argued that an intermediate rate of immigration should lead to the greatest scope for adaptation to sink environments, because very low rates of immigration lead to very little genetic variation being available (a genetic effect), and high rates of immigration lead to higher population size and depressed local fitnesses (an ecological effect). Our results here suggest that immigration may at times also facilitate local adaptation via increased abundance, given Allee effects. In other words, if there is little immigration, species with Allee effects may find it difficult to adapt to habitats outside their preexisting niches. Because sink populations are typically expected to be at low densities, the crucial empirical question is to

characterize how density dependence operates at low densities.

These results should be broadly applicable to evolution in a wide range of taxa, in light of the numerous different mechanisms that can generate Allee effects. Some mechanisms reflect species' intrinsic properties. Allee himself (Allee et al. 1949) focused on reduced cooperative interactions at low densities. Examples include meerkats (Clutton-Brock et al. 1999), African wild dogs (Courchamp et al. 2000), white-winged choughs (Heinsohn 1992), and social spiders (Aviles 1997). As assumed in some of our simulations, in sexual species, reproductive output is depressed at low abundances, simply because it is difficult to find mates (e.g., Lamont et al. 1993; Fauvergue et al. 1995; Kindvall et al. 1998; Levitan 2002) or because sex ratios are imbalanced (as in the black-eared miner: Ewen et al. 2001; this may explain failure of biological control programs that release insects in small numbers: Hopper and Roush 1993). Some mechanisms underlying Allee effects are very subtle. For instance, if organisms draw information from each other about the state of the environment ("conspecific cuing"; Kiester 1979), they may be less effective at habitat selection in low-density habitats (for an example in swallows, see Brown et al. 2000). Sexual selection via female choice may be less effective at low numbers, since females have fewer males among which to choose (Moller and Legendre 2001).

Other mechanisms generating Allee effects arise from interspecific interactions or ecosystem impacts. If predators have saturating functional responses, low-density prey populations may suffer higher per capita mortality. This mechanism occurs in mammalian predation on New Zealand birds (Jones 2002), mast-seeding in cycads (Donaldson 1993), and even lobsters (which enjoy lower predation risk when clustered in large "dens"; Childress and Herrnkind 2001). Plants dependent on animal pollination may suffer reduced reproductive success at low densities because of disrupted pollination syndromes (e.g., Widen 1993; Kunin 1997; Groom 1998; Knight 2003). A species may also positively alter the abiotic environment, facilitating its own growth, survival, or reproduction. For instance, Ferson and Burgman (1990) showed that at low densities, hemlock (*Tsuga heterophylla*) is less able to acidify the soil and sequester water in upper soil horizons. Fire-obligate plants such as wiregrass must occur at sufficiently high densities to facilitate the spread of fire (Malaiakal et al. 2000). Ecosystem impacts and interspecific interactions may combine to generate Allee effects. For instance, many exotic species can modify the environment and drive native species extinct once they reach high enough densities (Gordon 1998). Interspecific competition and mutualism implicitly embody Allee effects. If species A and B are competing, an increase in A reduces B, which

in turn relaxes the competitive impact of B on A; this is a form of indirect positive density dependence (DeAngelis et al. 1986; Holt 1992). When interspecific interactions create Allee effects, however, there may be a time lag between the change in population density and the change in individual fitnesses of a focal species.

This wide range of mechanisms that can generate Allee effects suggests that the evolutionary phenomenon we have identified could arise in a diverse range of taxa and ecosystems. A number of studies have examined how immigration can hamper local adaptation via the "swamping" of locally adapted alleles by maladapted immigrants (see review by Lenormand 2002) or how immigration may enhance local adaptation by reducing inbreeding depression (Spielman and Frankham 1992; Ball et al. 2000; Richards 2000). However, we are unaware of any studies of empirical systems that have explicitly examined the evolutionary phenomenon we have identified here. We suggest that examples of the facilitation of adaptation by immigration should be sought in sink environments where populations cannot persist at all without immigration and are being maintained by low to moderate rates of immigration.

One intriguing implication of our results is that the mating system of a species may influence how likely it is to adapt to a new environment. Here, we have demonstrated that dioecious sink populations likely require much more migration from a source population to adapt than do hermaphroditic sink populations. This results from an increased difficulty in finding mates and unequal sex ratios at low population size. Even more subtle types of mating system differences could also change the probability of adaptation. Indeed, Proulx (1999) showed that species with assortative mating are less likely to adapt in sinks, simply because individuals are less likely to mate with individuals with a novel, adaptive phenotype. Alternatively, adaptation may be more likely in species with sexual selection if females in the sink population selectively mate with locally adapted males (Proulx 1999, 2002). In addition, different dispersal rates among sexes could compound Allee effects by generating unequal sex ratios in sink populations, thereby hampering the evolution of local adaptation to sink habitats.

Small populations are prone to inbreeding depression (Byers and Waller 1999; Cronkrak and Roff 1999). Inbreeding depression should cause a decrease in the fitness of individuals. Because the sink population size is often well below carrying capacity, species that are likely to experience inbreeding depression (if deleterious alleles have not already been purged from the source population) would enjoy another added demographic benefit of increased immigration into sinks, because outbreeding is more likely if there are more immigrants per generation. The positive genetic effect of immigration via reduced in-

breeding depression complements the one we have explored involving ecological sources of Allee effects.

Anthropogenic use of the environment often causes degradation of a portion of a species' range, creating potential sink habitats. Because other portions of the species' range may later suffer comparable degradation, the long-term viability of a species may depend on whether or not populations in these sink habitats can adapt to their new environment (Holt and Gomulkiewicz, in press). Species with Allee effects may have a particularly difficult time adapting to novel sink conditions. For such species, it may be important to maintain corridors among habitats, permitting immigration to facilitate the evolutionary rescue of populations.

These results may also have implications for management strategies aimed at preventing noxious species from expanding their ranges. For instance, many specialist herbivorous insects introduced to control exotic plant species have expanded their host ranges to include nontarget species (van Klinken and Edwards 2002). Reducing connectivity may make such host range shifts less likely. An understanding of Allee effects may help explain why range shifts occur in some taxa but not others. In conclusion, we suggest that Allee effects may play a significant role in the interplay of the forces of gene flow, selection, and demography that govern the evolutionary response of species to spatially heterogeneous environments.

Acknowledgments

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APPENDIX

Individual-Based Models of Sink Evolution

We used an individual-based model in which every individual and gene was tracked to determine the effect of immigration on the probability of sink adaptation with and without positive density dependence. The basic model assumptions are those used by Burger and Lynch (1995), as modified (and described in detail) in Holt et al. (2003b) and Holt and Gomulkiewicz (in press; all these assume hermaphrodites and no positive density dependence). Here we simply highlight the main features and assumptions of the simulations.

We simulated two habitats, an initially populated source at mutation-selection-drift equilibrium and an initially empty sink that had a different optimum phenotype. Each

generation, a constant number of individuals from the source immigrated to the sink with no back migration. We assumed a constant environment in both habitats and calculated the probability of adaptation to the sink as a function of various parameters, in particular the immigration rate.

Generations were discrete. Selection was on offspring survival, determined by a single polygenic character composed of 10 freely recombining diploid loci with additive allelic effects within and among loci (i.e., no dominance or epistasis). The phenotypic value for an individual, z , was the sum of the contribution of each of its alleles and a zero mean, unit variance, normally distributed environmental effect. The survival probability of an individual with phenotype z in habitat i (source or sink) was

$$W_i(z) = (1 - ae^{-cN_i}) \exp\left[-\frac{(z - \theta_i)^2}{2\omega^2}\right],$$

where ω determines the strength of selection (we used $\omega = 1$, corresponding to fairly strong selection) and θ_i is the optimum phenotype in habitat i ; N_i is the total number of offspring at the beginning of a generation in habitat i . The optimal source phenotype was 0; θ_{sink} measured the degree of maladaptation in the sink experienced by immigrants. The first term was used to produce positive density dependence. If $a = 0$, there is no Allee effect on individual survival. If $a > 0$, there is an Allee effect, the strength of which is determined by a and c . We present results for $a = 1$ and two values for c , 0.1 and 0.05; the latter corresponds to a stronger Allee effect. (We also varied the strength of the Allee effect by varying a . The results were similar to those obtained by varying c and therefore are not presented.)

In addition to the positive density dependence included in the expression for W_i , we assumed "ceiling" density-dependent regulation of the number of breeding pairs. A maximum of K individuals was allowed to breed in each habitat. Mating pairs were formed randomly from all adults surviving selection. In some simulations, individuals were hermaphrodites, so any pair could mate, while in other simulations, two sexes were simulated, so a mating pair had to consist of a male and a female. When there were two sexes, the sex of each individual was assigned randomly, and there was no positive density dependence in survival. Each pair produced eight offspring. During reproduction, each haplotype had a probability of mutation of $n\mu$ (0.01 for results presented here; μ is the mutation rate per locus and n is the number of loci = 10). The size of a mutation was normally distributed, with mean 0 and variance α^2 (0.05 for all results here). When a mutation occurred, the size of its effect was added to

the previous value of a randomly chosen locus on that haplotype.

We began with K individuals in the source and no individuals in the sink. We assigned initial genotypes using the expected stochastic "house of cards" genetic variance (using eq. [14] in Burger and Lynch 1995). We then allowed the source population to go through 1,000 generations so that it reached a mutation-selection-drift equilibrium before any immigration to the sink occurred. We then began immigration and simulated an additional 1,000 generations. A constant number I of immigrants was randomly chosen from survivors of selection in the source habitat (with no mortality in transit). Immigrants were moved to the sink before parents were selected in the source and sink, so immigrants could mate in the sink with each other or with sink residents. We considered four different immigration rates: 2, 4, 8, and 16 individuals per generation.

Typically, in these simulations, a sink population either remained small with an average genotype near that of the source or at some point greatly increased in abundance and reached an average genotype close to the sink optimum. Populations in the latter state were considered adapted. For each parameter set, we simulated 400 replicate sink populations and from them determined the probability of adaptation after 1,000 generations (the number of populations with an average genotype closer to the sink optimum phenotype, divided by 400). Figure 4 gives results from our simulations. It should be noted that all these individual-based simulations involve the impact of demographic stochasticity at low population sizes.

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