Evolutionary Consequences of Asymmetric Dispersal Rates

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ABSTRACT: We study the consequences of asymmetric dispersal rates (e.g., due to wind or current) for adaptive evolution in a system of two habitat patches. Asymmetric dispersal rates can lead to overcrowding of the "downstream" habitat, resulting in a source-sink population structure in the absence of intrinsic quality differences between habitats or can even cause an intrinsically better habitat to function as a sink. Source-sink population structure due to asymmetric dispersal rates has similar consequences for adaptive evolution as a source-sink structure due to habitat quality differences: natural selection tends to be biased toward the source habitat. We demonstrate this for two models of adaptive evolution: invasion of a rare allele that improves fitness in one habitat but reduces it in the other and antagonistic selection on a quantitative trait determined by five additive loci. If a habitat can sustain a population without immigration, the conditions for adaptation to that habitat are most favorable if there is little or no immigration from the other habitat; the influence of emigration depends on the magnitude of the allelic effects involved and other parameters. If, however, the population is initially unable to persist in a given habitat without immigration, our model predicts that the population will be most likely to adapt to that habitat if the dispersal rates in both directions are high. Our results highlight the general message that the effect of gene flow upon local adaptation should depend profoundly on the demographic context of selection.

Keywords: adaptation, dispersal, gene flow, marginal habitats, heterogeneous environments, source-sink structure.

It is a trivial fact of ecology that a change in the population density at a given locality reflects the balance between local births, local deaths, immigration, and emigration. A local population can thus remain stable even though its local birth rate does not equal its local death rate. Populations living in heterogeneous environments can thus exhibit a source-sink structure, with a net flow of dispersers from some (source) habitats to other (sink) habitats (Lidicker 1975; Holt 1985; Pulliam 1988; Kawecki 1995; Dias 1996). According to the broad definition we adopt here, a habitat is a sink if the number of immigrants it receives from other habitats exceeds the number of individuals that successfully emigrate from it to other habitats. Our definition of sink habitats thus includes habitats unable to sustain a population without immigration (absolute sinks) as well as habitats good enough to sustain a population that become sinks as a result of high immigration and density dependence (relative sinks; Watkinson and Sutherland 1995 call them "pseudosinks"). Conversely, source habitats are net producers of migrants (for a caveat concerning the above definition when there are more than two habitats, see Rousset 1999).

As a consequence of a source-sink structure, a stable population may be maintained in an absolute sink (i.e., a habitat unable to sustain a population in the absence of immigration; Lidicker 1975; Järvinen and Väisänen 1984; Pulliam 1988; Robinson et al. 1995). In a habitat that is a relative sink, the population is maintained above the local carrying capacity (the density at which deaths balance births), while the reverse holds for a source habitat (e.g., Holt 1985; Watkinson and Sutherland 1995; Dias 1996). Some models predict that source-sink dynamics can have a stabilizing effect on population dynamics (Holt and Hassell 1993; Doebeli 1995; Gomulkiewicz et al. 1999).

Source-sink population structure also has important consequences for adaptive evolution. Source habitats tend to contribute more to the future gene pool of the entire population than do sink habitats. Most individuals in a sink habitat trace their ancestry to immigrants from a source habitat. The resulting asymmetric gene flow makes natural selection on performance in a sink habitat relatively ineffective (Holt and Gaines 1992; Kawecki and Stearns 1993; Kawecki 1995; Holt 1996a, 1996b). A population in a sink habitat may thus persist in a state of permanent maladaptation, a pattern confirmed by an in-

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creasing number of empirical studies (e.g., Stearns and Sage 1980; Dhondt et al. 1990; Blondel et al. 1992; Stanton and Galen 1997).

Predictions concerning the evolutionary consequences of source-sink population structure have to date largely been based on models in which the net flow of dispersers from source to sink habitats results from a difference in habitat quality. Under that scenario, more offspring are produced in the better habitat at equilibrium. Therefore, if the propensity to disperse is habitat independent, more individuals move from the better to the poorer habitat than in the opposite direction, simply because the pool of potential dispersers is greater in the former than in the latter.

However, the number of dispersing individuals is the product of the number of potential dispersers (propagules) and their propensity to disperse (dispersal rate). An asymmetry in the number of dispersing individuals will thus also arise, even in the absence of differences in habitat quality if the dispersal rate from habitat i to habitat j (i.e., the probability that a propagule produced in habitat i disperses to habitat j) is greater than the dispersal rate in the opposite direction. As a result of this asymmetry, the population density in habitat i will become reduced below the local carrying capacity, while habitat j will become overcrowded. The overcrowding will depress the reproductive success in habitat j until, at equilibrium, the difference between the reproductive outputs of the two habitats compensates for the asymmetric dispersal. Habitat i will thus become a source and habitat j a sink (Doebeli 1995). This can be true even if habitat i has the lower carrying capacity.

In general, whether there is a net flow of dispersers (i.e., whether there is a source-sink structure), and in which direction, will depend on differences in both habitat quality and dispersal rates. If there are no costs of dispersal and the individuals have perfect control over their dispersal, natural selection is expected to adjust dispersal rates in such a way that there is no sink structure; that is, for each habitat, the number of immigrants from other habitats equals the number of emigrants that move to other habitats (McPeek and Holt 1992; Doebeli 1995; Lebreton et al. 2000; Holt and Barfield 2001). When habitats differ in quality, the dispersal rates required for this "balanced dispersal" scenario are asymmetric: a propagule produced in a poorer habitat must be more likely to move to another habitat than a propagule produced in a better habitat. This asymmetry of dispersal rates must be so adjusted that differences in population density exactly compensate for differences in habitat quality and the expected lifetime reproductive success is the same in all habitats (Lebreton et al. 2000; Holt and Barfield 2001). The outcome is an ideal free distribution (Fretwell and Lucas 1970).

Since organisms are usually neither ideal nor free, the balanced dispersal scenario is likely to be uncommon in nature (though examples seem to exist for vertebrates, e.g., Diffendorfer 1998; Lin and Batzli 2001). Asymmetries in dispersal rates can also arise from social interactions (Pulliam 1988; Holt 1996a) or the directional influence of environmental agents of dispersal, for example, gravity, river or ocean current, or prevailing wind direction. For instance, asymmetric dispersal due to ocean currents has long been recognized as an important factor that affects the distribution, abundance, and genetic variation of marine benthic invertebrates with planktonic larvae (e.g., Scheltema 1986). A recent study of mtDNA in two barnacle and one sea urchin species off California found a signature of an excess of southward over northward dispersal, consistent with the pattern of currents (Wares et al. 2001). Similar patterns should be expected in river invertebrates. On land, asymmetric dispersal due to wind should play an important role on dunes and other exposed coastal habitats. Among the few cases of well-studied source-sink dynamics in natural populations, asymmetric dispersal due to wind has a crucial impact on distribution and abundance in the sand dune plant *Cakile edentula* (Keddy 1981, 1982; Watkinson 1985). In that system, the windward (seaward) side of the dunes is the source habitat, where most of the seeds are produced, but because most of them are transported by wind to the sink habitat around the dune crests, plant density in the latter habitat is considerably higher than in the windward habitat. At the same time, the seed emigration from the windward habitat reduces competition and boosts the reproductive output from that habitat.

An asymmetry of dispersal rates can thus create a source-sink structure in the absence of differences in habitat quality. Where habitats do differ in quality, asymmetry of dispersal rates can amplify the source-sink structure if its direction is opposite to that required for balanced dispersal, as in the *C. edentula* example mentioned above. Dispersal rates asymmetric in the direction predicted by the balanced dispersal scenario may reduce the source-sink structure, but if the asymmetry is greater than required under the balanced dispersal model, the source-sink structure will be reversed: the poorer habitat will become the source, and the better one, the sink. Unbalanced dispersal is also likely in recently changed landscapes, where dispersal syndromes may be maladapted to current conditions.

In this article we study the effect of asymmetries in dispersal rates on adaptation in the face of a trade-off in fitness between habitats. Only a few models have explicitly addressed this issue. Holt (1996b) studied the consequences of asymmetric dispersal rates in a two-patch source-sink model and concluded that the conditions for adaptation to the sink are most favorable when the dis-

persal rates in both directions are high. That model assumes, however, that one of the two habitats is unable to sustain a population without immigration and thus must be a sink if the population persists at all, irrespective of dispersal rates. Furthermore, the fitness sensitivity approach taken by Holt (1996*a*, 1996*b*) is equivalent to considering the fate of rare alleles with infinitesimal effects on fitness. Yet, dispersal rate may affect the fate of rare alleles with small and large effects in qualitatively different ways (Kawecki 2000*a*). A special, extreme case of dispersal rate asymmetry is one-way dispersal, resulting in a "black hole" sink, which receives dispersers from a source but sends no successful dispersers back. Theoretical aspects of the population dynamics and adaptive evolution in black hole sinks have been extensively studied by Gomulkiewicz and coworkers (Holt and Gomulkiewicz 1997; Gomulkiewicz et al. 1999; LoFaro and Gomulkiewicz 1999). They showed that this form of source-sink structure has qualitatively similar consequences for adaptive evolution in the sink as the source-sink structure because of differences in habitat quality. Yet they have not studied whether allowing for some dispersal back into the source (i.e., relaxing the "black hole" assumption) makes the conditions for adaptive evolution in the sink more or less stringent.

Our aim in this article is to generalize the qualitative conclusions reached in those papers regarding the evolutionary consequences of the source-sink structure to source-sink structure caused or modified by dispersal rate asymmetry. We combine a two-patch source-sink model that has an arbitrary combination of dispersal rates with explicit one-locus and multilocus population genetic approaches. In the next section we describe the model of population dynamics that we assume. In the following section genetic variance is introduced in the form of a rare allele that improves fitness in one habitat but reduces it in the other. We study how the conditions under which this allele is favored depend on the combination of the dispersal rates. The last section considers the evolution of a quantitative trait with antagonistic effects on fitness in the two habitats. These two approaches—invasion of a mutant allele and the evolution of a quantitative trait—provide two complementary ways to study whether and how asymmetric dispersal rates and the resulting source-sink structure promote or hinder habitat-specific adaptation.

The Model of Population Dynamics

Our model of population dynamics follows that of Doebeli (1995). We consider a population with discrete generations, living in two habitat patches connected by passive dispersal. Each individual completes its development within a single habitat patch, during which time it is sub-

ject to density dependence and selection (the latter introduced in the following section, "Invasion of a Rare Allele"). The equations for population dynamics are compatible with three modes of dispersal. First, adults mate and reproduce in the habitat in which they developed; the zygotes (seeds, eggs, etc.) then disperse. Second, adults mate within the habitat of origin; mated females disperse and oviposit after dispersal. And third, adults of both sexes disperse; mating and reproduction take place after dispersal. In the two latter cases, the performance of the dispersing adults is assumed to be only affected by the conditions and density in the habitat of origin and not by the habitat of destination. The census takes place at the zygote stage (after dispersal if zygotes disperse). Conditions are constant in time, and the population is assumed to be large enough for stochastic effects to be ignored. The dynamics of the two subpopulations can be described by the matrix equation (Doebeli 1995)

$$\begin{pmatrix} N_1' \\ N_2' \end{pmatrix} = \begin{pmatrix} f_1(N_1)(1 - m_{12}) & f_2(N_2)m_{21} \\ f_1(N_1)m_{12} & f_2(N_2)(1 - m_{21}) \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}, \quad (1)$$

where N_i is the size of the subpopulation in habitat i at census time, the prime denotes population size in the next generation, $f_i(N_i)$ is the density-dependent expected lifetime reproductive success of individuals developing in habitat i, and m_{ij} is the dispersal rate from habitat i to habitat j (i.e., the probability than an individual present in habitat i before dispersal migrates to habitat j). Density dependence here may act on survival from zygote to adult. Alternatively, it can be interpreted as affecting adult fecundity; in the latter interpretation, however, the density-dependent component is a function of the number of juveniles present in the habitat at the census time, not the number of breeding adults. To obtain the numerical results, we implement a form of density dependence proposed by Maynard Smith and Slatkin (1973):

$$f_i(N_i) = \frac{R_i}{1 + cN_i^b}, \quad (2)$$

where c and b are constants, for simplicity assumed to be equal for both habitats.

Throughout the article we restrict our analyses to parameter values for which the system described by equations (1) and (2) has a stable nonzero equilibrium. The condition for the existence of a nonzero equilibrium (i.e., persistence of the population) is derived in the appendix. If the equilibrium exists, it is always stable if $b \leq 2$; the conditions for stability of the equilibrium were studied by Doebeli (1995).

In the absence of dispersal, the form of density depen-

dence described by equation (2) leads to equilibrium densities of

$$K_i = [(R_i - 1)/c]^{1/b}. \qquad (3)$$

We refer to K_i as the carrying capacity of habitat i. When there is dispersal, the equilibrium densities ($\hat{N}_1$, $\hat{N}_2$) will equal the carrying capacities if the dispersal rates satisfy $K_1 m_{12} = K_2 m_{21}$, which, given equation (3), simplifies to

$$(R_1 - 1)^{1/b} m_{12} = (R_2 - 1)^{1/b} m_{21}. \qquad (4)$$

This is the special case of balanced dispersal: the number of migrants in both direction is the same, and there is thus no source-sink structure (McPeek and Holt 1992; Doebeli 1995; Diffendorfer 1998; Lebreton et al. 2000). If equation (4) is not satisfied and its left-hand side is greater than its right-hand side, habitat 1 will be a source and habitat 2, a sink; otherwise, the opposite holds. Except for special cases (e.g., one-way dispersal), the equilibrium densities ($\hat{N}_1$, $\hat{N}_2$) can only be found numerically.

Invasion of a Rare Allele

The Model

In this section we consider a mutant allele beneficial in habitat 2 but deleterious in habitat 1 and study how the conditions for invasion of such an allele are affected by dispersal rates in the two-patch system described above. As a caveat on the results described here, it should be noted that a rare allele that satisfies the condition for invasion derived in this deterministic model is still prone to be lost because of drift. Therefore, the condition for invasion might be better interpreted as the condition for the allele not to be deterministically eliminated by selection.

We consider a nonrecessive mutant allele, present at a low frequency in an otherwise monomorphic equilibrium population whose dynamics follow the assumptions of the previous section ("The Model of Population Dynamics"). The absolute fitness (expected reproductive success) of the heterozygous carriers of the mutant allele in habitat 1 is $f_1(N_1)(1 - s_1)$. The multiplicative relation between the density-dependent and the genotype-dependent components of fitness means that the selection coefficient against the mutant allele in habitat 1 is s_1, irrespective of density. The allele improves performance in habitat 2; there the fitness of the heterozygotes is $f_2(N_2)(1 + s_2)$. The conditions for invasion of this allele can thus be formulated in terms of a critical value of s_1, denoted s_1^*, such that the mutant allele is favored when rare if and only if $s_1 < s_1^*$. In other words, s_1^* is the maximum selection coefficient against the rare allele habitat 1 that is still outweighed by the beneficial

effect on fitness in habitat 2, s_2, such that the rare allele can invade. If $s_1^* = 1$, the rare allele will invade even if it is lethal in habitat 1. The question addressed in this section can thus be formulated like this: How is s_1^* affected by the dispersal rates m_{12}, m_{21}, as well as by s_2 and the population growth parameters defined above?

As usual when considering the fate of a rare allele, the frequency of mating between two heterozygotes and the frequency of homozygotes for the mutant allele are assumed negligible. With this assumption it does not matter whether mating takes place before or after dispersal; that is, the results hold for all three modes of dispersal considered in the previous section ("The Model of Population Dynamics"). Also, because the allele is rare, the effect of the heterozygotes on the population densities can be neglected. That is, as long as the mutant allele is rare, the population densities remain at $\hat{N}_1$ and $\hat{N}_2$, the equilibrium densities of a population monomorphic for the common homozygote. With these assumptions, the dynamics of the density of heterozygous individuals in the two habitats, M_1 and M_2, are described by the set of recurrence equations

$$\begin{pmatrix} M_1' \\ M_2' \end{pmatrix} = \begin{pmatrix} f_1(\hat{N}_1)(1 - s_1)(1 - m_{12}) \\ f_1(\hat{N}_1)(1 - s_1)m_{12} \end{pmatrix}$$

$$\begin{pmatrix} f_2(\hat{N}_2)(1 + s_2)m_{21} \\ f_2(\hat{N}_2)(1 + s_2)(1 - m_{21}) \end{pmatrix} \begin{pmatrix} M_1 \\ M_2 \end{pmatrix}, \qquad (5)$$

where the prime again denotes the number in the next generation. (This equation can easily be reformulated in terms of allele frequencies, leading to identical results.) Equation (4) is linear in (M_1, M_2). This means that, after converging to a stable distribution between the habitats, M_1 and M_2 will grow (or decline) exponentially with the rate given by the dominant eigenvalue λ_M of the matrix in equation (5). Because the densities of the resident homozygotes ($\hat{N}_1$, $\hat{N}_2$) remains constant at the equilibrium, λ_M gives the rate of change of both the number of heterozygotes and the frequency of the mutant allele, as long as $M_1 \ll \hat{N}_1$ and $M_2 \ll \hat{N}_2$. The allele is thus favored when rare if $\lambda_M > 1$. Note that $\lambda_M = 1$ implies $\det(\mathbf{A} - \mathbf{I}) = 0$, where $\mathbf{A}$ is the matrix in equation (5) and $\mathbf{I}$ is an identity matrix. This equation can be solved for s_1 to yield

$$s_1^* = 1 - \frac{1 - f_2(\hat{N}_2)(1 - m_{21})(1 + s_2)}{f_1(\hat{N}_1)[1 - m_{12} - f_2(\hat{N}_2)(1 - m_{12} - m_{21})(1 + s_2)]};$$

$$(6)$$

the rare allele can invade if the selective cost it experiences in habitat 1 satisfies $s_1 < s_1^*$.

Analytical Considerations

Although expression (6) is general, it is not sufficient for analyzing the net effect of dispersal rates on evolution, because the magnitudes of dispersal enter expression (6) not only directly but also indirectly through effects on $\hat{N}_1$, $\hat{N}_2$. Before using expression (6) to obtain numerical results, we describe some analytical insights concerning the relative weight of the two selection coefficients and some special cases.

The stable (asymptotic) fraction of carriers of the rare allele present in each habitat $\mathbf{q} = (q_1, q_2)$ is the right eigenvector corresponding to λ_M, normalized to make the sum of its elements equal 1 (Caswell 1989). Note that, by definition,

$$\mathbf{Aq} = \lambda_M \mathbf{q}. \tag{7}$$

By adding up the elements of the resulting vectors on both sides of the equation and using the fact that $q_1 + q_2 = 1$, one can show that

$$\lambda_M = q_1 f_1(\hat{N}_1)(1 - s_1) + q_2 f_2(\hat{N}_2)(1 + s_2) \tag{8}$$

(see Liberman 1988 for a formal derivation). In determining the ultimate growth rate of the frequency of the allele, the two selection coefficients are thus weighted by the products of the density-dependent components of fitness (which convert the relative selection coefficients into absolute differences in reproductive success) and the proportions of carriers exposed to each habitat. Note that the carriers of the rare allele not only have local fitnesses different from the common genotype but also are differently distributed between the habitats: $\mathbf{q}$ is a function of the selection coefficients s_1, s_2. The dispersal rates affect the fate of the rare allele through $\hat{N}_1$, $\hat{N}_2$, and thus $f_1(\hat{N}_1)$, $f_2(\hat{N}_2)$, but also through their effect on how the distribution of the carriers of the rare allele between the habitats deviates from that of the common genotype. If $m_{12} + m_{21} < 1$, which should usually be the case in nature, q_1 is smaller than the analogous proportion for the common resident genotype (assuming, as we do throughout, that $s_1, s_2 > 0$), and the difference increases as the sum $m_{12} + m_{21}$ decreases. The reason is that if dispersal is limited, the distribution of the allele will tend to be biased toward the habitat where it is relatively more fit. The reverse holds when $m_{12} + m_{21} > 1$. At the borderline ($m_{12} + m_{21} = 1$), which includes the complete mixing case ($m_{12} = m_{21} = 0.5$), it can be shown that $(q_1, q_2) = (m_{21}, m_{12})$ and, thus, that $f_1(\hat{N}_1)m_{21} + f_2(\hat{N}_2)m_{12} = 1$. Only in this special case is the weight given to the two selection coefficients independent of the coefficients themselves, and equation (6) simplifies to

$$s_1^* = \frac{f_2(\hat{N}_2)m_{12}}{f_1(\hat{N}_1)m_{21}} s_2. \tag{9}$$

In other cases ($m_{12} + m_{21} \neq 1$), the critical value of s_1 that still allows the rare allele to invade is not proportional to s_2. In the limit of weak selection, after expanding λ_M in a Taylor series around ($s_1 = 0$, $s_2 = 0$), one can show that

$$\lim_{s_2 \to 0} \left(\frac{s_1^*}{s_2} \right) = \frac{1 - f_1(\hat{N}_1)(1 - m_{12})}{1 - f_2(\hat{N}_2)(1 - m_{21})}; \tag{10}$$

numerical results show this to be a good approximation for alleles with s_2 of the order of 0.01 or less.

Another special case is for the common genotype at equilibrium to exhibit balanced dispersal (i.e., to satisfy eq. [4]). This implies that $f_1(\hat{N}_1) = f_2(\hat{N}_2)$, and the two selection coefficients of the rare allele are now weighted by proportion of carriers exposed to each habitat (q_1, q_2). Note however, that q_1, q_2 will not, in general, be proportional to the carrying capacities (equilibrium densities predicted under no dispersal) of the common genotype nor to those for the rare genotype. Although the common genotype is at balanced dispersal equilibrium, dispersal will not ultimately be balanced for the carriers of the rare allele: when the rare allele settles into its stable habitat distribution, it will be relatively more common in the habitat where it is fitter, leading, in turn, to a net flow of the carriers from habitat 2 to habitat 1. In the limit of weak selection with balanced dispersal, we have $s_1^*/s_2 = m_{12}/m_{21} = K_2/K_1$, which states that selection is biased in favor of the habitat with the higher carrying capacity.

Finally, we consider the special case of unidirectional dispersal. At the limit $m_{12} = 0$, what happens in habitat 1 has no influence on habitat 2, so we can consider habitat 2 alone. Thus, $f_2(\hat{N}_2)(1 - m_{21}) = 1$ at the equilibrium, and the growth rate of a rare heterozygote is $f_2(\hat{N}_2)(1 - m_{21})(1 + s_2)$, which is independent of s_1 and which exceeds unity for all $s_2 > 0$. Hence, the scope for adaptation to habitat 2 is unaffected by the coupling between habitat 2 and habitat 1. Habitat 1 is a black hole sink, so any deleterious effects of local adaptation in habitat 1 are irrelevant to evolution in habitat 2 because of the absence of feedback. Note, however, that for the population to persist, the intrinsic growth rate in habitat 2, R_2, must exceed unity by a margin large enough to compensate for the loss of individuals to emigration. If the population persists only in habitat 1, the allele is eliminated for any $s_1 > 0$. At the analogous limit $m_{21} = 0$, habitat 2 is a black hole sink (again assuming that the local population in habitat 1 persists). As shown by Holt and Gomulkiewicz (1997), the rare allele will only increase if $f_2(\hat{N}_2)(1 + s_2) > 1$. Since

$f_2(\hat{N}_2) < 1$ in a black hole sink, s_2 must be greater than a threshold value even if $s_1 = 0$.

Numerical Results

The numerical results were obtained with the Mathematica 3.0 software package (Wolfram 1996). Density dependence was implemented as defined in equation (2) with $c = R_1 - 1$; this parameter has only a scaling effect, and its value does not affect any of the results presented below. For each set of parameter values, we first numerically found the equilibrium densities of a population composed of the common genotype, $\hat{N}_1$ and $\hat{N}_2$, which were then substituted into equation (6). Representative results are shown in figure 1 (which assumes habitats of equal quality, i.e., $R_1 = R_2$) and figure 2 (for cases with unequal habitat quality, $R_1 > R_2$). For each of several sets of the "ecological" parameters (R_1, R_2, and b), we show three plots. The first (left-hand side) plot shows the fraction of the total population of the resident genotype present in habitat 1 at equilibrium, $p_1 = \hat{N}_1/(\hat{N}_1 + \hat{N}_2)$, as a function of the dispersal rates m_{12} and m_{21}, with other parameters kept constant. The condition for invasion of the rare allele is then plotted as s_1^*—the maximum deleterious effect in habitat 1 for which the mutant can invade—as a function of m_{12} and m_{21}. Greater s_1^* means a more favorable condition for maintenance of the mutant allele in the gene pool; $s_1^* = 1$ implies that the allele can invade even if it is lethal in habitat 1. The results are given for a mutant allele with a "small" ($s_2 = 0.05$ or 0.1) and a "large" ($s_2 = 0.5$ or 1.0) beneficial effect on fitness in habitat 2. While a 5% or 10% improvement of fitness is not necessarily a small effect, smaller s_2 yielded very similar results qualitatively. The results are plotted for $0 \le m_{12}, m_{21} < 1$. If the environment is strongly conductive to one-way dispersal (current, wind), it is conceivable that more than half, or even almost all, of the propagules produced in one habitat are carried to the other one. This justifies considering that $m_{ij} > 0.5$. On the other hand, systems where both m_{12} and m_{21} are greater than 0.5 are likely to be rare in nature; results for that parameter range are plotted for the sake of mathematical completeness but are not discussed.

The dispersal rates affect the equilibrium distribution of individuals between the habitats in a consistent manner: the fraction of the population occupying habitat 1 at census increases with m_{21} and decreases with m_{12} (left-hand-side panels in figs. 1, 2). As expected, when the habitats differ in quality, the dispersal from the better to the poorer habitat has a larger effect on the equilibrium distribution of individuals than the dispersal rate in the opposite direction (fig. 2). If the exponent $b = 1$, and at least one habitat is of high quality (R_1 or $R_2 \gg 1$), the relationship is almost perfectly linear (fig. 1A; fig. 2A, 2B, *left panels*),

with the proportion of individuals present in habitat 1 at census, p_1, given by

$$p_1 \approx \frac{(R_1 - 1)(1 - m_{12}) + (R_2 - 1)m_{21}}{R_1 + R_2 - 2} \quad (11)$$

(relationship fitted to the numerical results). The heavy solid line in figure 2A corresponds to the balanced dispersal scenario; beyond the line, habitat 1 is a sink despite being of higher quality ($R_1 > R_2$). If $R_2 < 1$ (fig. 2B), habitat 2 can only exist as a sink; that is, no combination of dispersal rates could result in balanced dispersal. If the habitats are of the same quality ($R_1 = R_2$), the conditions for balanced dispersal are satisfied along the diagonal (solid line in fig. 1). It should be noted that the relationship between the dispersal rates and the absolute numbers of individuals present in each habitat or the total population size is not monotonic (not shown; see also Holt 1985; Doebeli 1995).

The numerical results in figures 1 and 2 demonstrate that the fraction of individuals exposed to selection in each habitat does not predict the relationship between the dispersal rates and the condition for invasion of the rare allele even qualitatively. If it were so, the condition for invasion of the rare allele should become less stringent (s_1^* should increase) as the fraction of the population present in habitat 1 at equilibrium (p) decreases. This is the case for the entire range of dispersal rates only if habitat 2 is an absolute sink ($R_2 < 1$; fig. 2B). In other cases, the relationship between the dispersal rates and the condition for invasion of the rare allele is not monotonic. The shape of this relationship is strongly affected by the ecological parameters (R_1, R_2, and b) as well as the magnitude of its beneficial effect (s_2). We can draw the following generalizations, based on the results shown in figures 1 and 2 and other numerical results not reported here.

First, as expected from analytical considerations, if the population in habitat 2 can persist in the absence of immigration ($R_2 > 1$), the condition for invasion of the rare allele is most favorable when there is no dispersal from habitat 1 ($m_{12} = 0$). The allele can then invade even if it is lethal in habitat 1 ($s_1^* = 1$; left rear edges of graph boxes in figures 1 and 2A). This prediction is not affected by dispersal in the opposite direction (m_{21}) as long as the subpopulation in habitat 2 can persist despite the drain imposed by emigration, that is, as long as $m_{21} < 1 - 1/R_2$; otherwise, the subpopulation becomes extinct, and $s_1^* = 0$. The optimal conditions for the invasion extend over a range of nonzero m_{12}, whose width increases with s_2 and the R_2/R_1 ratio but decreases with m_{21}. If the beneficial effect on fitness in habitat 2 (s_2) is small, this region is very narrow, and even m_{12} of the order of 0.05 makes the condition for the invasion much more stringent (see
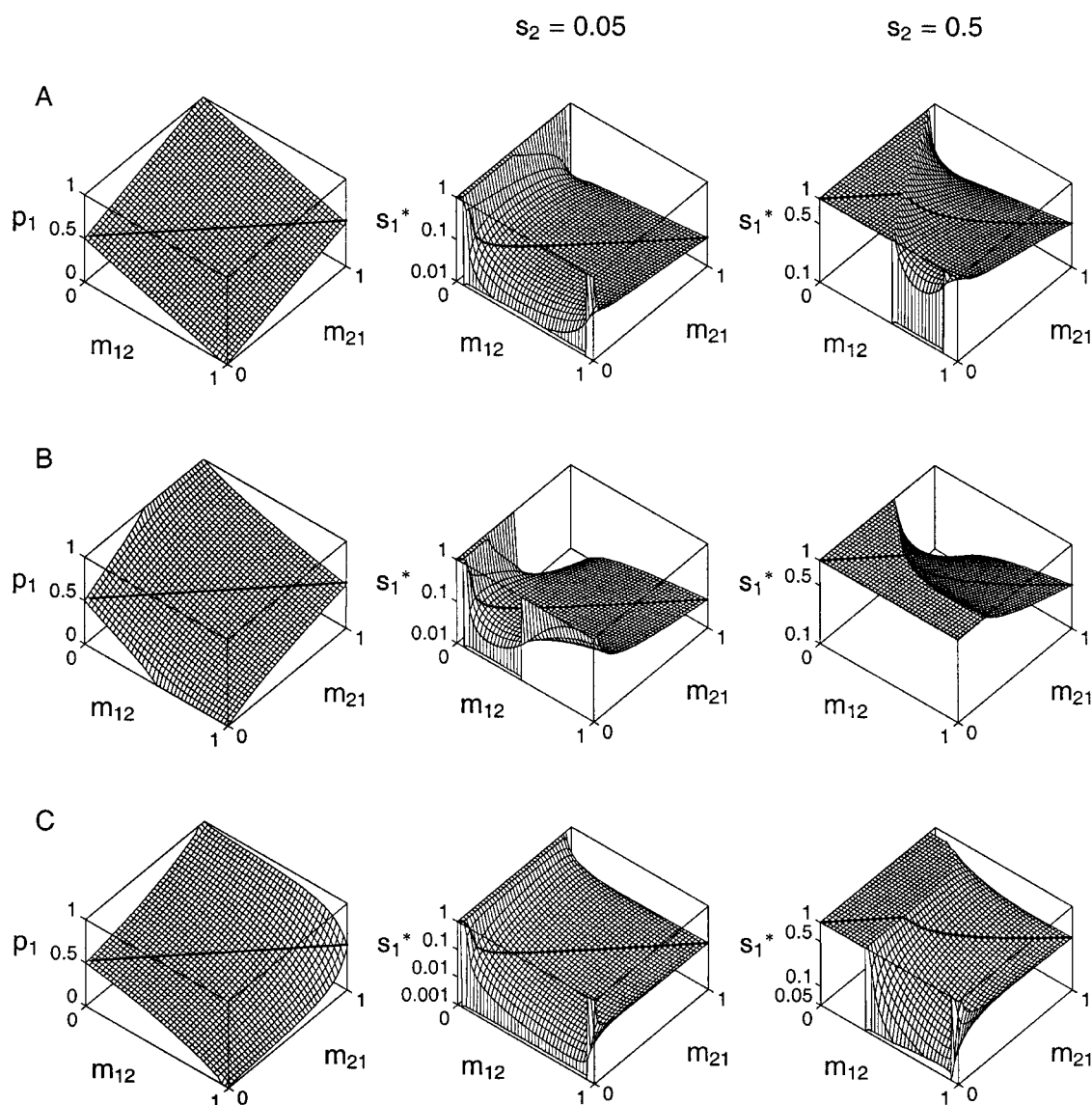
Figure 1: Fraction of the population present in habitat 1 at equilibrium, $p_1 = \hat{N}_1/(\hat{N}_1 + \hat{N}_2)$ (*left-hand-side graphs*), and the condition for invasion of an allele deleterious in habitat 1 and beneficial in habitat 2 (*center and right-hand-side graphs*), as functions of the dispersal rates between the habitats when both habitats are of the same quality ($R_1 = R_2$). The condition for invasion is expressed as the maximum selection coefficient against the rare allele in habitat 1, s_1^*, which permits the allele to increase in frequency when rare (i.e., the rare allele invades in the region of the parameter space under the surface). *A*, $R_1 = R_2 = 20$, $b = 1$; *B*, $R_1 = R_2 = 2$, $b = 1$; *C*, $R_1 = R_2 = 20$, $b = 2$. The center and right graphs differ with respect to the selection coefficient in favor of the allele in habitat 2, s_2. Along the diagonal ($m_{12} = m_{21}$, *solid lines on the graph surfaces*), dispersal is balanced; that is, there is no source-sink structure.

the central panels in fig. 1). This is even more pronounced when habitat 2 is of lower quality ($R_2 < R_1$; fig. 2*A*). If $R_2 < 1$, habitat 2 cannot sustain a population without immigration, so obviously the rare allele cannot invade if $m_{12} = 0$ (fig. 2*B*).

Second, consider the other limiting case: one-way dispersal from habitat 1 to habitat 2 ($m_{21} = 0$; front left edge

of each graph in figs. 1 and 2). Here three outcomes are possible. (1) If $m_{12} > 1 - 1/R_1$ and $R_2 < 1$, the whole population goes extinct. (2) If $m_{12} > 1 - 1/R_1$ and $R_2 > 1$, the population only persists in habitat 2, and the spread of the rare allele is not hampered by gene flow from habitat 1; the allele invades even if it is lethal in habitat 1. For reasonably large R_1, this only occurs at extremely large m_{12}.
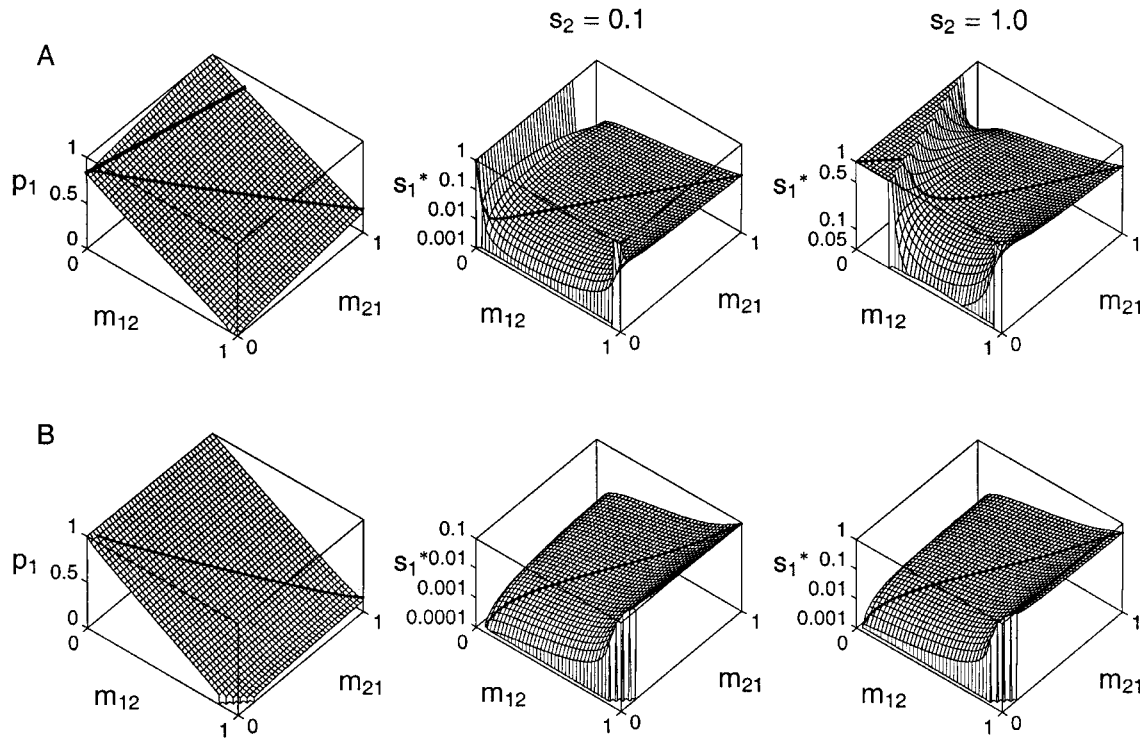
Figure 2: Fraction of the population present in habitat 1 at equilibrium and the condition for invasion of a rare allele when habitat 1 is of better quality ($R_1 > R_2$). *A*, $R_1 = 20$, $R_2 = 5$, $b = 1$; *B*, $R_1 = 10$, $R_2 = 0.5$. Equal dispersal rates ($m_{12} = m_{21}$, *thin solid lines*) do not result in balanced dispersal when $R_1 > R_2$. Dispersal is balanced along the heavy solid line in panel *A* (habitat 1 is a sink for dispersal rates beyond the line); in panel *B* a balanced dispersal scenario is impossible: habitat 2 is an absolute sink. Other explanations as in figure 1.

(3) If $m_{12} < 1 - 1/R_1$, habitat 2 is a black hole sink as defined by Gomulkiewicz et al. (1999), who studied in detail the fate of alleles advantageous in a black hole sink. They have shown that the rare allele will be eliminated from habitat 1 and will only persist in habitat 2 if $f_2(\hat{N}_2)(1 + s_2) > 1$. This is an absolute fitness criterion, independent of s_1 (see Gomulkiewicz et al. 1999 for a discussion of the implications). For a mutation with a small beneficial effect in habitat 2 (small s_2), this criterion can only be satisfied for very small m_{12}, and only when $R_2 > 1$ (central panels of figs. 1, 2*A*). An allele with a larger s_2 can invade in a black hole sink under a broader range of m_{12} (the right-hand-side panels in fig. 1*A*, 1*C*; fig. 2*A*), or even for the entire range of m_{12} (fig. 1*B*). In turn, if $R_2 < 1$, alleles with quite large positive effect in the black hole sink will often be deterministically eliminated from the gene pool no matter how small m_{12} is (fig. 2*B*), although alleles with extremely large s_2 may be maintained (see Gomulkiewicz et al. 1999 for a thorough discussion).

Third, how the dispersal rate from habitat 1 to habitat 2 (m_{12}) affects the condition for invasion of the rare allele depends on whether habitat 2 can sustain a population in the absence of immigration. Consider the biologically most relevant quadrant $0 < m_{12}, m_{21} < 0.5$. If $R_2 \gg 1$, the condition for the invasion becomes more favorable with decreasing m_{12}, and below a certain m_{12}, the allele will invade even if it is lethal in habitat 1 ($s_1^* = 1$; fig. 1*A*, 1*C*). In contrast, if $R_2 < 1$, the condition becomes more favorable with increasing m_{12} (fig. 2*B*). The cases where R_2 is larger than 1, but not by much, especially if also $R_1 > R_2$ (figs. 1*B*, 2*A*), are intermediate: the condition is most favorable at low m_{12}, but s_1^* tends to be a U-shaped function of m_{12}. For example, in the central panel of figure 2*A*, for a given m_{21} the condition is more favorable at $m_{12} \approx 0.5$ than at $m_{12} \approx 0.25$. Note that areas of parameter space where s_1^* is an increasing function of m_{12} also occur in examples in figures 1*A*, 1*C*, but only for $m_{12} \gg 0.5$.

Fourth, the qualitative effect of dispersal rate in the opposite direction (m_{21}) on the condition for invasion of the rare allele seems to depend on R_1 and the magnitude of the effect of the rare allele (s_2) but also on parameter b, which describes the shape of density dependence. If R_1 is large and s_2 is small, the condition tends to become more favorable with increasing m_{21}, at least for m_{12},

$m_{21} < 0.5$ (the central panels in fig. 1*A*, 1*C*). If $R_1 \gg R_2$, this also holds for alleles with a large s_2 (fig. 2*B*). The opposite seems to hold when R_1 is not substantially larger than R_2, s_2 is large, and $b = 1$ (the right panels in fig. 1*A*, 1*B*). Note that the density dependence parameter b has an effect on this relationship for alleles with a large, but not small, s_2 (cf. fig. 1*A*, 1*C*).

As discussed in the introduction, if the habitats are of the same quality ($R_1 = R_2$), habitat 1 is a source and habitat 2 is a sink if $m_{12} > m_{21}$ (in front of the solid line in each graph in fig. 1). The opposite is the case when $m_{12} < m_{21}$. Previous studies have shown that source-sink population dynamics resulting from differences in habitat quality make it difficult for an allele advantageous in the sink but deleterious in the source to be established in the gene pool (Holt and Gaines 1992; Kawecki 1995, 2000*a*; Holt 1996*a*, 1996*b*). Inspection of figure 2 suggests that the same holds when the source-sink structure results solely from asymmetric dispersal rates, at least for alleles with relatively small effects (small s_2) and for m_{12}, $m_{21} \leq 0.5$.

Finally, it is of interest to analyze briefly how the condition for invasion of the rare allele depends on a dispersal rate that is the same in both directions ($m_{12} = m_{21} = m$), that is, along the diagonal lines in figures 1 and 2. If both habitats are of the same quality ($R_1 = R_2$), there is no source-sink structure under symmetric dispersal rates; the condition is most favorable under complete isolation and becomes less favorable as m increases (solid lines in fig. 1). If $R_1 > R_2 > 1$, the condition is still most favorable under complete isolation but is least favorable under an intermediate dispersal rate, which is smaller for alleles with smaller effects (the solid line in the central graph in fig. 2*A* reaches a minimum at $m_{12} = m_{21} \approx 0.05$; that in the right graph, at $m_{12} = m_{21} \approx 0.30$). If $R_1 > 1 > R_2$ (fig. 2*B*), habitat 2 cannot sustain a population in complete isolation, and the condition for invasion of an allele with a small effect is least favorable under low m and becomes more favorable as the symmetric dispersal m increases. These results resemble those obtained in a different, time-continuous model of a two-patch source-sink system (Kawecki 2000*a*); the interpretation and implications of those results are extensively discussed in that paper.

A Quantitative Character under Antagonistic Selection

The Model

In this section we consider a quantitative character under antagonistic selection in the two habitats. If the optima of the trait differ between the habitats, gene flow will prevent the local populations from simultaneously attaining their respective optima, which results in mean fitness reduction.

We ask how the equilibrium adaptedness of the two local populations, measured as the relative mean fitness, depends on the dispersal rates.

A comprehensive analysis of the evolution of a quantitative character in a two-patch source-sink system goes well beyond the scope of this article; here we only analyze a simple case. We assume that the character, denoted Z, is determined by five unlinked diploid loci with identical effects, each with two alleles, "+" and "−." We assume additivity both within and between loci and no environmental variance: the genotypic value of Z equals the phenotypic value and ranges between 0 (homozygote for allele "−" at all loci) and 1 (homozygote for allele "+" at all loci). The expected reproductive success of an individual with phenotype Z in habitat i is $f_i(N_i)w_i(Z)$, where the genotype-independent component of the reproductive success $f_i(N_i)$ is given by equation (2), as before. The relative fitness $w_i(Z)$ of genotype Z in the two habitats is given by

$$w_1(Z) = 1 - sZ^\gamma, \tag{12a}$$

$$w_2(Z) = 1 - s(1 - Z)^\gamma, \tag{12b}$$

where s describes the strength of selection ($0 \leq s \leq 1$) and γ, the shape of the fitness function. Note that equations (12) imply antagonistic directional selection on Z (down in habitat 1, up in habitat 2); $\gamma > 1$ implies diminishing fitness returns as the trait changes in the direction of increased fitness. In contrast to the previous sections, it does matter whether mating takes place before or after dispersal. We assume here that adults disperse and mate randomly after dispersal; with this assumption, the genotype frequencies within a habitat before selection follow the Hardy-Weinberg expectations. The consequences of other mating systems will be the subject of future study. The dynamics of the whole population are given by equation (1) with each $f_i(N_i)$ replaced by $f_i(N_i)\bar{w}_i$, where $\bar{w}_i$ is the mean relative fitness of the local population in habitat i (ranging from $1 - s$ to 1).

For studying the dynamics of the system we used deterministic computer simulations. This approach, described in more detail elsewhere (Kawecki 1998, 2000*b*), iterates the multilocus genotype frequencies and the population density in both habitats. It is thus more direct and flexible than the traditional statistical quantitative genetic approach. Each iteration began with arbitrary haplotype frequencies and continued until none of the allele frequencies changed by more than 10^{-8} in one generation, at which point the system was considered to have converged to an equilibrium. The adequacy of this criterion was checked by running longer simulations for several sets

of parameter values. All results described below assume that $s = 0.5$ and $\gamma = 2$.

The Results

The results are presented in figure 3 as plots of the equilibrium mean relative fitness of the local population at each habitat at the time of census, $\bar{w}_1$ and $\bar{w}_2$, as functions of the two dispersal rates, m_{12} and m_{21}. The graphs are limited to m_{12}, $m_{21} \leq 0.5$; as noted above, this range is biologically most relevant. Convergence to the equilibrium took between several hundred and several tens of thousands of generations. We observed three types of equilibria. Type 1 is a boundary equilibrium, with all loci fixed for the "−" allele (mean trait value $\bar{Z} = 0$ for all individuals, $\bar{w}_1 = 1$, $\bar{w}_2 = 1 − s$) or all loci fixed for the "+" allele ($\bar{Z} = 1$, $\bar{w}_1 = 1 − s$, $\bar{w}_2 = 1$), which implies maximum adaptation to one habitat. In the limiting case of complete isolation ($m_{12} = m_{21} = 0$), all loci could become fixed for the "−" allele in habitat 1 and the "+" allele in habitat 2 (provided that $R_1 > 1$ and $R_2 > 1$). Type 2 is an intermediate equilibrium ($0 < \bar{Z} < 1$) with all loci polymorphic and allele frequency identical across loci (hypergeometric equilibrium; Shpak and Kondrashov 1999). Type 3 is an intermediate equilibrium ($0 < \bar{Z} < 1$) with at most one locus polymorphic; with no locus polymorphic, some loci are fixed for the "+" allele and others for the "−" allele.

Alternative equilibria are likely in multilocus models (Gimelfarb 1998), especially ones involving source-sink structure (Ronce and Kirkpatrick 2001). However, for each set of parameter values reported here, our model seemed to have a unique stable equilibrium distribution of trait Z, and thus unique equilibrium mean fitness values, irrespective of the initial genotype frequencies. Which particular locus would remain polymorphic when the equilibrium was of type 3 depended, of course, on the initial genotype frequencies, but given the identical effects of all loci, this had no effect on the equilibrium distribution of trait Z and the mean fitnesses. Generally, hypergeometric (type 2) equilibria were the outcome for lower dispersal rates than type 3 equilibria. The boundary separating the regions of parameter space with these two types of equilibria (indicated as light solid line in fig. 3A–3C) is sharp; we did not observe other types of equilibria (e.g., with two polymorphic loci). Genetic variance of trait Z tends to be larger at a type 2 than at a type 3 equilibrium, which led to discontinuity of equilibrium variance at the boundary between the two equilibria types (not shown). This, however, did not result in discrete change of mean fitnesses at the boundary.

If both habitats can well sustain a locally adapted population without immigration (R_1, $R_2 \gg 1$; fig. 3A, 3C), the mean relative fitness in habitat 2 at the equilibrium tends to increase with decreasing dispersal rate from habitat 1 to habitat 2 and with increasing dispersal rate from habitat 2 to habitat 1. The reverse applies to the mean fitness in habitat 1. In contrast, if habitat 2 cannot sustain a population ($R_2 < 1$; fig. 3D), the mean relative fitness in habitat 2 either is constant or increases with both dispersal rates; the mean fitness in habitat 1 is either constant or declines with both dispersal rates, although the decline is very slight. In intermediate cases, if R_i is only slightly larger than 1 for one or both habitats, the pattern may be more complicated, that is, saddle shaped (as in fig. 3B). In this case, the dispersal rate from habitat 2 to habitat 1 at which the mean fitness in habitat 2 is maximized depends on the dispersal rate in the opposite direction.

Overall, the results of this section and the "Invasion of a Rare Allele" section seem qualitatively similar. The relative equilibrium fitness in habitat 2 (fig. 3, *center panels*) depends on the dispersal rates in a similar way as the condition for invasion of a rare allele with a small advantageous effect in habitat 2 (figs. 1, 2, *left panels*). Parameter values that here lead to a low mean relative fitness in habitat 2 and a high relative fitness in habitat 1 tend to be unfavorable for invasion of a rare allele deleterious in habitat 1 and beneficial in habitat 2 (cf. fig. 3 with figs. 1, 2). In contrast, however, to the previous section, increasing b (the shape parameter of density dependence) from 1 to 2 had little effect on the equilibrium mean fitness; only results for $b = 1$ were thus included in figure 3. Finally, if dispersal rates are constrained to be symmetric ($m_{12} = m_{21} = m$), the mean fitness is highest in both habitats under complete isolation if R_1, $R_2 > 1$, but if $R_1 > 1 > R_2$, the mean fitness in habitat 2 is highest under the maximum dispersal rate.

How does the ability of trait Z to evolve modify the source-sink population structure? As the trait Z affects the reproductive success in a habitat-specific way, it is possible that a habitat becomes a sink because the local population becomes grossly maladapted, even though it would be a source if the trait had no effect on fitness. Inspection of figure 3, however, reveals that the relative mean fitness at the equilibrium is usually larger in the habitat than would be the source even if the relative mean fitness were 1 in both habitats. (If $\bar{w}_1 = \bar{w}_2 = 1$, the model reduces to the ecological model given by equation [1].) The evolutionary response of the quantitative trait thus further reduces the contribution of the sink habitat to the future gene pool, deepening the source-sink structure of the population. Note that this also applies if both habitats are of the same quality and the source-sink structure is solely a result of asymmetric dispersal rates (fig. 3A, 3B). An exception to this pattern occurs for a narrow parameter range if $R_1 > R_2 > 1$; in figure 3C this is the case between the heavy solid
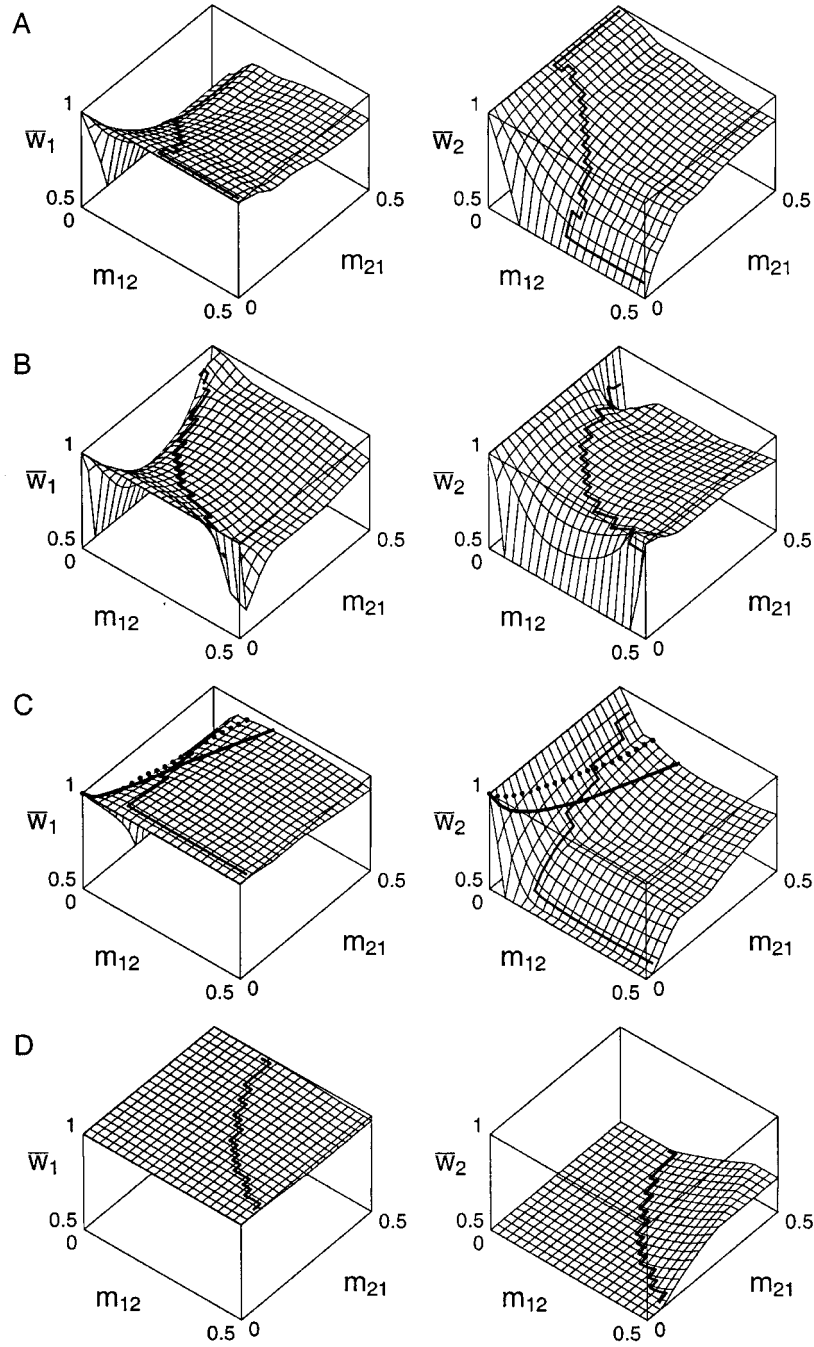
Figure 3: Mean fitness of the population in habitat 1 (*left*) and habitat 2 (*right*) at the equilibrium under antagonistic selection on an additively determined quantitative character, as functions of the dispersal rates. *A*, $R_1 = R_2 = 20$; *B*, $R_1 = R_2 = 2$; *C*, $R_1 = 20$, $R_2 = 10$; *D*, $R_1 = 2$, $R_2 = 0.5$. In all panels, $b = 1$, $s = 0.5$, $\gamma = 2$. The light solid line in each panel separates the regions with different types of equilibria: to the left of the line, an equilibrium with allele frequencies identical across loci (type 1 or type 2 equilibrium), to the right, an intermediate equilibrium with at most one locus polymorphic (type 3 equilibrium). In panel *D*, all intermediate ($\bar{w}_1 < 1$, $\bar{w}_2 > 1 - s$) equilibria are of type 3. The heavy line in panel *C* connects the combinations of dispersal rates resulting in balanced dispersal (i.e., for which neither habitat is source or sink) at the equilibrium under selection on trait *Z*. The dotted line indicates the combinations of dispersal rates that would have led to balanced dispersal if $\bar{w}_1 = \bar{w}_2 = 1$.

and dotted lines. For these combinations of dispersal rates, habitat 1 would be a sink if $\bar{w}_1 = \bar{w}_2 = 1$ despite its superior quality but becomes a source as a result of the evolution of trait Z, resulting in $\bar{w}_1 > \bar{w}_2$. Local adaptation of a quantitative character thus narrows the range of parameters under which the better habitat is a sink, at least under the assumption of this model. Note also that for some combinations of dispersal rates immediately beyond the heavy solid line in figure 3C, $\bar{w}_1 > \bar{w}_2$ despite habitat 1 being a sink. For most of the parameter space, however, the response to natural selection enhances the source-sink structure: habitats that are sinks tend to become deeper sinks.

Discussion

In this article we show that asymmetric dispersal rates have important consequences for adaptive evolution given a trade-off in adaptation to different habitats. These consequences result not only from asymmetric gene flow but also from demographic effects of dispersal rate asymmetry. As noted by Doebeli (1995) and Lebreton et al. (2000), asymmetric per capita dispersal rates (e.g., caused by current or wind) result in a source-sink structure in the absence of quality differences between habitats and may cause a "downstream" habitat of better intrinsic quality to become an effective sink, that is, a net importer of migrants. This occurs if the asymmetric dispersal causes the density in the "downstream" habitat to exceed its carrying capacity. As a result of this overcrowding, the per capita birth rate in the downstream habitat falls below the death rate, with the net immigration from the upstream habitat compensating for the difference.

If the population is originally equally well adapted to both habitats, but there is an emergent source-sink structure as a result of asymmetric dispersal rates, natural selection is biased toward favoring adaptation to the habitat that acts as a source. The condition for invasion of an allele advantageous in habitat 2 but deleterious in habitat 1 tends to be more favorable if habitat 2 is the source and habitat 1 is the sink than if the reverse is the case (fig. 1). A similar conclusion applies to adaptation mediated by a quantitative trait under directional selection in opposite directions in the two habitats: the equilibrium mean fitness is higher in the source than in the sink, even though the habitats are of the same intrinsic quality (fig. 3A, 3B). Asymmetric dispersal may even make selection in a lower quality habitat more effective than in the better habitat if the asymmetry is strong enough (region of $m_{12} \ll m_{21}$ in fig. 3C).

Previous models have shown that source-sink structure due to habitat quality differences tends to make natural selection in the sink less effective than in the source (Holt

and Gaines 1992; Kawecki and Stearns 1993; Kawecki 1995; Holt 1996a, 1996b). This study thus suggests that this conclusion extends to source-sink population dynamics due to asymmetric dispersal rates. This was not a foregone conclusion. In a source-sink system caused by differences in habitat quality with equal dispersal rates, $m_{12} = m_{21} < 0.5$, population density is greater in the source than in the sink habitat. If both habitats cover the same area, more individuals experience the source than the sink habitat. In contrast, when source-sink structure is the result of asymmetric dispersal rates, with no differences in habitat quality, density is greater in the sink. Thus, in our model, source-sink structure tends to favor adaptation to the source habitat even though more individuals experience the sink.

Which combination of dispersal rates creates conditions most favorable for adaptation to a given habitat? The above results suggest that the answer depends on whether the population is initially adapted to that habitat well enough to persist there without immigration. If it is, conditions for adaptation to that habitat are most favorable if there is little or no immigration from other habitats. This applies to the condition for invasion of a rare allele (figs. 1, 2A) as well as to local adaptation mediated by a quantitative trait (fig. 3A–3C). High emigration to the other habitat seems favorable for invasion of rare alleles with small effects but not necessarily with large effects (fig. 1); high emigration from the focal habitat is also favorable in the polygenic model (fig. 3A–3C). If, on the other hand, the focal habitat cannot sustain the initial population without immigration and thus can only be a sink, conditions for adaptation to that habitat are most favorable if dispersal rates in both directions are high. This again holds for both models of adaptation: invasion of a rare allele (fig. 2B) and adaptation mediated by a quantitative trait (fig. 3D). This confirms the qualitative results of a fitness sensitivity analysis by Holt (1996b), generalizing them to alleles with finite effects and to polygenic traits. For a range of cases where the focal habitat can sustain a population but is of a lower quality than the other habitat, conditions for adaptation to the focal habitat seem most stringent at intermediate rates of dispersal from the other habitat (see fig. 2A). That conditions for adaptation to a marginal habitat may be least favorable under intermediate dispersal rates has been previously found in a continuous time model with symmetric dispersal (Kawecki 2000a).

The relationship between the dispersal rates and adaptation studied in this article is not simple because of the manifold effects of dispersal. On the one hand, dispersal leads to gene flow, which brings into the population alleles that have undergone selection elsewhere and are potentially locally maladaptive. On the other hand, immigration into a habitat results in more individuals being

exposed to selection in that habitat. The latter factor is of crucial importance if the original population cannot persist in the focal habitat without immigration. Even if this population harbors rare alleles that, when brought together by selection and recombination, would create a genotype able to persist, the population is likely to go extinct before that happens (Gomulkiewicz and Holt 1995). Too much immigration results in overcrowding, which is likely to reduce the reproductive output even of locally well adapted genotypes. Conversely, emigration reduces local competition, but this also means that a given number of immigrants will constitute a greater fraction of the remaining population. These opposing effects of dispersal have been considered previously in models assuming symmetric dispersal (Holt 1996*a*; Kawecki 2000*a*) and strictly one-way dispersal (Holt and Gomulkiewicz 1997; Gomulkiewicz et al. 1999); the model presented here fills the parameter space between these special cases.

The above results and conclusion are based on only two aspects of adaptive evolution—invasion of rare alleles and selection on an additively determined quantitative trait under antagonistic selection. This is an obvious limitation, and the results may prove qualitatively different in other scenarios if, for example, epistasis is assumed or stochastic effects are included. Nonetheless, it is encouraging to find that the qualitative picture from the analysis of the antagonistic selection on a quantitative trait broadly resembles that from analyzing the condition for invasion of a rare allele with antagonistic pleiotropy, at least when the allele has a small to moderate effect.

Natural selection is biased toward source habitats, and under most scenarios, source habitats are those to which the population is already better adapted, that is, those at the center of the species' ecological niche. It has therefore been postulated that source-sink population structure favors evolutionary conservatism of ecological niches (Holt and Gaines 1992; Holt 1996*b*) except in species with active interference leading to nonideal habitat distributions (Holt 1996*a*). Environmentally imposed asymmetric dispersal can lead to a situation in which a "downstream" habitat acts as a sink even though the population is better adapted to that habitat than to an "upstream" source habitat. Our results suggest that such a "reverse" source-sink structure would promote, rather than hinder, niche evolution, favoring adaptation to the upstream habitat at the expense of adaptation to the downstream habitat. If adaptation to the upstream habitat is not prevented by lack of genetic variation, the "reverse" source-sink structure should thus be transient: species should eventually become better adapted to the upstream habitat. Within the framework of this article, this is only possible when the species initially performs sufficiently well in the upstream habitat to be able to maintain local population there despite the drain

imposed by the net immigration. In particular, it cannot work for habitats initially outside the species' niche (i.e., those in which $R_0 < 1$), which cannot act as sources. Whether a similar mechanism would promote an "upstream" niche shift along a continuous environmental gradient seems to be a promising direction in which this model could be extended. More broadly, our results contribute to the growing recognition of the importance of demographic context and asymmetries in channeling or modifying the direction of adaptive evolution (Vermeij 1999).

APPENDIX

When Can the Coupled Populations Persist if $R_2 < 1$?

The lifetime reproductive success in both habitats is a strictly decreasing function of density (no Allee effect). Therefore, for the existence of an equilibrium with $N_1, N_2 > 0$, it is necessary and sufficient that the dominant eigenvalue of the Jacobian matrix of derivatives corresponding to equations (1), evaluated at $(N_1, N_2) = (0, 0)$, is greater than 1 (Edelstein-Keshet 1988). The Jacobian is $J(0, 0) = \{[R_1(1 - m_{12}), R_2 m_{21}], [R_1 m_{12}, R_2(1 - m_{21})]\}$, and its dominant eigenvalue equals

$$\lambda(0, 0) = \frac{1}{2}\Big[R_1(1 - m_{12}) + R_2(1 - m_{21})$$

$$+ \sqrt{[R_1(1 - m_{12}) - R_2(1 - m_{21})]^2 + 4R_1 R_2 m_{12} m_{21}}\Big]. \tag{A1}$$

The eigenvalue gives the asymptotic rate of increase of the coupled population at densities close to zero. With some algebraic manipulation one can show that $\lambda(0, 0) > 1$ if

$$\frac{R_1 m_{12}}{R_1 - 1} < 1 + \frac{R_2 m_{21}}{1 - R_2}. \tag{A2}$$

From inequality (A2) it follows that, as expected, a smaller R_2 must be compensated by a larger R_1 (i.e., a better-quality source habitat) if the coupled populations are to persist.

The minimum R_1 needed to maintain nonzero equilibrium densities increases with increasing m_{12} and with decreasing m_{21}. A sufficient condition for persistence is $R_1(1 - m_{12}) > 1$; in this case, the species can persist in habitat 1, regardless of what happens in habitat 2. Finally, for given R_1 and R_2, the maximum m_{12} that permits persistence is a linearly increasing function of m_{21}.

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