VOL. 160, NO. 2 THE AMERICAN NATURALIST AUGUST 2002

Metapopulation Structure Favors Plasticity over Local Adaptation

Sonia E. Sultan[1,*] **and Hamish G. Spencer**[2,†]

1. Department of Biology, Wesleyan University, Middletown, Connecticut 06459;
2. Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Submitted April 10, 2001; Accepted January 11, 2002

ABSTRACT: We describe a model for the evolutionary consequences of plasticity in an environmentally heterogeneous metapopulation in which specialists for each of two alternative environments and one plastic type are initially present. The model is similar to that proposed by Moran (1992) but extends her work to two sites. We show that with migration between sites the plastic type is favored over local specialists across a broad range of parameter space. The plastic type may dominate or be fixed even in an environmentally uniform site, and even if the plasticity has imperfect accuracy or bears some cost such that a local specialist has higher fitness in that site, as long as there is some migration between sites with different distributions of environmental states. These results suggest that differences among taxa in dispersal and hence realized migration rates may play a heretofore unrecognized role in their patterns of adaptive population differentiation. Migration relaxes the thresholds for both environmental heterogeneity and accuracy of plastic response above which plasticity is favored. Furthermore, small changes in response accuracy can dramatically and abruptly alter the evolutionary outcome in the metapopulation. A fitness cost to plasticity will substantially reduce the range of conditions in which the plastic type will prevail only if the cost is both large and global rather than environment specific.

Keywords: phenotypic plasticity, metapopulation, variable environments, population divergence, ecotypes, environmental cues.

Individual plasticity has been increasingly recognized as a major source of phenotypic variation in natural populations. When phenotypic responses to environment are functionally adaptive, plasticity allows individual genotypes to maintain fitness under diverse environmental conditions (Travis 1994 and references therein; Sultan 1995 and references therein). By broadening the environmental tolerance of genotypes, such adaptive plasticity may have important consequences for the evolutionary divergence of populations in distinct habitats. Selection in any population will favor individuals that produce a phenotype appropriate to the local environment; when alternative phenotypes are required in different environmental states and each genotype is associated with a single phenotype, this process is expected to produce genetically distinct, locally specialized ecotypes (references in Nagy and Rice 1997). However, if individuals are sufficiently plastic to produce phenotypes appropriate to more than one environment, this type of adaptive population differentiation may be obviated (Levin 1988; Jain 1990; Novak et al. 1991). Thus, adaptive plasticity may have important implications for patterns of local ecotypic diversification and ultimately allopatric speciation (Sultan 2000). Although numerous models have been developed to examine the conditions favoring the evolution of plasticity within a population (reviewed in Scheiner 1993; Schlichting and Pigliucci 1998; see also Tufto 2000), the potential impact of plasticity on population differentiation has not been directly tested.

In this article, we examine the consequences of phenotypic plasticity for a metapopulation of a species living in a spatially variable environment. Previous studies incorporating the effects of population structure into models of plasticity evolution have examined the evolution of reaction norms over subpopulations varying in their optimum phenotype (e.g., Scheiner 1998; de Jong 1999; Tufto 2000). Our work, in contrast, investigates these effects by realistically expanding Moran's (1992) single-population model to a two-site metapopulation: two geographical locations connected by migration and differing in the frequency of environmental states. We address for the first time the following question: When sites differ, will local populations evolve toward distinct monophenic specialists, or can a single plastic strategist be favored in both? Migration has a profound effect on local differentiation (Wright 1931; Hamrick et al. 1995); in the case of a plastic type, this effect may be far more complex than a simple

[*] Corresponding author; e-mail: sesultan@wesleyan.edu.

[†] E-mail: h.spencer@otago.ac.nz.

Am. Nat. 2002. Vol. 160, pp. 271–283.

selection-migration balance (Scheiner 1998). We examine how evolution in the metapopulation will be influenced by migration rates, the degree and pattern of environmental heterogeneity, limits to the response accuracy of the plastic type, possible fitness costs to plasticity, and the interaction of these biologically critical parameters. These parameters are briefly explained below.

In contrast to early estimates based on observed dispersal, indirect methods for measuring gene flow show that populations of many plant and animal species are linked by substantial migration (reviewed by Slatkin 1985; Hamrick et al. 1995). However, migration rates vary widely from species to species as well as among different habitats and years. By testing different migration rates, our model offers insight into the impact of plasticity in taxa with different dispersal abilities and, hence, realized rates of gene flow. We also examine the effect of one-way (directional) gene flow between populations, which may be common in natural systems as a result of factors such as wind direction and differences in site quality (Nagy and Rice 1997; Stanton and Galen 1997; Turelli 1997).

Previous models have found that greater environmental variability favors plasticity within populations (reviewed by Scheiner 1993; see also Scheiner 1998). To examine the possible impact of plasticity on population divergence in a range of ecological situations, we test various spatial distributions of alternative environmental states in two sites, from the extreme case of completely environmentally distinct sites to maximally heterogeneous sites. We also examine cases where the sites differ in heterogeneity, which are undoubtedly an important set of scenarios in nature (Bazzaz 1996).

Also critical to the adaptive success of a plastic strategy is the organism's accurate perception of and response to environmental conditions. Response accuracy depends on both the predictability of environmental variation and the organism's system of perception and response (Moran 1992; DeWitt et al. 1998). Unreliable cues (the decoupling of the developmental and selective environments) can significantly constrain the evolution of plasticity (Lively 1986; de Jong 1999; Tufto 2000). Accuracy may be inherently limited in highly labile environments or when the required phenotypic response entails a long lag time (Kingsolver and Huey 1998); in other cases, accuracy may improve as a result of selective evolution of the organism's perception or response mechanisms (Moran 1992). We test the evolutionary impact of a range of response accuracies as well as of slight (e.g., evolved) shifts in accuracy. Since sites may differ in environmental distribution, we also test the effect of unequal accuracies in different environments.

Finally, we specifically test the evolutionary effects of different possible costs of plasticity (discussed in DeWitt et al. 1998). The idea is widespread that the capacity for plastic response requires inherently costly genetic and cellular machinery, resulting in a universal or global cost of plasticity (Scheiner 1993). Not surprisingly, such a global cost has a powerful impact on evolutionary predictions since, in this case, the fitness of a plastic individual will be less than that of a specialist in every lineage and every environment, even if the accuracy of plastic response is perfect (Van Tienderen 1991). At present, little empirical evidence exists for such inherent costs of plasticity (Tufto 2000 and references therein). However, environment-specific or local costs may be more likely. For instance, a plastic response to an extreme environment may be less adaptively effective than the phenotype of a local specialist (Newman 1992; Reboud and Bell 1997). In such cases, a plastic individual will have lower fitness than a specialist in one but not all environments. We test both global and local costs of plasticity to understand how either inherently costly plasticity mechanisms or environment-specific fitness decrements would influence adaptive divergence. We also examine how the magnitude of each type of plasticity cost affects the evolutionary outcome.

Model

We modeled a clonally reproducing metapopulation spread over two disjunct sites, A and B. At both sites, two environmental states, 1 and 2, occurred at constant frequencies r_s and $1 - r_s$, respectively, where the subscript, s, denotes the site (A or B). Following Moran (1992), three types of organisms were hypothesized: two monophenic specialists, 1 and 2 (one for each environmental state) and one plastic type, P. The specialists always produced the same phenotype, i ($i \in \{1, 2\}$) regardless of the environmental state, whereas the plastic type responded to environmental cues in producing its phenotype. This response was appropriate for the environmental state (i.e., phenotype 1 was produced in environmental state 1 and 2 in 2) a proportion, a_j, of the time, in which j is the environmental state (i.e., $j \in \{1, 2\}$). These two parameters can be thought of as the accuracy of the plastic response. Inaccuracy can arise either because the environmental cues are misleading or because the individual fails to correctly perceive and/or respond to a reliable cue. The relative fitness of a (monophenic) specialist with phenotype i in environmental state j was given by the constant f_{Mij} ($i, j \in \{1, 2\}$). We always assumed that $f_{M11} > f_{M21}$ and $f_{M22} > f_{M12}$, which simply says that a specialist does better in its appropriate environmental state than a specialist for another state. The comparable fitnesses of the plastic type were the constants f_{Pij}. If there is an inherent (global) cost to plasticity, $f_{Pij} < f_{Mij}$ for all i and j; no cost means that (as in Moran 1992) $f_{Pij} = f_{Mij}$.

In site A, therefore, the relative viabilities of the plastic and two specialist types were

$$\begin{aligned} w_{\mathrm{PA}} &= r_{\mathrm{A}}[a_1 f_{\mathrm{P11}} + (1 - a_1) f_{\mathrm{P21}}] \\ &\qquad + (1 - r_{\mathrm{A}})[a_2 f_{\mathrm{P22}} + (1 - a_2) f_{\mathrm{P12}}], \\ w_{1\mathrm{A}} &= r_{\mathrm{A}} f_{\mathrm{M11}} + (1 - r_{\mathrm{A}}) f_{\mathrm{M12}}, \\ w_{2\mathrm{A}} &= r_{\mathrm{A}} f_{\mathrm{M21}} + (1 - r_{\mathrm{A}}) f_{\mathrm{M22}}, \end{aligned} \tag{1}$$

and similar equations (with B in place of A) applied in site B. These equations are simply those of Moran (1992), with the subscripts A and B added to denote the two sites.

At each generation, a certain proportion, m_s ($s \in \{\mathrm{A}, \mathrm{B}\}$), of the population at each site was derived by migration from the other site. If the two sites are isolated from each other, say because of distance (so that $m_{\mathrm{A}} = m_{\mathrm{B}} = 0$), then our model reduces to two cases of Moran's (1992) model, in which one type always wins out. Moran showed that the plastic type will be favored only if the fitness cost of mismatch phenotypes produced by the specialist is greater than the total fitness decrement to the plastic type due to mismatches (inaccuracy) and/or inherent cost. With nonzero migration rates, however, the situation is considerably more complicated: more than one type may persist at a site. More surprising, a type that is not favored within a site may be fixed: for instance, the plastic type may be fixed at a site even if its fitness is lower than that of a monomorphic specialist at that site.

We were unable to fully solve this model analytically, and so we explored parameter space using simulation (a listing of the PASCAL computer program may be obtained on request from H. G. Spencer). In doing so, we assumed that generations are separate and that in each generation the proportions of the three types in a site change according to their relative fitnesses, before migration occurs. For example, the frequency of the plastic type in site A in the subsequent generation, n'_{PA}, is given by

$$\begin{aligned} n'_{\mathrm{PA}} &= (1 - m_{\mathrm{A}}) \frac{n_{\mathrm{PA}} w_{\mathrm{PA}}}{n_{\mathrm{PA}} w_{\mathrm{PA}} + n_{1\mathrm{A}} w_{1\mathrm{A}} + n_{2\mathrm{A}} w_{2\mathrm{A}}} \\ &\qquad + m_{\mathrm{A}} \frac{n_{\mathrm{PB}} w_{\mathrm{PB}}}{n_{\mathrm{PB}} w_{\mathrm{PB}} + n_{1\mathrm{B}} w_{1\mathrm{B}} + n_{2\mathrm{B}} w_{2\mathrm{B}}}, \end{aligned} \tag{2}$$

in which n_{is} is the proportion of type i in site s. This set of equations was iterated until the changes in proportions were very small, at which point an equilibrium was considered to have been reached. (In practice, since the proportions at each site sum to 1, just the absolute values of differences between the proportions of the plastic type and type 1 at each site were calculated. The sum of these four numbers was required to be less than a threshold, usually 5×10^{-8}.) Any runs apparently not reaching equilibrium were investigated further: all runs did eventually reach equilibrium (i.e., no cases of cycling were discovered).

Because we could not be sure whether the equilibrium reached for a particular set of parameter values was globally or just locally stable, we simulated 200 replicate runs that differed only in their initial proportions. We drew initial values for the types at each site from a uniform distribution by using the broken-stick method (Marks and Spencer 1991). The required pseudorandom numbers were produced by the lagged-Fibonacci generator of Marsaglia et al. (1990). In all of our simulations, a unique equilibrium was reached, although convergence was sometimes very slow. Hence, we could ignore any effects of initial proportions when discussing equilibria. Nevertheless, the equilibrium threshold sometimes needed to be set very low (for one set of parameters $< 5 \times 10^{-20}$) so that the simulations did not stop at frequencies different from the true equilibrium values. As part of our program validation, we verified that when there was no migration (i.e., $m_{\mathrm{A}} = m_{\mathrm{B}} = 0$) and no cost to plasticity (i.e., $f_{\mathrm{P}ij} = f_{\mathrm{M}ij}$) we obtained results consistent with Moran's (1992) findings at each site. Similarly, when migration between the two sites was great enough ($m_{\mathrm{A}} = m_{\mathrm{B}} = 0.5$), our system converged to a single-site system, consistent with Moran's (1992) results.

Finally, we investigated special cases of equations (2) with standard analytical techniques, enabling us to draw the figures exactly. All results were consistent with simulations.

Results

Migration in an Environmentally Heterogeneous Metapopulation Favors Plasticity

In Moran's (1992) single-site model, just one of the three types would be favored and, hence, in the equivalent of our simulations, become fixed. In the two-site metapopulation, however, more than one type can be present in the system at equilibrium. Not surprisingly, population structure in conjunction with environmental differences will maintain phenotypic variation: with no migration, a different type can be maintained at each site (for suitable parameter values), an outcome that can be expected to be robust to low levels of migration. As the migration rate increases, however, eventually a point is reached where only one type can be maintained; of course, once m reaches 0.5, the system essentially behaves as a single-site model. For a wide range of parameters, the plastic strategist is likely to be the type that is fixed because metapopulation structure often leads to a high degree of environmental variation.

An example is shown in figure 1: with no migration, we get fixation (in all runs) of the type with the highest

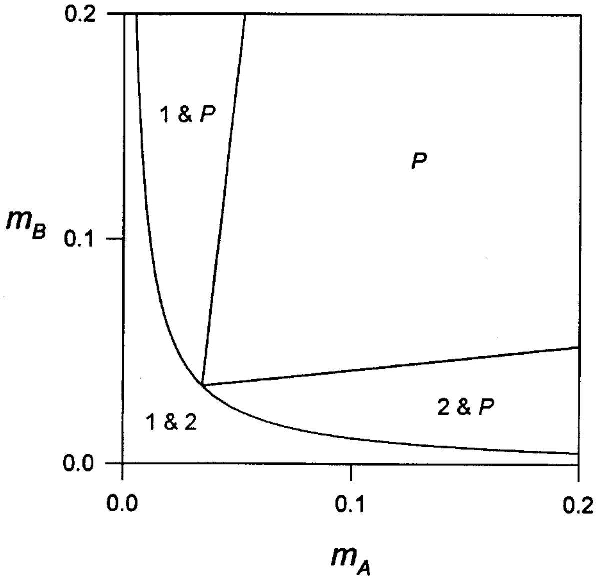

Figure 1: The effect of changing the migration rates between the two environmentally different sites on the type(s) (1, 2, and P) present at equilibrium. The proportion of migrants each generation at site A is given by m_A; that at site B, by m_B. Other parameter values were constant at $r_A = 0.9$, $r_B = 0.1$, $a_1 = a_2 = 0.8$, $f_{P11} = f_{P22} = f_{M11} = f_{M22} = 1.0$, and $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$.

fitness at each site, which in the case of the parameters chosen (low plasticity accuracy and predominance of a different environment at each site) is a different specialist for each site. When the two-way migration is increased to cross a critical threshold, the plastic type becomes fixed at both sites (in all runs), even though it is not the best type anywhere. With the symmetries $m_A = m_B = m$, $r_B = 1 - r_A$, $a_1 = a_2 = a$, $f_{P11} = f_{P22} = f_{M11} = f_{M22} = f_{11}$, and $f_{P12} = f_{M12} = f_{P21} = f_{M21} = f_{12}$, this migration threshold is given by

$$m = \frac{(f_{11} - f_{12})[a(1 - a) - r_A(1 - r_A)]}{af_{11} - f_{12}(1 - a) - 2(f_{11} - f_{12})r_A(1 - r_A)}. \tag{3}$$

In other words, despite limited accuracy and low environmental heterogeneity within sites, conditions in which specialists have higher fitness within each site, a plastic type will be fixed throughout the metapopulation as long as there is a modest rate of migration between the sites. The precise migration threshold favoring plasticity depends on both response accuracy and environmental distribution (fig. 2). With greater accuracy of plastic response, a lower migration threshold is sufficient for the plastic type to be fixed in the system; as response accuracy decreases, higher migration rates are required for the plastic type to predominate. Similarly, as sites approach complete environmental distinctness, higher migration rates are required for the plastic type to be fixed. Nevertheless, these migration thresholds can be surprisingly low. For example, even when two sites consist completely of contrasting environments (i.e., $r_A = 1.0$ and $r_B = 0.0$)—a scenario expected to lead to ecotypic divergence—10% migration in each direction is sufficient to fix a cost-free plastic type in both sites if the plastic response is accurate as little as 67.30% of the time. In figure 1, where two sites have different predominant environmental states and a cost-free plastic type has low response accuracy, a migration rate of only 3.5% in both directions allows the plastic strategist to be fixed throughout the system, even though this type is not the "best" in either site compared with local specialists.

In none of our simulations were all three types present at equilibrium. Since only one type can be favored at a site, the greatest number that can be favored in our two-site model is two. Of course, it is quite likely that a more finely divided population (say, with three sites) would maintain all three types (as might frequency-dependent, density-dependent, or temporally variable fitnesses).

One-Way Migration Can Overwhelm Local Selection

In the case where only one of the sites receives migrants (say, because it is downwind or downstream from the

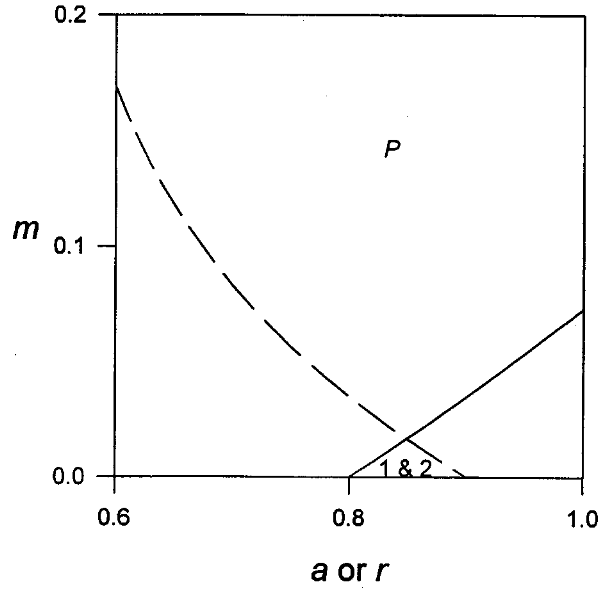

Figure 2: The effect of environmental predictability ($r = r_A = 1 - r_B$; *solid line*) and the plastic type's accuracy ($a_1 = a_2$; *dashed line*) on the migration threshold (given by eq. [3]) above which plasticity is favored. When r was varied, a was fixed at 0.8; when a was varied, r was fixed at 0.9. Other parameter values were $f_{P11} = f_{M11} = f_{P22} = f_{M22} = 1.0$ and $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$.

source site), the result depends on the direction of migration with respect to site heterogeneity. At the source site, Moran's model applies, and whichever type is favored there becomes fixed. If the source site is homogeneous and (in the absence of immigration) a specialist is fixed there, high migration is required for this type to displace the plastic type from a heterogeneous site. However, even low levels of migration from a heterogeneous site where a plastic type is favored can cause this type to be fixed over a local specialist with higher fitness. As a concrete example, suppose that $m_A = m > 0$ and $m_B = 0$ and, in order to keep things tractable, that we have certain other parameter symmetries: $a_1 = a_2 = a$, $f_{P11} = f_{P22} = f_{M11} = f_{M22} = f_{11}$, $f_{P12} = f_{M12} = f_{P21} = f_{M21} = f_{12}$. Following Moran (1992), it is simple to see that the plastic type will be favored and hence fixed at site B if $a > \max(r_B, 1 - r_B)$; if we also have $a > \max(r_A, 1 - r_A)$, it is also fixed at site A. If, however, $r_A > a > 1 - r_A$, such that specialist type 1 is favored at site A, this type will be present at site A only for low values of m. The boundary between these low and high migration rates is given by

$$m = \frac{(f_{11} - f_{12})(r_A - a)}{f_{12} + r_A(f_{11} - f_{12})}. \tag{4}$$

Below this value, the equilibrium proportion of the plastic type is given by

$$\hat{n}_{PA} = \frac{m[f_{12} + r_A(f_{11} - f_{12})]}{(f_{11} - f_{12})(r_A - a)}, \tag{5}$$

a simple increasing linear function of m. (The absence of r_B from eqq. [4] and [5] is due to the fixation of the plastic type at site B.) And even very infrequent migration (e.g., 0.5%) from a site where a plastic type is fixed into a totally homogeneous site (e.g., $r_A = 1$) will maintain both the plastic type and the local specialist at intermediate frequencies in a stable equilibrium.

Migration Relaxes the Environmental Heterogeneity Threshold to Favor Plasticity

As has been shown in single-population models, plasticity is favored by increasing environmental heterogeneity in the metapopulation. However, migration among sites relaxes the heterogeneity threshold for the plastic type to persist in or dominate the system. Figure 3 presents a representative example. Moderate rates of migration (in this case 10% in both directions) cause the plastic type to be fixed throughout the system in a broad range of environmental distributions, even when only one site is heterogeneous (r_A or r_B = 1 or 0). When environmental state 2 predominates throughout the metapopulation (r_A and r_B are both small), type 2 is fixed at both sites, as one would expect. As environmental state 1 becomes increasingly common at either site, initially the plastic type and type 2 coexist at intermediate frequencies, and then only the plastic type is present. As r_A and r_B increase, type 1 appears in the equilibrium, and eventually (as they approach 1) it is fixed throughout.

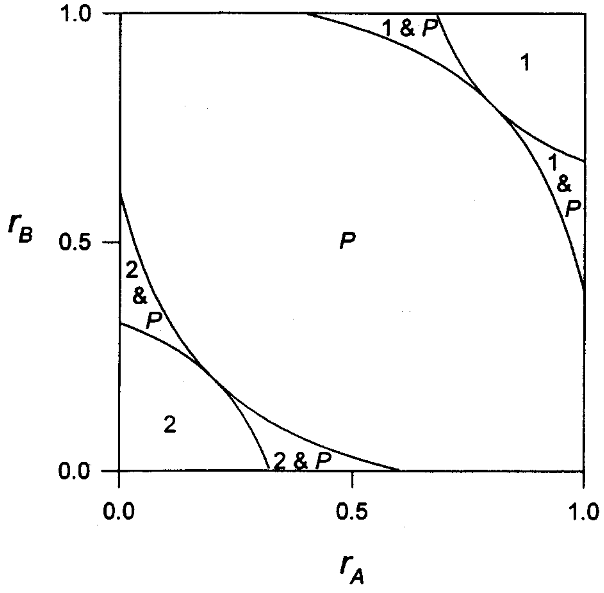

Figure 3: The effect of changing the frequencies of the alternative environmental states at the two sites on the type(s) (1, 2, and P) present at equilibrium. The frequency of state 1 at site A is given by r_A; that at site B, by r_B. Other parameter values were constant at $m_A = m_B = 0.1$, $a_1 = a_2 = 0.8$, $f_{P11} = f_{P22} = f_{M11} = f_{M22} = 1.0$, and $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$.

Metapopulation Structure Permits Suboptimal Types to Fix

As noted above, migration between sites may allow a type to be fixed at a site even when it does not have the highest fitness at that site. In figure 3, for instance, with $r_A = 0.0$ and $r_B = 0.3$, only type 2 is present at equilibrium in both sites, yet $w_{PB} = 0.94 > w_{2B} = 0.91$ ($> w_{1B} = 0.79$). The combination of two-site selection and migration can also favor the plastic type: for example, with $r_A = 0.0$ and $r_B = 0.7$, the plastic type is everywhere fixed, yet $w_{PA} = 0.94 < w_{2A} = 1.00$.

Accuracy of Plastic Response Is a Crucial Parameter

Small changes in the accuracy parameters can cause abrupt rather than gradual replacements. When only the two specialists are present, they occur at equilibrium frequencies unaffected by changes in a_1 and a_2 (since these parameters affect only the viability of the absent plastic type). As a threshold in response accuracy is crossed, one specialist (or both) abruptly becomes extinct, and the frequency of the other may also drop. For example, in figure 4, with a_1 fixed at 0.60, $a_2 \leq 0.73$ gave $\hat{n}_{1A} = \hat{n}_{2B} = 0.716$, $\hat{n}_{1B} = \hat{n}_{2A} = 0.284$ and $\hat{n}_{PA} = \hat{n}_{PB} = 0.000$ (the symmetry of the equilibrium values reflecting that of the parameter values), yet $a_2 = 0.74$ gave $\hat{n}_{PA} = 0.794$, $\hat{n}_{1A} = 0.206$, $\hat{n}_{PB} = 0.919$, $\hat{n}_{1B} = 0.081$, and $\hat{n}_{2A} = \hat{n}_{2B} = 0.000$. Increasing a_2 further led to even lower equilibrium frequencies of type 1. Thus, small differences in the accuracy with which a plastic genotype responds to an environmental cue can lead to wholesale changes in the genetic composition of the system.

Not surprisingly, when the accuracy of response to at least one environmental state is no better than random (a_1 or $a_2 = 0.5$), the specialists are favored; as the accuracy of response to environment increases, the plastic type displaces the specialist for that environmental state. However, as we discuss below, accuracy need not be particularly high for the plastic type to be present or even fixed.

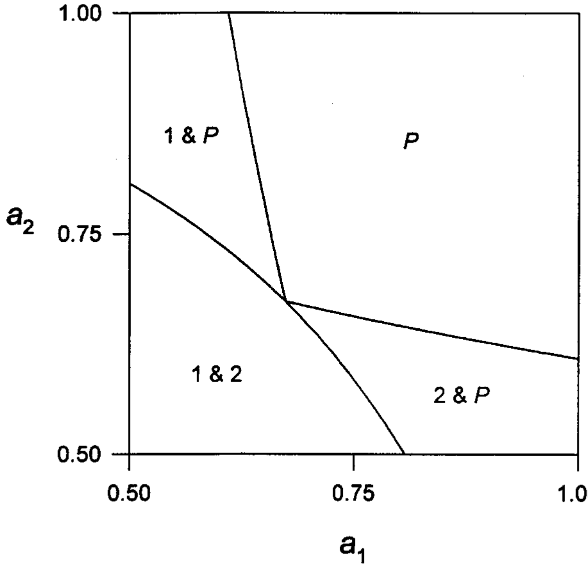

Figure 4: The effect of changing the accuracies with which the plastic type produces the appropriate phenotype on the type(s) (1, 2, and P) present at equilibrium. The accuracy of matching state 1 is given by a_1; that of matching state 2, by a_2. Other parameter values were constant at $m_A = 0.1$, $m_B = 0.1$, $r_A = 0.9$, $r_B = 0.1$, $f_{P11} = f_{P22} = f_{M11} = f_{M22} = 1.0$, and $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$.

Metapopulation Structure Allows Less Accurate Plastic Types

In Moran's (1992) single-site model, the environmental distribution and plastic accuracy parameters, r and a, interacted so that a change in the value of one led to changes in the range of the other that favored plasticity. A similar result occurs in our two-site model, as illustrated in the numerical example of figure 5 (in which $m_A = m_B = m$ and $r = r_A = 1 - r_B$). With low plastic accuracy and environmentally distinct, internally homogeneous sites (r close to 0), only the two specialists will be present. Plasticity is favored above the critical value for a_1 $(= a_2)$ given by

$$a_1 = \frac{f_{11} - f_{12} - m(f_{11} + f_{12}) + \left[(f_{11} - f_{12})^2(1 - 2r)^2(1 - 2m) + (f_{11} + f_{12})^2 m^2\right]^{1/2}}{2(f_{11} - f_{12})}. \tag{6}$$

In essence, the greater the environmental heterogeneity within the two sites (r approaching 0.5), the less accurate the plastic type needs to be in order to prevail over the specialists. (Note that as r increases from 0, both sites become maximally heterogeneous [$r = 0.5$] and therefore more environmentally similar to each other.) The effect of migration can be seen by comparing the lines for $m = 0$ (in which case eq. [6] simplifies to $a_1 = 1 - r$, as in Moran 1992) and $m = 0.1$. The connected population structure allows a less accurate plastic type to succeed for a given level of environmental variation within sites (and a given level of difference in environmental distribution between sites). This effect is most pronounced when the two sites consist entirely of distinct environmental states. Although this situation would tend to favor specialists whenever the accuracy of plastic response is less than perfect, a 10% migration rate reduces to only 0.75 the level of accuracy required to fix the plastic type in both sites.

When response accuracies to both environments are equal, only two outcomes are possible: depending on accuracy, environmental distribution, and migration, either the system will include only the two specialists or the plastic type will be fixed throughout (fig. 5). When the accuracies in different environments are unequal, however, the plastic type may coexist at intermediate frequencies with the specialist for the environment to which plastic response is inaccurate. This polymorphic condition is restricted to a relatively narrow range of parameter space (see also Lively 1986; Wilson and Yoshimura 1994 for similar results regarding coexistence of plastic and monomorphic types). Indeed, even if the accuracy to one environment is extremely poor or even random, the plastic type will be fixed throughout the system as long as the response to the other environment is relatively accurate (fig. 5). This result agrees with Lively (1986), who found

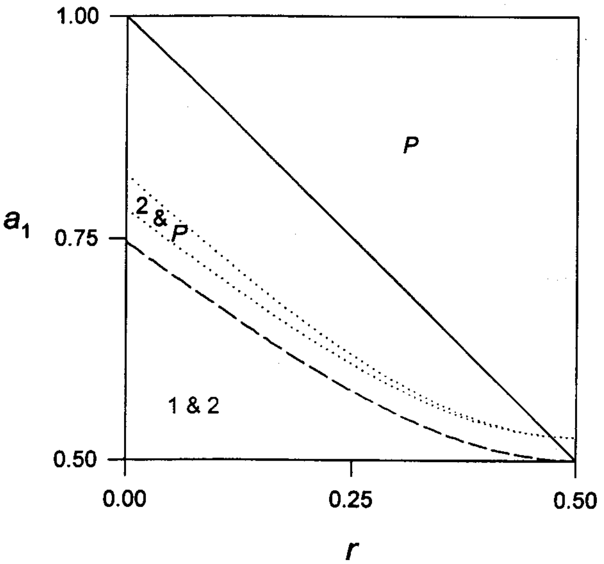

Figure 5: The interactive effect of changing the frequency of alternative environmental states at the two sites and the accuracy with which the plastic type produces the appropriate phenotype on the type(s) (1, 2, and P) present at equilibrium. The two sites have complementary distributions of the two environmental states: the frequency of state 1 at site A is given by r; that at site B, by $1 - r$. The accuracy of plastically matching states 1 and 2 is given by a_1 and a_2, respectively. When $a_2 = a_1$, there are just two regions, one with just type P present and one with types 1 and 2. The solid line shows the demarcation between these two regions when $m = m_A = m_B = 0$; the dashed line, when $m = m_A = m_B = 0.1$. When $a_2 < a_1$, a third region, in which types 2 and P coexist, is present. The boundaries of this region are shown for $a_2 = 0.9a_1$ and $m = 0.1$ by the dotted lines. The fitnesses were constant at $f_{P11} = f_{P22} = f_{M11} = f_{M22} = 1.0$ and $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$.

that plasticity could persist as an evolutionarily stable strategy despite very poor accuracy in one of two environments, providing the average accuracy across environments was greater than random (50%).

Lower Migration May Favor the Origination of Plasticity

We can also use our model to examine constraints on how plasticity may evolve. Suppose that a specialist type 1 is fixed in both sites but that the environment is more variable at the second site. A plastic type, which can better accommodate environmental variation, may evolve from the specialist, but whether it persists in the system will depend both on the accuracy of its response to the environmental variation and on the level of migration between the two sites. As a concrete example, consider figure 6 (*solid lines*), in which site A is overwhelmingly of environmental state 1 ($r_A = 0.9$) but site B is maximally variable ($r_B = 0.5$). A plastic type evolving from the specialist is likely to have a high accuracy in environmental state 1 (say, $a_1 = 0.9$), but it will not survive unless its accuracy in state 2 is greater than some threshold dependent on m. With modest levels of migration (~0.015 in this example), plasticity may be fixed even when the accuracy of response to environmental state 2 is low, indeed, even when it is worse than random ($a_2 < 0.5$). Because a low level of appropriate response is better than none at all, the plastic type is sufficiently favored over the inappropriate specialist at site B that a modest level of migration allows it to prevail also at site A, where it is at a slight fitness disadvantage. Note, however, that increasing migration will raise the threshold value of a_2 above which the plastic type can coexist with the specialist, which indicates that low levels of migration may be necessary for a very inaccurate plastic type to initially persist in a population. This last result is particularly interesting because it shows that, in certain cases, higher migration rates may hinder rather than favor plasticity. Once the plastic type

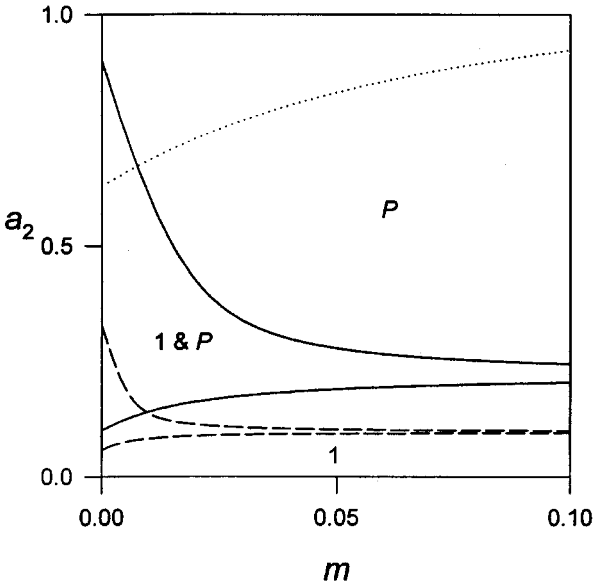

Figure 6: The effect of migration ($m = m_A = m_B$) and the accuracy with which the plastic type produces the appropriate phenotype in environmental state 2 (a_2) on the type(s) (1, 2, and P) present at equilibrium. The solid lines show the boundaries between the (labeled) regions for which type 1 and the plastic type are fixed and coexist for $a_1 = 0.9$ and no cost to plasticity ($f_{P11} = f_{P22} = f_{M11} = f_{M22} = 1.0$, $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$). The dashed lines show the boundaries between these (unlabeled but analogous) regions for $a_1 = 1.0$ and a 1% global cost to plasticity ($f_{M11} = f_{M22} = 1.0$, $f_{M12} = f_{M21} = 0.7$, and $f_{Pij} = 0.99f_{Mij}$ for all i and j). The dotted line shows the boundary between the region in which type 1 is fixed (below the line) and that in which it coexists with the plastic type (above the line) for $a_1 = 1.0$ and a 10% global cost to plasticity ($f_{M11} = f_{M22} = 1.0$, $f_{M12} = f_{M21} = 0.7$, and $f_{Pij} = 0.9f_{Mij}$ for all i and j). Other parameter values were constant at $r_A = 0.9$ and $r_B = 0.5$.

is present, however, an increase in migration rate will favor its fixation throughout the system.

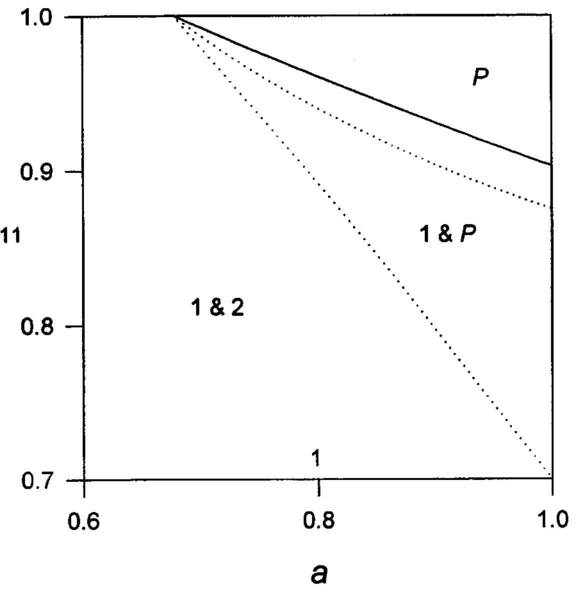

Figure 7: The effect of a trade-off between plastic accuracy ($a = a_1 = a_2$) and the fitness of the appropriate plastic phenotype f_{P11} on the types present at equilibrium for global versus local costs of plasticity. The solid line shows the boundary between the regions for which the plastic type is fixed (above the line) and types 1 and 2 coexist (below the line) for a global cost to plasticity ($f_{\mathrm{M11}} = f_{\mathrm{M22}} = 1.0$, $f_{\mathrm{M12}} = f_{\mathrm{M21}} = 0.7$, and $f_{\mathrm{P}ij} = f_{\mathrm{P11}} f_{\mathrm{M}ij}$ for all *i* and *j*). The dotted lines show the boundaries between the labeled regions with an environmentally specific cost to plasticity in which just the appropriate phenotype in environmental state 1 has a cost ($f_{\mathrm{P22}} = f_{\mathrm{M11}} = f_{\mathrm{M22}} = 1.0$, $f_{\mathrm{P12}} = f_{\mathrm{M12}} = f_{\mathrm{P21}} = f_{\mathrm{M21}} = 0.7$). Other parameter values were constant at $m_{\mathrm{A}} = m_{\mathrm{B}} = 0.05$, $r_{\mathrm{A}} = 0.8$, and $r_{\mathrm{B}} = 0.2$.

Difference between Global and Environmentally Specific Costs of Plasticity Is Crucial

If plasticity itself bears a cost, such a fitness cost can occur in two distinct ways. First, it can be global, due to inherent costs of environmental perception and response mechanisms. In this case, the fitness of the plastic types will be some constant proportion, *c*, of all the corresponding fitnesses of the specialists: $f_{\mathrm{P}ij} = cf_{\mathrm{M}ij}$ for all *i* and *j* and $0 \leq c < 1$. Alternatively, the cost of plasticity may be environment specific; for instance, an extreme environment may demand a distinctive phenotype that only a canalized specialist can produce, while there may be no fitness decrement in more moderate conditions.

Our results show that a substantial, global cost can severely reduce the ability of plasticity to prevail over specialization. In figure 6, for instance, when the cost is small (1%; $c = 0.99$), the pattern of transitions is the same as with no cost: low accuracy ($a_2 \approx 0$) leads to type 1 being fixed, and as accuracy increases, the plastic type coexists with and finally displaces it completely. With a higher cost, however, the boundaries can move quite dramatically. With a 10% global cost to plasticity ($c = 0.9$), the plastic type is never fixed (since its fitness is always less than that of type 1 even in site A); at best (if it is sufficiently accurate), it coexists with type 1. This result suggests that a substantial cost of plasticity may be a greater hindrance to its evolution than an inaccurate response to environmental cues. Of course, this conclusion depends on the scales on which these two factors are measured, but our scales seem natural in that they are relative to the optimal value for each factor (e.g., perfect accuracy and relative fitness of 1, or no cost).

Compared to a global cost, an environmentally specific cost to plasticity leads to a smaller reduction in the proportion of parameter space in which plasticity is fixed (see, e.g., fig. 7). Note that an environmentally specific cost has an asymmetric impact (fig. 7): there is now a region of parameter space in which the plastic type and type 1 coexist, type 2 being forced out by the plastic type over a wider range of parameter space (because the plastic type bears no cost in producing phenotype 2). This difference, however, may be trivial or even nonexistent if the accuracy of the plastic type's response is poor; for higher accuracies, by contrast, the two types coexist for a wide range of local costs.

A cost to plasticity also raises the threshold for environmental heterogeneity necessary to favor the plastic type (fig. 8): in more homogeneous environments, specialists are favored unless the cost of plasticity is low, this effect being stronger for global rather than environmentally specific costs. Likewise, the migration rate required for the plastic type to dominate the system is greater with an increasing cost to plasticity (fig. 9). Again, this effect is far more pronounced with a global than a local cost. Figures 8 and 9 (like fig. 7) show that intermediate environmentally specific costs permit the coexistence of the plastic type with one specialist. Figures 7–9 also confirm that changes in accuracy, levels of environmental heterogeneity, and migration rates all appear to have less effect on whether or not plasticity is favored than do changes in the cost of plasticity, particularly global cost.

Real Populations May Not Be at Predicted Equilibria

One aspect of the model that at first appears a technical matter but that almost certainly has biological relevance is the slow convergence to equilibrium (see "Model"). If fitness differences among different types are small (as would seem likely if we consider parameter values to be evolvable), many systems need not be at or even close to

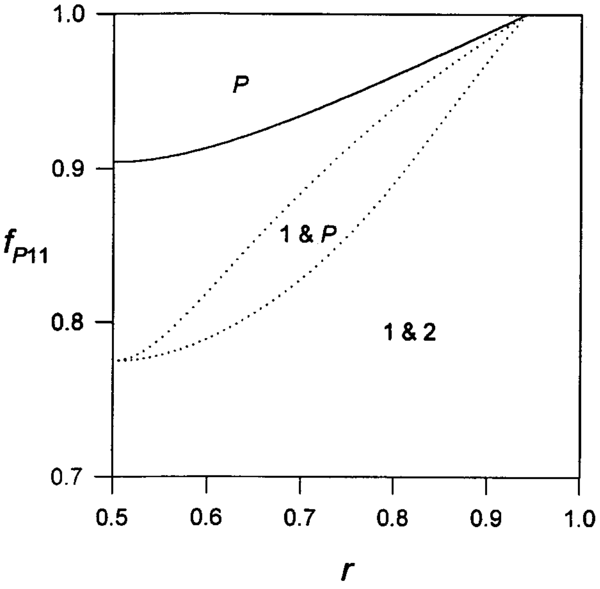

Figure 8: The effect of a trade-off between environmental predictability ($r = r_A = 1 - r_B$) and the fitness of the appropriate plastic phenotype f_{P11} on the types present at equilibrium, for global versus local costs of plasticity. The solid line shows the boundary between the regions for which the plastic type is fixed (above the line) and types 1 and 2 coexist (below the line) for a global cost to plasticity ($f_{M11} = f_{M22} = 1.0$, $f_{M12} = f_{M21} = 0.7$, $f_{Pij} = f_{P11} f_{Mij}$ for all i and j). The dotted lines show the boundaries between the labeled regions with an environmentally specific cost to plasticity in which just the appropriate phenotype in environmental state 1 has a cost ($f_{P22} = f_{M11} = f_{M22} = 1.0$, $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$). Other parameter values were constant at $m_A = m_B = 0.05$ and $a_1 = a_2 = 0.8$.

equilibrium. Furthermore, in any finite population, different equilibria could be reached. If, at some point, the proportion of one of the types falls below the value corresponding to a single individual, that type would become extinct. In the infinite-population model, however, this type would still be present at the predicted equilibrium.

Discussion

Our model of a two-site metapopulation with two specialists and a plastic type provides several new and fundamental insights into the evolutionary dynamics of phenotypic plasticity and local adaptation. In a metapopulation with migration, plasticity is favored over local specialists in a surprisingly broad range of conditions. In particular, the threshold for accuracy of plastic response is much relaxed in a metapopulation as a result of migration, as is that for environmental heterogeneity. These results reveal for the first time the importance of metapopulation structure to the evolution of plasticity. One key implication is that differences among taxa in among-site migration rates may play a heretofore unrecognized role in their patterns of adaptive population differentiation. Our results also show that a high, inherent cost powerfully constrains the evolution of plasticity, such that evolved plasticity is likely to bear only environment-specific or negligible global costs.

Plasticity versus Local Specialization: The Effect of Migration

In previous models of plasticity evolution within one site (reviewed by Scheiner 1993), any inaccuracy or cost to plasticity is likely to reduce the fitness of a plastic type below that of a local specialist as long as one environment is more frequent than the other. These models suggest that plasticity will be favored only in very variable environments, or with extremely high accuracy and negligible cost. Introducing migration among populations, however, dramatically broadens the conditions in which plasticity may be favored. Despite limited accuracy and low environmental heterogeneity within sites—conditions in which local specialists have higher fitness within each site—a

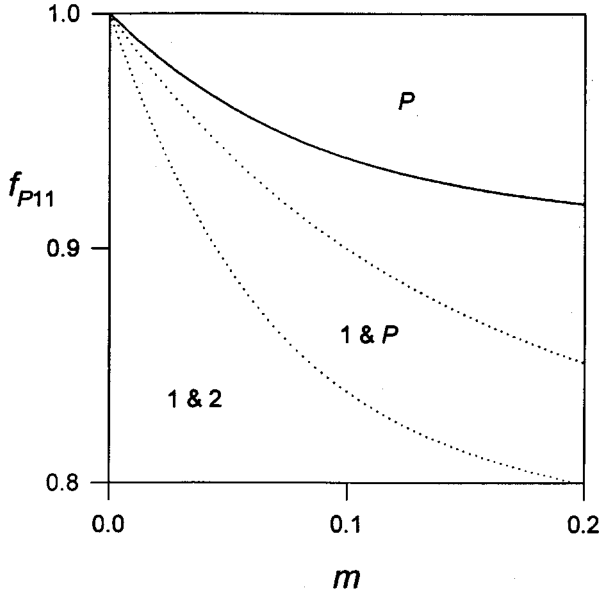

Figure 9: The trade-off between migration rate ($m = m_A = m_B$) and the fitness of the appropriate plastic phenotype f_{P11} on the types present at equilibrium for different costs of plasticity. The solid line shows the boundary between the regions for which the plastic type is fixed (above the line) and types 1 and 2 coexist (below the line) for a global cost to plasticity ($f_{M11} = f_{M22} = 1.0$, $f_{M12} = f_{M21} = 0.7$, and $f_{Pij} = f_{P11} f_{Mij}$ for all i and j). The dotted lines show the boundaries between the labeled regions with an environmentally specific cost to plasticity in which just the appropriate phenotype in environmental state 1 has a cost ($f_{P22} = f_{M11} = f_{M22} = 1.0$, $f_{P12} = f_{M12} = f_{P21} = f_{M21} = 0.7$). Other parameter values were constant at $a_1 = a_2 = 0.8$, $r_A = 0.8$, and $r_B = 0.2$.

plastic type will be fixed throughout the metapopulation as long as there is a modest rate of migration between sites. Scheiner's (1998) model of a one-dimensional cline with postplasticity dispersal also showed that, in general, higher migration rates favor plasticity (but see de Jong 1999 and Tufto 2000 for limits to this model).

Our results suggest that the inclusion of realistic migration rates may substantially alter evolutionary predictions regarding plasticity versus local specialization in systems where plastic genotypes are available and reasonably accurate. (Note that in contrast to some previous evolutionary models of plasticity vs. specialization—e.g., Van Tienderen 1991—in most of our simulations we assume a conservative plasticity accuracy of 80%.) The evolutionary implications of these results depend on the extent of interpopulation migration in diverse taxa, a subject about which much remains to be learned (Cain et al. 2000). Migration distances depend on population size and habitat as well as on the dispersal capacity, life history, and behavior of the species (Slatkin 1985; Hamrick et al. 1995; Goodell et al. 1997). In both animals and plants, indirect multilocus estimates reveal extensive gene flow among natural populations in many taxa (ranging from 1%–80%; references in Slatkin 1985; Broyles et al. 1994; Hamrick et al. 1995). Thus, the migration rates explored in our model fall well within the range of naturally occurring rates in animal and plant populations.

If, as our model shows, migration may promote plasticity over local specialization, differences among taxa in migration rates may contribute to differences in patterns of population (and ultimately species) differentiation. Taxa with greater dispersal capacities may be more likely to consist of plastic individuals rather than locally specialized ecotypic populations. In plants, high migration rates are characteristic of weedy, colonizing species (Baker 1965, 1974) as a result of both long-range propagule dispersal and relatively continuous distribution of populations across wide geographic ranges (Levin 1981, 1995). Along with high interpopulation migration, colonizing species are characterized by unusually broad plasticity and often show little ecotypic differentiation (Levin 1988; Novak et al. 1991; Bazzaz 1996). This well-known suite of traits may thus reflect the evolutionary interaction of migration and plasticity revealed by the model. It would be interesting to examine the relation of plasticity to migration rates in widespread animal taxa as well. It is also worth noting that in both plants and animals, plasticity may be promoted by habitat fragmentation, since interpopulation gene flow often increases markedly among small, patchily distributed populations (Nason and Hamrick 1997 and references therein). Thus continued human-mediated habitat disruption may increasingly promote the evolution of plasticity over local ecotypes in surviving taxa.

We also examined the evolutionary effects of directional (one-way) gene flow, which is likely to be common in nature (Stanton and Galen 1997; Turelli 1997). Previous models have shown that such migration bias can oppose local adaptation to poor environmental patches (Pulliam 1988; Kawecki 1995). We show that the specific direction with respect to site heterogeneity will have a key impact on the evolution of the metapopulation. Even low levels of migration from a heterogeneous site (where the plastic type is favored) can cause this type to be fixed over a local specialist with higher fitness or, with extremely low migration, to persist with it in a stable equilibrium. The latter result is particularly significant because, in nature, occasional gene flow may occur from many sources. Hence, rare migration events may maintain genetic variation for plasticity even in environmentally homogeneous populations.

Accuracy of Plastic Response

As in Moran's (1992) single-site model, we found that the greater the environmental heterogeneity in the system, the less accurate the plastic type must be to prevail over local specialists. Furthermore, our results show that the presence of migration relaxes the thresholds for both accuracy and environmental variability. Indeed, given moderate migration rates, plasticity will be fixed throughout the system despite considerable inaccuracy and consequent phenotypic mismatches. The surprisingly low accuracy threshold suggests that plasticity may be favored in metapopulation systems even when environmental cues are unreliable, when organisms do not always perceive those cues accurately, or when the response lag time is long enough that the environment may have changed (Newman 1992; DeWitt et al. 1998; Kingsolver and Huey 1998). This result is particularly interesting since response inaccuracy can significantly constrain the evolution of plasticity within populations (Moran 1992; Scheiner 1993; Padilla and Adolph 1996; de Jong 1999; Tufto 2000).

In nature, the external and organismic factors that influence plastic response accuracy may well differ among environments (Lively 1986; Weinig 2000). By independently varying the two response accuracies in our model, we found that plasticity could be favored even with random accuracy to one environment, provided that environment was relatively infrequent or the response to the other environment was good. Thus, a plastic type may dominate a heterogeneous metapopulation despite surprisingly poor adaptive plasticity to one environment.

Our results also show that subtle changes in plastic accuracy can profoundly affect the evolutionary outcome in the metapopulation. For example, slight increases in accuracy can lead to the abrupt replacement of the specialists by the plastic type throughout the system. This suddenness is particularly interesting because such subtle increases might result from adaptive evolution of the plastic organism's environmental sampling or perception ability (Moran 1992; Tufto 2000; see Newman 1992; Tauber and Tauber 1992; Tollrian and Harvell 1999 for examples of complex cue systems) or of its response timing (Eiguchi et al. 1993). Accuracy might also slightly increase in just one environment because of selective change in the organism's response to a particular cue or because of an external change that increases that cue's reliability. In this case, our model predicts that either one or both specialists may be abruptly replaced, depending on response accuracy to the second environment. Note that response accuracy may also decrease slightly in a population such that the plastic type will be lost, for instance if habitat disturbance causes greater environmental unpredictability (Moran 1992).

The role of response accuracy in this and previous models suggests some general predictions as to the traits and taxa in which plasticity rather than local specialists would be predicted to evolve. Response lag time sufficient to reduce accuracy below the critical threshold may be most likely in the case of certain developmental traits, while physiological and behavioral aspects of plasticity may be extremely rapid (Kingsolver and Huey 1998; see references in Sultan 1995; Tollrian and Harvell 1999). Patterns of plasticity versus specialization may also differ among taxa for a given trait, since even congeneric species may differ in the rapidity of a particular plastic response (Bell and Sultan 1999).

Possible Costs of Plasticity

Our results for a metapopulation confirm previous one-site quantitative genetic and optimality models (Lynch and Gabriel 1987; Van Tienderen 1991; Moran 1992) in showing that a cost to plasticity may have a powerful impact on evolutionary outcomes regarding plasticity versus environmental specialization. Our results clarify that this impact depends on both the magnitude of such fitness costs and on whether they occur globally (in all environments) or only locally. We found that plasticity cost may interact with response accuracy: the greater the cost, the greater the accuracy required for the plastic type to be fixed (see Moran 1992 for a similar result within a single population). Thus a plastic type bearing a high fitness cost is unlikely to persist unless it provides highly accurate environmental matching. In general, the negative impact of increased cost (especially global cost) on the fixation or persistence of a plastic type is greater than that of reduced response accuracy (presumably since such a fitness cost applies to every plastic individual in the system while inaccuracy affects only some proportion). For instance, a 10% plasticity cost in all environments can completely prevent the plastic type from being fixed. However, such powerful evolutionary effects depend on the magnitude of the cost: even a global cost will have little effect if it is small (e.g., 1% fitness reduction in all environments). This result agrees with that of Gomulkiewicz and Kirkpatrick (1992), who argued that global plasticity costs will not substantially constrain the evolution of adaptive plasticity unless they are large. Thus, to understand the potential evolutionary importance of plasticity costs, it is essential to know their likely magnitude.

Global plasticity costs could arise if there were an intrinsic "maintenance" cost to the genetic, cellular, or biochemical mechanisms of plastic response (discussed by DeWitt et al. 1998). At present, empirical evidence in support of such global fitness costs is scant (Dorn et al. 2000; Tufto 2000 and references therein). Moreover, even if the capacity for plastic response did bear inherent costs, it seems unlikely that such costs would be sufficient to markedly reduce fitness—or, as our model predicts, plastic genotypes of this type would not persist. Indeed, one reason that global maintenance costs may be difficult to detect empirically (Gomulkiewicz and Kirkpatrick 1992) is that they may be extremely small in magnitude (Sultan 1992 and references therein).

Our results show that environment-specific costs of plasticity constitute a far weaker constraint on the success of plastic organisms in a metapopulation. Such local plasticity costs may be biologically realistic, since the environmental sampling and response costs of plasticity may vary from one environmental state to another (DeWitt et al. 1998 and references therein; Kingsolver and Huey 1998). A fitness disadvantage relative to local specialists (a functional cost or limit to plasticity) may occur for certain traits in those environments in which either range of phenotypic expression or speed of response is likely to be critical (Newman 1992). Note too that fitness costs or limits to plasticity arising from genetic architecture, trait correlations, or response mechanisms and timing are themselves modifiable by natural selection (Van Tienderen and Koelwijn 1994; DeWitt et al. 1998; Schlichting and Pigliucci 1998). Thus, many costs to plasticity are likely to be environment specific rather than global and to be selectively minimized, conditions that would reduce their impact as constraints to the spread of plastic organisms. The great interest in plasticity costs may be in part because such costs offer an optimality explanation for the fact that ogranisms are not infinitely plastic (DeWitt et al. 1998). However, in addition to possible genetic, biochemical, or functional costs to plastic systems, a lack of appropriate genetic variation for these complex response systems (Tufto 2000 and references therein), together with inherent and external constraints on their accuracy, may account for the fact that plasticity, like other aspects of adaptation, is imperfect.

Acknowledgments

S.E.S.'s visit to the University of Otago was supported by a grant from the Department of Zoology's International Visitor Programme. The research was also supported by a grant to S.E.S. from the Andrew Mellon Foundation's Program in Conservation and the Environment. We thank two anonymous reviewers for thoughtful and constructive comments on the manuscript.

Literature Cited

Baker, H. G. 1965. Characteristics and modes of origin of weeds. Pages 147–172 *in* H. G. Baker and G. L. Stebbins, eds. The genetics of colonizing species. Academic Press, New York.

———. 1974. The evolution of weeds. Annual Review of Ecology and Systematics 5:1–24.

Bazzaz, F. A. 1996. Plants in changing environments: linking physiological, population and community ecology. Cambridge University Press, Cambridge.

Bell, D. L., and S. E. Sultan. 1999. Dynamic phenotypic plasticity for root growth in *Polygonum*: a comparative study. American Journal of Botany 86:807–819.

Broyles, S. B., A. Schnabel, and R. Wyatt. 1994. Evidence for long-distance pollen dispersal in milkweeds (*Asclepias exaltata*). Evolution 48:1032–1040.

Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87:1217–1227.

de Jong, G. 1999. Unpredictable selection in a structured population leads to local genetic differentiation in evolved reaction norms. Journal of Evolutionary Biology 12:839–851.

DeWitt, T. J., A. Sih, and D. S. Wilson. 1998. Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13:1–8.

Dorn, L. A., E. H. Pyle, and J. Schmitt. 2000. Plasticity to light cues and resources in *Arabidopsis thaliana*: testing for adaptive value and costs. Evolution 54:1982–1994.

Eiguchi, M., R. Sano, H.-Y. Hirano, and Y. Sano. 1993. Genetic and developmental bases for phenotypic plasticity in deepwater rice. Journal of Heredity 84:201–205.

Gomulkiewicz, R., and M. Kirkpatrick. 1992. Quantitative genetics and the evolution of reaction norms. Evolution 46:390–411.

Goodell, K., D. R. Elam, J. D. Nason, and N. C. Ellstrand. 1997. Gene flow among small populations of a self-incompatible plant: an interaction between demography and genetics. American Journal of Botany 84:1362–1371.

Hamrick, J. L., M. J. W. Godt, and S. L. Sherman-Broyles. 1995. Gene flow among plant populations: evidence from genetic markers. Pages 215–232 *in* P. C. Hoch and A. G. Stephenson, eds. Experimental and molecular approaches to plant biosystematics. Missouri Botanical Garden Press, St. Louis.

Jain, S. K. 1990. Variation and selection in plant populations. Pages 199–230 *in* K. Wohrmann and S. K. Jain, eds. Population biology: ecological and evolutionary viewpoints. Springer, Berlin.

Kawecki, T. J. 1995. Demography of source-sink populations and the evolution of ecological niches. Evolutionary Ecology 9:38–44.

Kingsolver, J. G., and R. B. Huey. 1998. Evolutionary analysis of morphological and physiological plasticity in thermally variable environments. American Zoologist 38:545–560.

Levin, D. A. 1981. Dispersal versus gene flow in plants. Annals of the Missouri Botanical Garden 68:233–253.

———. 1988. Plasticity, canalization and evolutionary stasis in plants. Pages 35–45 *in* A. J. Davy, M. J. Hutchings, and A. R. Watkinson, eds. Plant population ecology. Blackwell Scientific, Oxford.

———. 1995. Plant outliers: an ecogenetic perspective. American Naturalist 145:109–118.

Lively, C. M. 1986. Canalization versus developmental conversion in a spatially variable environment. American Naturalist 128:561–572.

Lynch, M., and W. Gabriel. 1987. Environmental tolerance. American Naturalist 129:283–303.

Marks, R. W., and H. G. Spencer. 1991. The maintenance of single-locus polymorphism. II. The evolution of fitnesses and allele frequencies. American Naturalist 138:1354–1371.

Marsaglia, G., A. Zaman, and W. W. Tsang. 1990. Toward a universal random number generator. Statistics & Probability Letters 9:35–39.

Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. American Naturalist 139:971–989.

Nagy, E. S., and K. J. Rice. 1997. Local adaptation in two subspecies of an annual plant: implications for migration and gene flow. Evolution 51:1079–1089.

Nason, J. D., and J. L. Hamrick. 1997. Reproductive and genetic consequences of forest fragmentation: two case studies of Neotropical canopy trees. Journal of Heredity 88:264–276.

Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. BioScience 42:671–678.

Novak, S. J., R. N. Mack, and D. E. Soltis. 1991. Genetic variation in *Bromus tectorum*: population differentiation in its North American range. American Journal of Botany 78:1150–1161.

Padilla, D. K., and S. C. Adolph. 1996. Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. Evolutionary Ecology 10:105–117.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Reboud, X., and G. Bell. 1997. Experimental evolution in *Chlamydomonas*. III. Evolution of specialist and generalist types in environments that vary in space and time. Heredity 78:507–514.

Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. Annual Review of Ecology and Systematics 24:35–68.

———. 1998. The genetics of phenotypic plasticity. VII. Evolution in a spatially structured environment. Journal of Evolutionary Biology 11:303–320.

Schlichting, C. D., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer, Sunderland, Mass.

Slatkin, M. 1985. Gene flow in natural populations. Annual Review of Ecology and Systematics 16:393–430.

Stanton, M. L., and C. Galen. 1997. Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup *Ranunculus adoneus*. American Naturalist 150:143–178.

Sultan, S. E. 1992. Phenotypic plasticity and the neo-Darwinian legacy. Evolutionary Trends in Plants 6: 61–71.

———. 1995. Phenotypic plasticity and plant adaptation. Acta Botanica Neerlandica 44:1–21.

———. 2000. Phenotypic plasticity for plant development, function and life-history. Trends in Plant Science 5: 537–542.

Tauber, C. A., and M. J. Tauber. 1992. Phenotypic plasticity in *Chrysoperla*: genetic variation in the sensory mechanism and in correlated reproductive traits. Evolution 46:1754–1773.

Tollrian, R., and D. C. Harvell, eds. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, N.J.

Travis, J. 1994. Ecological genetics of life-history traits: variation and its evolutionary significance. Pages 171–204 *in* L. A. Real, ed. Ecological genetics. Princeton University Press, Princeton, N.J.

Tufto, J. 2000. The evolution of plasticity and nonplastic spatial and temporal adaptations in the presence of imperfect environmental cues. American Naturalist 156: 121–130.

Turelli, M. 1997. Environmental heterogeneity, maternal effects, and spatial patterns of genetic variation. Evolution 51:93–94.

Van Tienderen, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. Evolution 45:1317–1331.

Van Tienderen, P. H., and H. P. Koelewijn. 1994. Selection on reaction norms, genetic correlations and constraints. Genetical Research 64:115–125.

Weinig, C. 2000. Plasticity versus canalization: population differences in the timing of shade avoidance responses. Evolution 54:441–451.

Wilson, D. S., and J. Yoshimura. 1994. On the coexistence of specialists and generalists. American Naturalist 144: 692–707.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.

Associate Editor: Johanna M. Schmitt