Evolution, 55(8), 2001, pp. 1520–1531

WHEN SOURCES BECOME SINKS: MIGRATIONAL MELTDOWN IN HETEROGENEOUS HABITATS

OPHÉLIE RONCE[1,2] AND MARK KIRKPATRICK[1,3]
[1]*Section of Integrative Biology C0930, University of Texas, Austin, Texas 78712*
[3]*E-mail: Kirkpatrick@mail.utexas.edu*

Abstract.—We consider the evolution of ecological specialization in a landscape with two discrete habitat types connected by migration, for example, a plant-insect system with two plant hosts. Using a quantitative genetic approach, we study the joint evolution of a quantitative character determining performance in each habitat together with the changes in the population density. We find that specialization on a single habitat evolves with intermediate migration rates, whereas a generalist species evolves with both very low and very large rates of movement between habitats. There is a threshold at which a small increase in the connectivity of the two habitats will result in dramatic decrease in the total population size and the nearly complete loss of use of one of the two habitats through a process of ''migrational meltdown.'' In some situations, equilibria corresponding to a specialist and a generalist species are simultaneously stable. Analysis of our model also shows cases of hysteresis in which small transient changes in the landscape structure or accidental demographic disturbances have irreversible effects on the evolution of specialization.

Key words.—Heterogeneity, local adaptation, migration, source-sink dynamics, specialization.

Received September 9, 2000. Accepted April 18, 2001.

Phytophagous insects feeding on different plant species and parasites exploiting different hosts face conflicting selection pressures due to the heterogeneous nature of their habitats. It is therefore not surprising that the study of such systems has led to so many fruitful insights (Futuyama and Moreno 1988; Jaenike 1990; Via 1991) and raised so many theoretical questions about broad issues, such as the evolution of source-sink dynamics (Pulliam 1988; Holt 1996b) and the evolution of ecological specialization (Levins 1968; Berenbaum 1996; Fry 1996). The nature of the genetic and ecological factors that limit the niche breadth of a species in a heterogeneous habitat still remains largely an open question. In this paper, we suggest that host range evolution may be very sensitive to demographic disturbances affecting both population densities and migration patterns in a heterogeneous habitat.

The present theoretical study is inspired by the dynamics and rapid evolution of a heterogeneous metapopulation of the checkerspot butterfly, *Euphydryas editha* (Singer and Thomas 1996; Thomas et al. 1996; Boughton 1999). Before 1989, larvae of *E. editha* were found on two host plants. Populations on *Collinsia torreyi* behaved as source populations exporting migrants to pseudo-sink populations on *Pedicularis semibarbata.* The accidental extinction of populations on *Collinsia*, due to an unusual summer frost in the early 1990s, was followed by a complete reversal in source-sink dynamics and a dramatic narrowing of the butterfly diet (Boughton 1999). Since the disturbance, local populations have not regained the ability to use their former host, *Collinsia.* This example suggests that demographic disturbances may play an important role in the evolution of ecological specialization leading to rapid shifts in host use.

Several models have explored how the interactions between demography and local adaptation may shape the niche of a species. Kirkpatrick and Barton (1997) used a quantitative genetic model to study the evolution of a species range in a spatially variable and continuous habitat with local migration. Because migration from a large central population prevented local adaptation in small peripheral populations, they found that increased migration limited the species range (see also García-Ramos and Kirkpatrick 1997). In contrast, models for the evolution of performance in patchy landscapes with discrete habitat types predict that increased migration between habitats may facilitate niche expansion (Holt and Gaines 1992; Kawecki 1995; Holt 1996a,b) and the evolution of generalists (Brown and Pavlovic 1992; Day 2000). Because those two classes of models differ both in assumptions concerning the landscape structure (patchy vs. continuous) and the genetic determinism of traits underlying performance (evolutionarily stable strategy models or single locus models vs. multiple loci), it is difficult to understand which assumptions are responsible for the discrepancies in their predictions.

Here we present a quantitative genetic model that bridges the gap between previous theoretical approaches. As in Holt and Gaines (1992), we consider the evolution of a species niche in a landscape with two discrete habitat types connected by migration. But as in Kirkpatrick and Barton (1997), we use a quantitative genetic model to study the joint evolution of a quantitative character determining performance in each habitat together with the changes in the population density in each habitat. We assume that the trait responsible for performance in each habitat is determined by multiple loci with small effects and that the trait is distributed normally with a constant genetic variance in each habitat. We later relax these assumptions and examine the impact on the evolutionary dynamics. We consider a species to be a specialist if, in a heterogenous environment, individuals of that species are found mostly in a single habitat. An example of this situation is when an insect feeds only on a small fraction of available hosts within its dispersal range (Futuyma and Moreno 1988; Jaenike 1990). In constrast, if the different habitats in the

---

[2] Present address: Institut des Sciences de l'Evolution de Montpellier, CC65, Université Montpellier II, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France; E-mail: ronce@isem.univ-montp2.fr.

environment are occupied, the species is considered as a generalist. A generalist species may be composed of generalist genotypes, or it may comprise a diversity of genotypes specialized on different habitats. Both situations occur in the case of phytophagous insects (Fox and Morrow 1981; Singer 1983). Our definition of the species niche is therefore based on the pattern of resource (or habitat) use at the scale of the landscape (for similar models of niche evolution, see Holt and Gaines 1992; Holt 1996a,b).

We find that specialist species with narrow niches evolve for intermediate migration rates, whereas both very low and very large rates of movement between habitats favor the evolution of generalist species. Increasing the connectivity of the two habitats above some threshold results in the collapse of the total population size and the complete loss of one of the two habitats. We call this process a ''migrational meltdown.'' Equilibria corresponding to a generalist and a specialist may be simultaneously stable. Random disturbances can then trigger rapid change in niche breadth, as observed in the case of the checkerspot butterfly (Boughton 1999). We show that small transient changes in the landscape structure may have irreversible effects on the evolution of specialization, illustrating a case of hysteresis.

A Quantitative Genetic Model

We consider a species living in a patchy landscape with two types of habitats. Local adaptation depends on a single quantitative character whose optimal values are different in the two habitats. For instance, beak length in the soapberry bug, *Jadera haematoloma*, is under stabilizing selection within populations feeding on a single host, but diverges strongly between populations feeding on different hosts (Carroll and Boyd 1992). We assume that the character has polygenic inheritance. Its expression is the same in the two habitats, as with beak length in the soapberry bug (Carroll et al. 1997). A key assumption of our model is that maladaptation, measured as departure from the local optimal phenotype, is a source of extra mortality affecting local population dynamics. For the sake of simplicity, we assume that the two habitats are in equal frequency and that each can support the same maximal number of individuals. There are no intrinsic differences in quality between the two habitats. (We will later relax this assumption.)

We consider continuously growing populations with overlapping generations. The fitness of an individual in habitat *i* depends both on its local adaptation and on the intensity of competition with other individuals in the same patch. These effects are additive. We assume that the expected Malthusian fitness per generation of an individual with phenotype *z* in habitat *i* is:

$$r(n_i, z) = r_0\left(1 - \frac{n_i}{K}\right) - \frac{\gamma}{2}(z - \theta_i)^2. \tag{1}$$

The first term in the right side of equation (1) describes the effect of density dependence and decreases with n_i, the number of individuals in habitat *i*. We here assume that density-dependent mortality has a logistic form, with r_0 the fitness at low density of an individual with the optimal phenotype and *K* the maximal number of perfectly adapted individuals that the habitat can support at equilibrium. The second term describes mortality caused by stabilizing selection on the trait *z*. The optimal phenotype in habitat *i* is θ_i, and γ measures the intensity of stabilizing selection around this optimum.

The rate of movement between the two habitats is *m* (i.e., the probability that an individual moves between the two habitats during a short period of time *dt* is *mdt.*). Movement is a diffusive process with no preference, and rates of emigration are the same for the two habitats. Migration has two consequences: it affects the local population dynamics, and immigrants originating from another habitat may have a different mean phenotype than residents. This will shift the mean phenotypic value and potentially decrease local adaptation.

Immigration may also affect the genetic and phenotypic variances in each population. In this section, we ignore these effects. More precisely, we assume that phenotypes and breeding values are distributed normally within each population and that both the phenotypic variance σ_p^2 and the additive genetic variance σ_g^2 are constant and identical in the two habitats (with $\sigma_p^2 = \sigma_g^2 + \sigma_e^2$, where σ_e^2 is the contribution of the environment and nonadditive genetic effects to the phenotypic variance). The response of the trait mean to selection is then given by the product of the additive genetic variance σ_g^2 and the selection gradient (Lande 1976). We will later relax the assumptions of a fixed genetic variance and normal distribution of phenotypes and examine the consequences for the evolutionary dynamics (see the section An Explicit Multilocus Genetic Model). Simulation results show that our main qualitative conclusions are not affected.

The equations describing the joint changes in population size, n_i, and mean phenotype, $\bar{z}_i$, within the habitat *i* then are:

$$\frac{d\bar{z}_i}{dt} = \sigma_{\mathrm{g}}^2\gamma(\theta_i - \bar{z}_i) + m\frac{n_j}{n_i}(\bar{z}_j - \bar{z}_i) \quad \text{and} \tag{2a}$$

$$\frac{dn_i}{dt} = \left[r_0\left(1 - \frac{n_i}{K}\right) - \frac{\gamma}{2}\sigma_{\mathrm{p}}^2 - \frac{\gamma}{2}(\bar{z}_i - \theta_i)^2\right]n_i + m(n_j - n_i). \tag{2b}$$

The second and third terms inside the square brackets in equation (2b) represent two different demographic loads. The first is due to stabilizing selection acting on variance around the mean phenotype, and the second is due to the difference between the mean and the optimum (the ''evolutionary load''; see Lande and Shannon 1996).

At this stage, it is useful to rescale the equations to reduce the number of parameters and simplify the interpretation of our results. Let r^* and K^* be, respectively, the rate of increase at low density and the equilibrium size for population whose mean phenotype is at the optimum. Equations (2a) and (2b) show that such an equilibrium is reached in the absence of migration between the two habitats, with:

$$r^* = r_0 - \frac{\gamma}{2}\sigma_{\mathrm{p}}^2 \quad \text{and} \tag{3a}$$

$$K^* = K\frac{r^*}{r_0}. \tag{3b}$$

Note that $r^* < r_0$ and $K^* < K$ because, even when the mean phenotype coincides with the optimum, there remains a load due to variance around the optimum. In the following we will assume that the additive genetic variance is positive. We then define the new dynamic variables as:

$$Z_1 \equiv \frac{\bar{z}_1 - \theta_1}{\sigma_g}, \tag{4a}$$

$$Z_2 \equiv \frac{\theta_2 - \bar{z}_2}{\sigma_g}, \quad \text{and} \tag{4b}$$

$$N_i \equiv \frac{n_i}{K^*}, \tag{4c}$$

where Z_i is a relative measure of maladaptation in habitat *i.* It measures the number of genetic standard deviations that separates the mean phenotype from the optimum in that habitat. Without loss of generality, we will assume that θ_1 is smaller than θ_2 (Z_1 and Z_2 are measured in opposite directions so that they are positive at equilibrium). N_i is the density in habitat *i* relative to the equilibrium population size in absence of migration. The new parameters are:

$$H \equiv \frac{\theta_2 - \theta_1}{\sigma_g}, \tag{5a}$$

$$\Gamma \equiv \frac{\sigma_g^2 \gamma}{r^*}, \tag{5b}$$

$$M \equiv \frac{m}{r^*}, \quad \text{and} \tag{5c}$$

$$T \equiv r^* t. \tag{5d}$$

The number of genetic standard deviations separating the optima corresponding to the two habitats, *H,* is a relative measure of habitat heterogeneity. The intensity of stabilizing selection, Γ, and the movement rate, *M,* are measured relatively to the intrinsic population growth rate and time is now measured in numbers of generations. The dynamic equations in (2) are equivalent to the rescaled equations:

$$\frac{dZ_i}{dT} = -\Gamma Z_i + M\frac{N_j}{N_i}(H - Z_i - Z_j) \text{ and} \tag{6a}$$

$$\frac{dN_i}{dT} = (1 - N_i)N_i - \frac{\Gamma}{2}Z_i^2 N_i + M(N_j - N_i). \tag{6b}$$

We now analyze the dynamic behavior of this system of equations as a function of the three parameters *H, M,* and Γ, instead of the seven original parameters.

RESULTS

A Symmetric Equilibrium

Equations (6a,b) show that the dynamic system reaches an equilibrium when both population maladaptation and population size in the two habitats are equal:

$$\hat{Z}_1 = \hat{Z}_2 = \frac{HM}{2M + \Gamma} \quad \text{and} \tag{7a}$$

$$\hat{N}_1 = \hat{N}_2 = 1 - \frac{\Gamma}{2}\hat{Z}_2^2. \tag{7b}$$

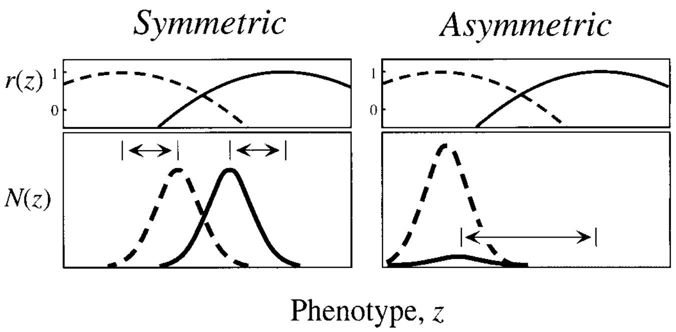

FIG. 1. Illustrations of the symmetric and asymmetric equilibria. The dashed curves correspond to habitat 1 and solid curves to habitat 2. The top panels show the rates of increase for phenotypes when population density is low, and the bottom panels show the phenotypic distributions at equilibrium. The arrows indicate the amount of maladaptation in each habitat. The optimum trait value is $\theta_1 = 20$ in habitat 1 and $\theta_2 = 27$ in habitat 2. Other parameters values are $K^* = 2.5$, $r^* = 1$, $\sigma_g = 1$, $\gamma = 0.1$, $m = 0.1$.

This situation is illustrated in Figure 1, left panel. In each habitat, the mean phenotype lies at the same distance from the local optimum. Exchanges between habitats are perfectly balanced. Because individuals are equally distributed in the two habitats, we consider the species to be a generalist. Stability of this symmetric equilibrium will be discussed shortly.

The equilibrium value of maladaptation in each habitat results from a balance between migration and selection. Maladaptation thus increases with increasing habitat heterogeneity, *H,* increasing movement rate, *M,* and decreasing intensity of stabilizing selection, Γ. Equation (7b) shows that higher levels of maladaptation at equilibrium decrease the density in each patch. The total population size thus decreases when the movement rate increases or when habitat heterogeneity increases.

The population size at equilibrium, however, varies nonmonotonically with the intensity of stabilizing selection Γ (eq. 7a,b). For $\Gamma < 2M$, the population decreases when Γ increases. When Γ is higher than this threshold, the population increases with increasing intensity of selection. This is because stabilizing selection has direct and indirect effects on population size. First, larger Γ results in higher mortality due to selection, thus decreasing the equilibrium population size. Second, the increasing intensity of selection also affects the evolution of the mean phenotype and reduces maladaptation, which has beneficial indirect effects on population size. When the intensity of selection is low relatively to the rate of movement ($\Gamma < 2M$), the first effect predominates because selection has little effect on maladaptation.

Increasing levels of maladaptation may lead to the extinction of the entire population. By setting $N_i = 0$ in equation (7b), we find the maximal sustainable habitat heterogeneity, H_v, above which the symmetric equilibrium is no longer viable:

$$H_v = \frac{2M + \Gamma}{M}\sqrt{\frac{2}{\Gamma}}. \tag{8}$$

Asymmetric Equilibria

Numerical integration of the system of dynamic equations (6a,b) reveals the existence of asymmetric equilibria for which population size and maladaptation differ between habitats. The right panel of Figure 1 illustrates such a situation. The mean phenotype of the population in habitat 1 is very close to its local optimum. In contrast, the population in habitat 2 is strongly maladapted. The density is much larger in the first habitat. Populations in habitat 1 behave as sources exporting migrants to sink populations in habitat 2. Which habitat behaves as a source or as a sink depends on initial conditions. Because individuals are mainly found in a single habitat (or, for a parasite, on a single host), we consider the species to be a specialist.

We were unable to find a general analytical expression for these asymmetric equilibria. Instead, we develop approximations for low rates of movement (see Appendix 1). We assume that adaptation is close to perfect for the population in habitat 1 and that this population is close to its maximal size. In contrast, we assume that the population in habitat 2 is poorly adapted and that its density is low. For a very low movement rate between habitats, a stable asymmetric equilibrium is then:

$$\hat{Z}_1 \approx 0,$$

$$\hat{Z}_2 \approx \frac{2 - 2\Gamma + 3\Gamma H^2 + \sqrt{(-2 + 2\Gamma + \Gamma H^2)^2 - 16H^2\Gamma^2}}{4H\Gamma} \tag{9a}$$

and

$$\hat{N}_1 \approx 1 - M,$$

$$\hat{N}_2 \approx \frac{4M}{-2 - 2\Gamma + \Gamma H^2 + \sqrt{(-2 + 2\Gamma + \Gamma H^2)^2 - 16H^2\Gamma^2}} \tag{9b}$$

(see Appendix 1). Conditions for the stability of this equilibrium are discussed in the next section.

Equations (9a,b) illustrate how the source-sink dynamics affect both population size and local adaptation in the two habitats. The density in habitat 1 declines with increasing rates of movement M because the small number of immigrants coming from the second habitat does not compensate for loss by emigration (eq. 9b). However, the density in habitat 2 is proportional to the movement rate (eq. 9b). This occurs because essentially all individuals are immigrants from the first habitat. The population size in habitat 2 is so small that it has little effect on the population dynamics and the evolution in the first habitat (see eq. 9a,b). This situation is very similar to the source-sink system with one-way migration described by Gomulkiewicz and Holt (1999).

The process by which such asymmetries evolve depends critically on the feedbacks between demography and phenotypic evolution embedded in our model. Recall that maladaptation at equilibrium in each habitat depends on the relative balance between migration and selection. Let us assume that population size in habitat 2 is initially smaller. Equation (6a) shows that the genetic migration rate into the population in habitat 2, that is, the proportion of immigrants in that population, is MN_1/N_2. Therefore, the larger the asymmetry between populations, the higher the genetic migration rate into the population in the second habitat. Higher migration rates cause the maladaptation in habitat 2 to increase, which in turn reduces even more the size of this population. This process is reminiscent of a ‘‘mutational meltdown’’ (Lynch and Gabriel 1990), the process in which deleterious mutations accumulate in small populations, or the mutational collapse in marginal habitats described by Kawecki et al. (1997). By analogy, we call this process a ‘‘migrational meltdown.’’

Equations (9a,b) show that maladaptation in the second habitat increases and population size decreases with increasing habitat heterogeneity, as they did in the case of the symmetric equilibrium. But, in contrast with the symmetric case, maladaptation in habitat 2 now increases and population size decreases when the intensity of selection increases (eq. 9). This occurs because migration is then a more powerful evolutionary force than selection. Indeed, at equilibrium, the genetic migration rate into populations in habitat 2 is approximately $M/\hat{N}_2$, with $\hat{N}_2$ much smaller than one, instead of M as in the symmetric equilibrium. Selection thus has little effect on maladaptation. The direct mortality effect of stabilizing selection on population size is now greater than its indirect effects on the evolution of the mean phenotype. As for the symmetric equilibrium, when the intensity of selection is low compared to the migration rate, the mortality cost of selection causes the population size in habitat 2 to decrease when the intensity of selection increases. This decrease in population size causes the genetic migration rate $M/\hat{N}_2$ to increase further. As a result, maladaptation in the second habitat increases when the intensity of selection increases. Holt (1996b) described a similar situation, where increasing intensity of selection has negative consequences for local adaptation in a sink-source system.

These results hold approximately when the relative movement rate is low. We now evaluate numerically the robustness of our predictions for the asymmetric equilibrium when the movement rate is larger. The dynamic equations (6a,b) were numerically integrated using Mathematica (Wolfram 1999). As the movement rate increases, population density in habitat 2 increases (Fig. 2, top panel), while population density in habitat 1 decreases, as predicted qualitatively by equation (9b). For large rates of movement between habitats, however, both populations converge toward the same equilibrium density, corresponding to the symmetric equilibrium. Our approximation for asymmetric equilibria thus gives accurate quantitative predictions only for very low rates of movement.

For low movement rates, the equilibrium maladaptation in habitat 2 depends little on the rate of movement, as predicted by our approximation (see eq. 9a and Fig. 2, bottom panel). A further increase in the rate of movement between habitats causes maladaptation to decrease in habitat 2 (Fig. 2, bottom panel). This is explained by the demographic consequences of dispersal, which tend to decrease asymmetries between populations. As the rate of movement between the two habitats is increasing, the genetic migration rate into populations in habitat 2, as measured by $M\hat{N}_1/\hat{N}_2$, is actually decreasing. Eventually, the expected value of maladaptation at equilibrium converges toward the value expected at the symmetric equilibrium (Fig. 2, bottom panel).

Stability of the Equilibria

The stability of the symmetric equilibrium defined by equations (7a,b) is analyzed in Appendix 2. When the rate of

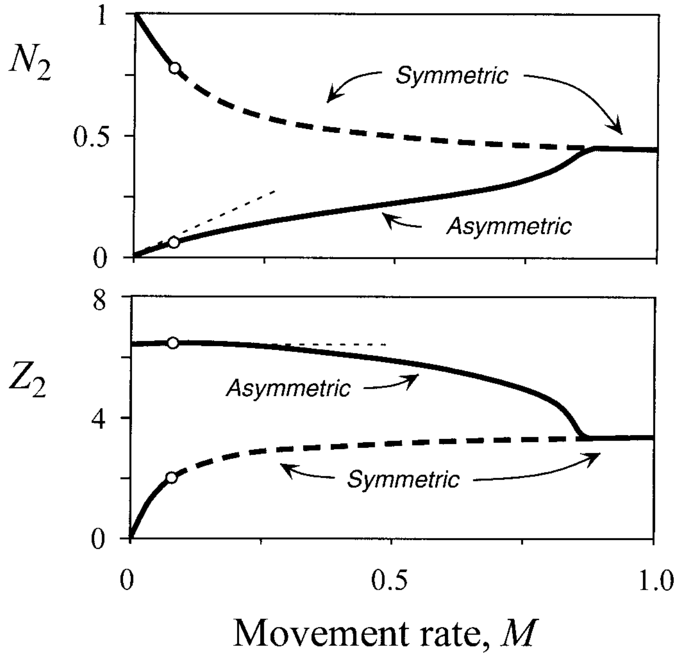

FIG. 2. The equilibrium in habitat 2 for population size N_2 and maladaptation Z_2 as functions of the movement rate between habitats. Results for the symmetric equilibrium are from equations (7a,b), whereas those for the asymmetric equilibrium were obtained by integrating equations (6a,b) over 1000 generations starting with a much higher density and lower maladaptation in habitat 1. The solid segments of each curve show stable equilibria; the long dashed segments are unstable equilibria. For very low movement rates ($M < 0.080$) both the symmetric and asymmetric equilibria are stable; the limit of this region is marked by open circles. Thin dashed lines show the low-movement approximations for the asymmetric equilibrium (from eq. 9). Parameter values are $H = 7$, $\Gamma = 0.1$.

movement between habitats is not too large ($M < 2$), a necessary and sufficient condition for the symmetric equilibrium to be stable is that the habitat heterogeneity be below a threshold:

$$H < H_{\max} = \sqrt{\frac{2M + 1}{5}}H_{\mathrm{v}}, \tag{10}$$

again, with H_{v} given by equation (8).

The threshold $H_{\max}$ is the maximal sustainable heterogeneity for which the symmetric equilibrium is stable. This threshold varies nonmonotonically with the rate of movement between the two habitats and with the intensity of stabilizing selection. When the relative movement rate is very high ($M > 2$), the condition for stability of the symmetric equilibrium reduces to the condition for its viability: $H < H_{\mathrm{v}}$ (see Appendix 2). Any viable symmetric equilibrium is then stable.

We were unable to derive a general condition for the stability of the asymmetric equilibria. Instead, we assume that the rate of movement between hosts is very low and use the same kind of approximation as described earlier (see Appendix 1). For low movement rates, a stable and viable asymmetric equilibrium exists only if:

$$H > H_{\min} = 2 + \sqrt{\frac{2(1 + \Gamma)}{\Gamma}}. \tag{11}$$

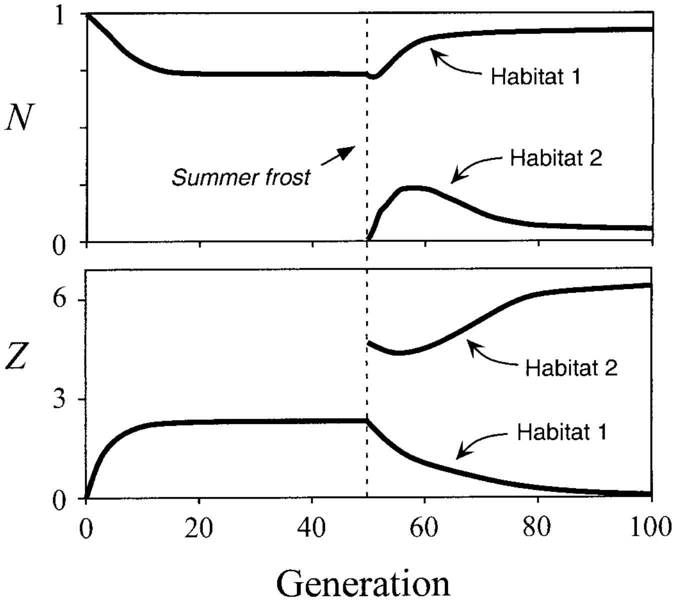

FIG. 3. Population sizes N and maladaptation Z in response to a demographic disturbance that causes extinction in habitat 2. The trait means in each habitat are initially at their local optima. Before the disturbance, the two populations have the same size and the same level of maladaptation. After 50 generations, the population in the second habitat goes extinct from the disturbance and never recovers its original density. The intensity of stabilizing selection is $\Gamma = 0.1$, the habitat heterogeneity is $H = 7$, and the movement rate is $M = 0.08$.

The threshold $H_{\min}$ corresponds to the minimal habitat heterogeneity above which the asymmetric equilibrium is stable and viable. This threshold is independent of the movement rate and it decreases when the intensity of selection increases. Equation (11) also indicates that, when movements between habitats are rare, the migrational meltdown associated with the asymmetric equilibrium may be observed only if local optima in the two habitats differ by more than two genetic standard deviations ($H_{\min} > 2$).

Comparison of equations (10) and (11) shows that, for low rates of movement between habitats, there always exists a range of intermediate habitat heterogeneity such that both symmetric and asymmetric equilibria are simultaneously stable. In this situation, the species may evolve as a specialist or a generalist depending on initial conditions. More precisely, coexistence of the three equilibria (one symmetric, plus two asymmetric) for low movement rate occurs when $H_{\min} < H < H_{\max}$.

Effect of Disturbances

When multiple equilibria are stable simultaneously, random disturbances can trigger rapid switch in habitat use and source-sink dynamics, as observed for *E. editha.* Consider an initial situation where, at equilibrium, populations in the two habitats have the same level of maladaptation and the same density. Figure 3 shows the evolution of the population size and maladaptation in the two habitats. After 50 generations we simulate a catastrophic event, such as the summer frost described by Boughton (1999), leading to the extinction of

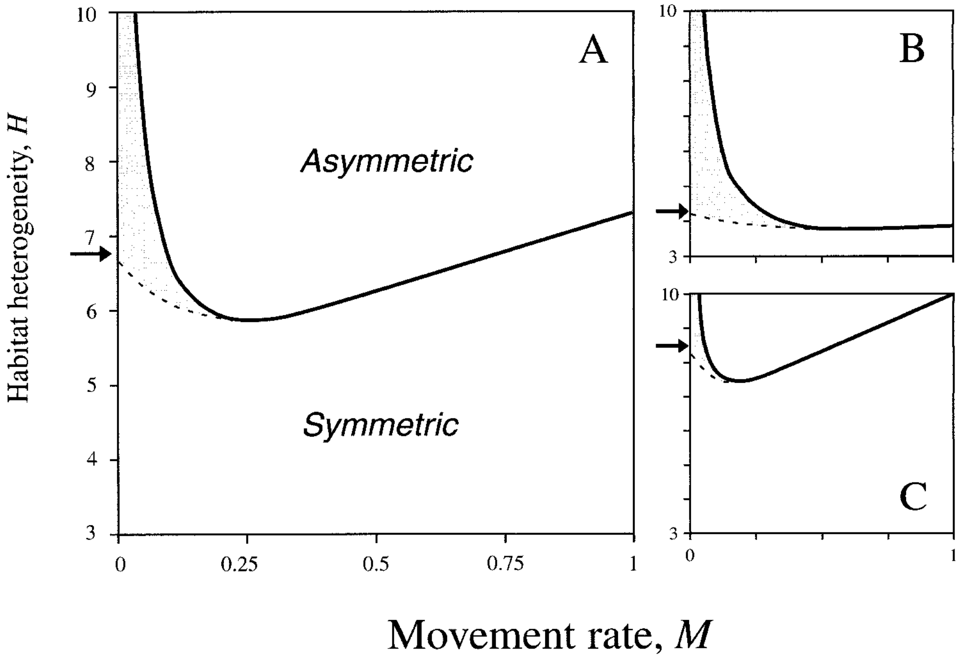

FIG. 4. Stability of the different equilibria as a function of habitat heterogeneity and rate of movement between habitats. The solid curves give the maximal value of the habitat heterogeneity, $H_{\max}$, for which the symmetric equilibrium is stable (from eq. 10). Above this threshold, asymmetric equilibria are stable (as determined by numerical integration). Arrows indicate the minimal value of habitat heterogeneity, $H_{\min}$, above which the asymmetric equilibria are stable at low rates of movement (from eq. 11). The shaded area corresponds to zones of the parameter space where both the symmetric and asymmetric equilibria are locally stable. The intensities of stabilizing selection are: (A) $\Gamma = 0.1$; (B) $\Gamma = 0.5$; (C) $\Gamma = 0.05$.

all populations in habitat 2. A new equilibrium is reached where the population in habitat 1 is close to its maximal size and almost perfectly adapted, whereas the population in habitat 2 never recovers from the disturbance and remains small and poorly adapted. Although the two populations exchanged an equal number of migrants before the extinction, the population in habitat 2 now functions as a sink (immigration outbalances emigration), and the population in habitat 1 acts as a source.

Migration and the Evolution of Specialization

We now investigate how changes in the movement rate between habitats affect the evolution of specialization. Figure 4 shows zones of the parameter space for which either one equilibrium (a generalist), two equilibria (each with one specialist), or three different equilibria (two with specialists and one with a generalist) are locally stable. When habitat heterogeneity is low, the species evolves to be a generalist. In contrast, when habitat heterogeneity is high, specialists mainly distributed in a single habitat evolve (see eq. 10). For intermediate habitat heterogeneity, evolution of niche breadth depends critically on the rate of movement between habitats. Equation (10) shows that the maximal sustainable heterogeneity for the symmetric equilibrium reaches a minimum for an intermediate value of the movement rate:

$$M^* = \frac{\Gamma}{2} + \frac{\sqrt{8\Gamma + \Gamma^2} - \Gamma}{4}. \qquad (12)$$

A generalist species may evolve both under very low and very high rates of movement between habitats, whereas a specialist species evolves with intermediate movement rates. The range of intermediate movement rates for which specialists will evolve also depends on the intensity of stabilizing selection (see eq. 12 and Fig. 4).

When movements rates are low with respect to the intensity of selection ($M < M^*$), the generalist species is composed of highly differentiated and strongly locally adapted populations. This kind of generalist species is actually a mixture of highly specialized genotypes. Such differentiation cannot be maintained in the face of more frequent movements between habitats. Increased movement rates then tend to destabilize the symmetric equilibrium (eq. 10).

When the movement rate between habitats is very high with respect to the intensity of stabilizing selection ($M > M^*$), a generalist species evolves that is almost genetically uniform with an intermediate phenotype representing a compromise between the conflicting selection pressures in each habitat. Increased movement rates then tend to reduce the difference in density between habitats and to stabilize the symmetric equilibrium (eq. 10). Specialists evolve when the movement rate is high enough so that genetic differentiation between populations cannot be achieved, but low enough so that differences in population sizes can be maintained. Note that the same kind of arguments apply for the effect of the intensity of stabilizing selection on the evolution of specialists and generalists.

Demographic Consequences of Migration

Evolutionary transitions from generalist to specialist have important consequences for the size of the total population

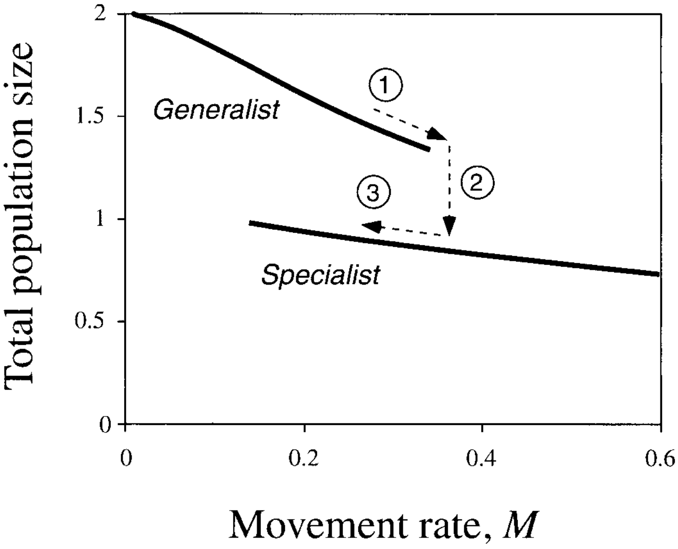

FIG. 5. Different stable equilibria for the total population size $N_1 + N_2$ as a function of the rate of movement between habitats. Arrows show a scenario that illustrates a case of hysteresis. We start initially with a generalist species with a large population size (1). The rate of movement between habitats is then increased by a small amount, causing the symmetric equilibrium to lose its stability (2). The species is now a specialist with a low total population size. Returning the movement rate between habitats to its initial value does not allow the species to recover the generalist status: The species remains a specialist with a much smaller population size than initially (3). The intensity of stabilizing selection is $\Gamma = 0.5$ and the habitat heterogeneity is $H = 4$.

at equilibrium (Fig. 5). In general, increasing the rate of movement between habitats decreases the total population size. At a threshold in the rate of movement, a collapse in the total population occurs (see Fig. 5). This happens when the increase in migration destabilizes the symmetric equilibrium. A small increase in the frequency of movements then results in a dramatic decline of niche breadth and later reduction in the total population, which is now restricted to a single habitat instead of two. In this example, the population will not evolve back to a generalist range when the rate of movement is returned to its initial value because the species is trapped in the basin of attraction corresponding to the specialist equilibrium. Only a large decrease in dispersal or some consequent disturbance can bring the population back to its original size. Thus, not only small change in dispersal may result in the shrinking in niche width and size of the total population, but such an effect may also be very difficult to reverse. This is a case of hysteresis where historical factors may have a large impact.

Note, however, that higher rates of movements may also help a specialist to broaden its niche. In that situation, an increase in migration may have positive consequences for the total population size (results not shown). In our numerical study, the range of parameters values for which migration had a globally beneficial effect was, however, quite narrow.

Differences in Quality between the Two Habitats

We next consider the effects of differences in carrying capacity between the habitats. We were unable to obtain analytical results. Instead, we numerically integrated the system of dynamic equations to test the robustness of our previous predictions. We wanted to know whether the existence of multiple equilibria was an artifact due to the symmetry of our model. Numerical studies show that, for small differences in intrinsic quality between the two habitats, there are still situations where three equilibria (one symmetric, two asymmetric) are simultaneously stable. For historical reasons, a species might specialize on the poorest habitat, leaving the best habitat almost unoccupied. Bias toward the best habitat, however, increases with increasing differences in quality. Only two equilibria, corresponding to a specialist of the best habitat and a generalist species, are simultaneously stable for large intrinsic differences in habitat quality (see also Van Tienderen 1991; Day 2000). Thus, even in the presence of intrinsic differences in habitat quality, we still predict that demographic disturbances are likely to cause rapid shifts in ecological range, source-sink dynamics, and total population size.

An Explicit Multilocus Genetic Model

In this section, we relax the assumption of a fixed genetic variance and normal distribution of phenotypes in each population. Instead, we simulate an explicit multilocus hypergeometric model (Barton 1992; Jenkins and Kirkpatrick 1995; Shpak and Kondrashov 1999). This allows us to follow the population and evolutionary dynamics without making assumptions about constancy or form of the phenotypic and genotypic distributions.

The hypergeometric model assumes that the phenotype z of an individual is determined by L haploid loci with equivalent and additive effects. We assume that there are two alleles (+/−) at each locus. Two individuals share the same phenotype as long as they share the same total number of + alleles, whatever the exact position of those alleles in their genotype. We assume equal allelic frequencies at all the loci, that all loci recombine freely, and that the trait is completely heritable.

We assume discrete time. The order of events in the life cycle is: (1) selection; (2) migration; (3) recombination; and (4) density regulation. Populations were sampled just before selection. We compared the predictions of the hypergeometric model to a discrete-time version of the Gaussian analytic model developed above. For each parameter set, the additive genetic variance at equilibrium predicted by the hypergeometric model was averaged across the two habitats. This value of the additive genetic variance was then used to generate predictions about maladaptation and population sizes with our Gaussian model.

Figure 6 shows examples of comparisons between the simulation and analytic models. The qualitative patterns observed in our simulations are consistent with the predictions of the previous quantitative genetics model. Generalist species with identical levels of maladaptation in the two habitats evolve when the optima in the two habitats are close to each other (Fig. 6, bottom panel). When they are distant, generalist species evolve under low and high migration rates, whereas specialists are found only for intermediate migration rates (Fig. 6, top panel). We found multiple cases where both types

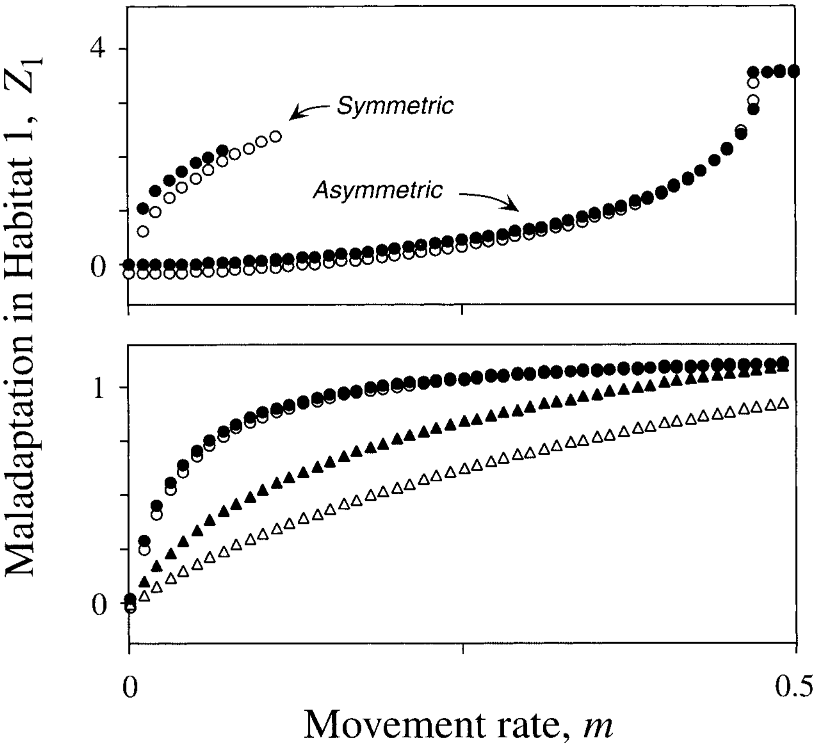

FIG. 6. Comparisons of results from the discrete time version of the Gaussian analytic model (solid symbols) and simulations of the hypergeometric model (open symbols). Maladaptation in habitat 1 is given as a function of the unscaled movement rate between habitats, *m.* Simulations of the hypergeometric model were run for 5000 generations and 30 loci. For each value of the movement rate, we started the simulations from two types of initial conditions: (1) both populations were perfectly adapted and at their maximal size; or (2) the population size was much smaller and maladaptation much larger in habitat 2 than in habitat 1. Top panel: A case where both the symmetric and asymmetric equilibria are stable at low movement rates. Parameter values are $r_0 = 1$, $K = 1$, $\theta_2 = 5$, $\theta_1 = 25$, $\gamma = 0.01$. Bottom panel: Two cases where only the symmetric equilibrium is stable. Parameter values are $r_0 = 1$, $K = 1$, $\theta_2 = 2$, $\theta_1 = 8$, $\gamma = 0.01$ (circles) and $\gamma = 0.1$ (triangles). Note the different scale for the y-axis on the two panels.

of equilibria are simultaneously stable (e.g., Fig. 6, top panel). Increasing movement between habitats generally resulted in a smaller total population size and higher maladaptation (Fig. 6, bottom panel), with the same kind of collapse for some threshold migration rate as described previously (Fig. 6, top panel). From a qualitative point of view, assumptions about the constancy of the genetic variance and normality of the phenotypic distribution seem to matter little.

Quantitative predictions of the hypergeometric model were in good agreement with the predictions of our simple quantitative genetics model when selection was weak and the habitat heterogeneity was low (Fig. 6, bottom panel; for identical conclusions, see also Tufto 2000). The fit is less good for stronger selection and or larger differences in the optima between habitats (Fig. 6, top panel). In particular, our simple model underestimates the migration rate at which the migrational meltdown occurs in the hypergeometric model.

Simulations using the hypergeometric model also show that the deleterious effects of dispersal on maladaptation and total population size depend strongly on the relative order of migration, selection, and recombination (results not shown). Selection is much more efficient when it acts just after migration rather than after an episode of recombination. Dispersal in the former situation has very little impact on local adaptation, and we observe a migrational meltdown only for very large migration rates. In the extreme case of a single haploid locus (and where recombination has no effect), we found that the asymmetric equilibrium was always unstable.

DISCUSSION

Dispersal and the Evolution of Specialization

Dispersal has a homogenizing effect on both genetics and population size in a heterogeneous habitat, with conflicting consequences for the evolution of a species' niche. Migration tends to attenuate demographic asymmetries between habitats, so that the strength of selection acting on performances in source and sink habitats becomes more similar. As a consequence, several models have found that high dispersal between habitats favors the evolution of generalist species with a broad niche (Brown and Pavlovic 1992; Holt and Gaines 1992; Kawecki 1995; Holt 1996a,b; Day 2000). However, dispersal can frustrate local adaptation in sink populations, which indirectly accentuates the demographic asymmetries (Gomulkiewicz and Holt 1999). Kirkpatrick and Barton (1997) found that increased dispersal can cause the evolution of limited geographical ranges for this reason. In our model, generalist species with a broad niche evolved for both very low and very high rates of movement between habitats, whereas specialist species evolved for intermediate dispersal.

As Kirkpatrick and Barton (1997), we found that increased dispersal may lead to the loss of local adaptation in some populations, the appearance of source-sink dynamics, and the evolution of narrow niches. We call this process a migrational meltdown, as small populations experience a downward spiral of maladaptation and shrinking size. In contrast to the mutational meltdown described by Lynch and Gabriel (1990), small, maladapted populations can be rescued by a further increase in dispersal that again equilibrates population sizes across habitats. Similarly, in Kirkpatrick and Barton's (1997) model, increased migration causes the range size to broaden again at the high migration limit. In their model, however, the whole population always goes extinct before that densities are equalized across space. This prediction is ultimately linked to their assumption of infinite space: The distance traveled by the migrants and thus the maladaptation of such migrants to local conditions increase indefinitely with the migration rate.

Our analysis shows that the net effect of dispersal on the evolution of the species niche depends critically on the intensity of stabilizing selection within each habitat. If the intensity of selection is weak, increased dispersal generally favors the evolution of generalists. The consequences of dispersal are then explained by their direct demographic effects. When the intensity of selection is strong, however, increased migration generally favors the evolution of narrow niches. The swamping effect of dispersal on adaptation then dominates the evolutionary dynamics. These results parallel those obtained by Kawecki (2000) in a simple one-locus haploid model of a source-sink habitat. Gabriel et al. (1993) similarly found that, in populations undergoing a mutational meltdown, the mean time to extinction was minimized at some intermediate selection intensity. The intensity of selection thus affects the migrational and the mutational meltdowns in similar ways.

Rescue Effect and Migrational Meltdown: The Impact of History

Maintaining connectivity between habitat patches is often identified as primary goal for conservation in fragmented landscapes, because dispersal between patches is thought to have direct positive consequences on the total population size in the network (the rescue effect of dispersal: Brown and Kodric-Brown 1977; Hanski 1985; Hanski and Gyllenberg 1993). In habitats that are both patchy and heterogeneous, our model suggests that dispersal may actually have detrimental effects on the demography and persistence of the species. Increased movement leads to higher total population size only under a limited set of conditions. Generally, dispersal has negative demographic consequences due to its effect on local adaptation. Several models (Hastings 1983; McPeek and Holt 1992; Wiener and Feldman 1993) have shown that constant dispersal rates were strongly selected against in spatially heterogeneous but temporally constant environments. Those conclusions might not hold in presence of kin competition, however, or when populations sizes fluctuate through time (Holt 1997). Migration behaviors are often habitat specific or density dependent, which is not accounted for in our model. The joint evolution of habitat selection or migration strategies with local adaptation remains to be investigated in more realistic ecological scenarios.

The negative demographic effects of dispersal can be particularly dramatic in our model. For some threshold dispersal rate, a small increase in the rate of movement between habitats results in a collapse of population size. Small modifications of the landscape resulting in an increase in the connectivity between different patches of habitat could thus have a huge impact. This causes concern because at the vicinity of such transition zones, we have shown that increasing and decreasing connectivity do not have symmetrical consequences. Evolving back to a higher population size by slightly decreasing the rate of movement between habitats may be impossible, and the species may be trapped in its new specialist status. This finding agrees with empirical and theoretical studies that view ecological specialization as a dead-end and reversion to a generalist lifestyle as unlikely (Fry 1996; Kelley and Farrell 1998). It also illustrates a case of hysteresis, where historical factors have a large impact on evolution and demography. Small past fluctuations in the landscape structure and connectivity could then explain differences among species living in otherwise identical conditions. Kawecki et al. (1997) described a similar case where transient changes in demography in an heterogeneous environment lead to the accumulation of deleterious mutations in marginal habitats with abrupt reduction in fitness in those habitats and irreversible consequences for the evolution of the niche. As in our case, the existence of multiple equilibria and the hysteresis property of their model are ultimately due to feedbacks between demography and genetics.

Shift in Host Range and Disturbance

An important finding of the present model is the existence of multiple simultaneously stable equilibria. Historical factors will then decide whether a species evolves to be a specialist or a generalist. Van Tienderen (1991) described a similar situation. Like us, he modeled the evolution of a quantitative trait in a heterogeneous environment where local population sizes depend on their level of maladaptation. In contrast to the present model, however, he assumed complete mixing and did not examine the effect of varying the rate of movement between habitats. Our model indicates that we are more likely to observe multiple equilibria for low to intermediate dispersal rates.

The existence of multiple equilibra means that the evolution of the species niche can be extremely sensitive to disturbances and historical effects. In the case of phytophagous insects, we would also expect a large amount of geographical variation in diet and diet breadth, as is indeed observed in the Melitaeine butterflies *E. editha* (Singer 1971, 1983; Singer and Parmesan 1993; Radtkey and Singer 1995) and *Melitea cinxia* (Kuussaari et al. 2000). Specialization is then the property of a set of populations in a geographical region rather than of the species on its whole range (Fox and Morrow 1981). Our theoretical findings as well as the empirical work on the Melitaeine butterflies point to the need to study specialization at several scales (at the level of genotypes, populations, metapopulations, or the whole species range).

The existence of several simultaneous equilibria also suggest that niche width could vary through time in unstable environments where perturbations of population sizes are not uncommon. Frequent shifts in host range such as that observed in *E. editha* (Radtkey and Singer 1995) make the formation of differentiated host-races and host-associated speciation less likely (M. C. Singer, pers. comm.). The shifts observed in our model mimic the inversion in source-sink dynamics and narrowing of the diet following a disturbance as described by Boughton (1999) in *E. editha.* The inability of the checkerspot butterfly to recolonize its former host plant is, however, more likely to be due to some environmental effects (see Boughton 1999) than to the genetic inability of colonizers, as assumed in our theoretical study. There is some circumstantial evidence that evolution of specialization in the bark beetle *Dendroctonus jeffreyi* was associated with a historical population bottleneck (Kelley et al. 2000).

Demographic Asymmetries

Most conclusions reached in this paper depend on the subtle interplay of population dynamics with genetics. Demographic asymmetries in particular play a central role. Like previous studies (Holt and Gaines 1992; Holt 1996b; García-Ramos and Kirkpatrick 1997; Gomulkiewicz and Holt 1999), we found that such asymmetries severely constrain the evolution of a species niche. Spatial variation in density and unequal migration rates are also responsible for counterintuitive predictions. In case of extreme asymmetry between habitats, we found that higher selection intensity and lower rates of movement between habitats could promote higher levels of maladaptation in the inferior habitat (see also Holt 1996a). These conclusions diametrically oppose the predictions reached when population densities are equal across space. The existence of multiple equilibria also relies on our assumption of feedbacks between demography, gene flow, and evolution. Note, however, that differences in local adaptation may not always translate into demographic differences. With pure soft selection, when maladaptation has no consequences on population sizes, only generalists evolve (Van Tienderen 1991). Conclusions of our model are therefore valid only for systems in which selection has a demographic cost. The consequences of interactions between maladaptation, demography, and population regulation should be explored further.

Local Adaptation and Genetics

Our theoretical study also indicates that predictions about local adaptation and demography in a heterogenous habitat depend on the genetic architecture of the trait under selection as well as on details of the life cycle. Assumptions about recombination appear to be critical. Our simulation results show that migrational meltdown is more likely to occur if the trait responsible for adaptation is determined by several loci with equivalent effects and migration and selection are separated by an episode of strong recombination. For phytophagous insects, this would mean that mating occurs after dispersal and that recombinant larvae are selected on the host plant. Insects who mate shortly after emergence on their native host plant, before dispersal, obviously violate this assumption. The hypergeometric model then shows that selection is much more efficient at eliminating poorly adapted immigrant genotypes, so that we rarely observe a migrational meltdown.

Our understanding of the impact of migration on local adaptation would be much improved by analytical insights on how genetic variance evolve in such heterogenous habitats. The genetic variance is likely to change with selection, recombination, and migration, as suggested by the hypergeometric model, but also with population sizes. Drift may be a powerful eroding force in small maladapted populations and so that our assumption of a constant genetic variance across habitats is questionable. Gomulkiewicz and Holt (1999) showed that migration from a large source population into a small, genetically depauperate sink may actually reintroduce some genetic variation and improve local adaptation in the sink. For the same reasons, in a temporally variable environment, Gandon et al. (1996) found that higher levels of migration for a parasite increased its probability to be adapted to its local but variable host. Those two models, together with the findings of the present paper, suggest that there is still much to learn about the impact of dispersal on evolutionary dynamics in heterogeneous habitats.

ACKNOWLEDGMENTS

We thank T. Bataillon for comments on the manuscript and R. Gomulkiewicz and R. D. Holt for discussions. We are very grateful to M. C. Singer, who was a great source of inspiration and exciting ideas. We also thank M. Whitlock, T. Kawecki, and an anonymous reviewer for helping us improve the manuscript. This research was supported by National Science Foundation grant DEB-9973221 and funds from the University of Texas.

LITERATURE CITED

Barton, N. H. 1992. On the spread of new gene combinations in the third phase of Wright's shifting balance. Evolution 46: 551–557.

Berenbaum, M. R. 1996. Introduction to the symposium: on the evolution of specialization. Am. Nat. 148:S78–S83.

Boughton, D. A. 1999. Empirical evidence for complex source sink dynamics with alternative states in a butterfly metapopulation. Ecology 80:2727–2739.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of migration on extinction. Ecology 58: 445–449.

Brown, J. S., and N. B. Pavlovic. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. Evol. Ecol. 6:360–382.

Carroll, S. P., and C. Boyd. 1992. Host race radiation in the soapberry bug: natural history with the history. Evolution 46: 1052–1069.

Carroll, S. P., H. Dingle, and S. P. Klassen. 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. Evolution 51:1182–1188.

Day, T. 2000. Competition and the effect of spatial resource heterogeneity on evolutionary diversification. Am. Nat. 155: 790–803.

Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? Science 211:887–893.

Fry, J. D. 1996. The evolution of host specialization: are trade-offs overrated? Am. Nat. 148:S84–S107.

Futuyma, D. J., and G. Moreno. 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 19:207–233.

Gabriel, W., M. Lynch, and R. Bürger. 1993. Müller's ratchet and mutational meltdowns. Evolution 47:1744–1757.

Gandon, S., Y. Capowiez, Y. Dubois, Y. Michalakis, and I. Olivieri.

1996. Local adaptation and gene-for-gene coevolution in a metapopulation model. Proc. R. Soc. Lond. B 263:1003–1009.

García-Ramos, G., and M. Kirkpatrick. 1997. Genetic models of rapid evolutionary divergence in peripheral populations. Evolution 51:21–28.

Gomulkiewicz, R., and R. D. Holt. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. Theor. Popul. Biol. 55: 283–296.

Hanski, I. 1985. Single-species dynamics may contribute to long-term rarity and commonness. Ecology 66:335–343.

Hanski, I., and M. Gyllenberg. 1993. Two general metapopulation models and the core-satellite species hypothesis. Am. Nat. 142: 17–41.

Hastings, A. 1983. Can spatial variation alone lead to selection for dispersal? Theor. Popul. Biol. 24:244–251.

Holt, R. D. 1996a. Adaptive evolution in source-sink environments: direct and indirect effects of density-dependence on niche evolution. Oikos 75:182–192.

———. 1996b. Demographic constraints in evolution: towards unifying the evolutionary theories of senescence and niche conservatism. Evol. Ecol. 10:1–11.

———. 1997. On the evolutionary stability of sink populations. Evol. Ecol. 11:723–731.

Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. Evol. Ecol. 6:433–447.

Jaenike, J. 1990. Host specialization in phytophagous insects. Annu. Rev. Ecol. Syst. 21:243–273.

Jenkins, C. D., and M. Kirkpatrick. 1995. Deleterious mutation and the evolution of genetic life cycles. Evolution 49:512–520.

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

———. 2000. Adaptation to marginal habitats: contrasting influence of the dispersal rate on the fate of alleles with small and large effects. Proc. R. Soc. Lond. B 267:1315–1320.

Kawecki, T. J., N. H. Barton, and J. D. Fry. 1997. Mutational collapse in marginal habitats and the evolution of ecological specialisation. J. Evol. Biol. 10:407–429.

Kelley, S. T., and B. D. Farrell. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52:1731–1743.

Kelley, S. T., B. D. Farrell, and J. B. Mitton. 2000. Effects of specialization on genetic differentiation in sister species of bark beetles. Heredity 84:218–227.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species range. Am. Nat. 150:1–23.

Kuussaari, M., M. Singer, and I. Hanski. 2000. Local specialization and landscape-level influence on host use in an herbivorous insect. Ecology 81:2177–2187.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution 30:314–334.

Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution 50:434–437.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton Univ. Press, Princeton, NJ.

Lynch, M., and W. Gabriel. 1990. Mutational load and the survival of small populations. Evolution 44:1725–1737.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. Am. Nat. 140: 1010–1027.

Pulliam, H. R. 1988. Source, sinks, and population regulation. Am. Nat. 132:652–661.

Radtkey, R. R., and M. C. Singer. 1995. Repeated reversals of host-preference evolution in a specialist insect herbivore. Evolution 49:351–359.

Shpak, M., and A. S. Kondrashov. 1999. Applicability of the hypergeometric phenotypic model to haploid and diploid populations. Evolution 53:600–604.

Singer, M. C. 1971. Evolution of food-plant preference in the butterfly *Euphydryas editha.* Evolution 25:383–389.

———. 1983. Determinants of multiple host use by a phytophagous insect population. Evolution 37:389–403.

Singer, M. C., and C. Parmesan. 1993. Sources of variation in patterns of plant-insect association. Nature 361:251–253.

Singer, M. C., and C. D. Thomas. 1996. Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. Am. Nat. 148:S9–S39.

Thomas, C. D., M. C. Singer, and D. A. Boughton. 1996. Catastrophic extinction of population sources in a butterfly metapopulation. Am. Nat. 148:957–975.

Tufto, J. 2000. Quantitative genetic model for the balance between migration and selection. Genet. Res. 76:285–293.

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

Via, S. 1991. The genetic structure of host plant adaptation in a spatial patchwork: demographic variability among reciprocally transplanted clones. Evolution 45:827–852.

Wiener, P., and M. W. Feldman. 1993. The effects of the mating system on the evolution of migration in a spatially heterogeneous population. Evol. Ecol. 7:251–269.

Wolfram, S. 1999. Mathematica. ver. 4.0. Cambridge Univ. Press, Cambridge, U.K.

Corresponding Editor: M. Whitlock

APPENDIX 1

An Approximation for the Asymmetric Equilibria at Low Movement Rates

We here derive approximations for the population sizes and maladaptation at the asymmetric equilibrium, as well as conditions for the stability of this equilibrium, when the rate of movement between habitats is very low. We assume that adaptation is almost perfect for the populations in habitat 1 and that these populations are also close to their maximal size. In contrast, the populations in habitat 2 are poorly adapted and their density is low. We further assume that the relative movement rate is small. Thus, we can write $Z_1 = \delta_{Z1}$, $N_1 = 1 + \delta_{N1}$, $Z_2 = H + \delta_{Z2}$, $N_2 = \delta_{N2}$, and $M = \delta_M$, where all the δ-values are much smaller than one. We also assume that the habitat heterogeneity, H, is large.

By neglecting terms of order δ^2, but retaining those involving H, we obtain the following set of dynamic equations:

$$\frac{dZ_1}{dT} \approx -\Gamma Z_1 \quad \text{and} \tag{A1}$$

$$\frac{dN_1}{dT} \approx -N_1 + 1 - M. \tag{A2}$$

The dynamics in habitat 1 are approximately independent of the population density and maladaptation in habitat 2. Populations in habitat 1 thus settle to their own equilibrium:

$$\hat{Z}_1 \approx 0, \quad \text{and} \tag{A3a}$$

$$\hat{N}_1 \approx 1 - M. \tag{A3b}$$

Inspection of equations (A1) and (A2) shows that this equilibrium is stable against small perturbations. Assuming that populations in habitat 1 are at equilibrium, and making the same approximations as previously, the dynamic equations for changes in habitat 2 are:

$$\frac{dZ_2}{dT} \approx -TZ_2 + \frac{M}{N_2}(H - Z_2) \quad \text{and} \tag{A4}$$

$$\frac{dN_2}{dT} \approx N_2\left(1 + \frac{1}{2}\Gamma H^2 - \Gamma H Z_2\right) + M. \tag{A5}$$

Here we present a graphical argument showing that there are at most two equilibria for this set of equations, one of them being always unstable. Equations (A4) and (A5) show that the equilibrium population size and maladaptation in habitat 2 satisfy:

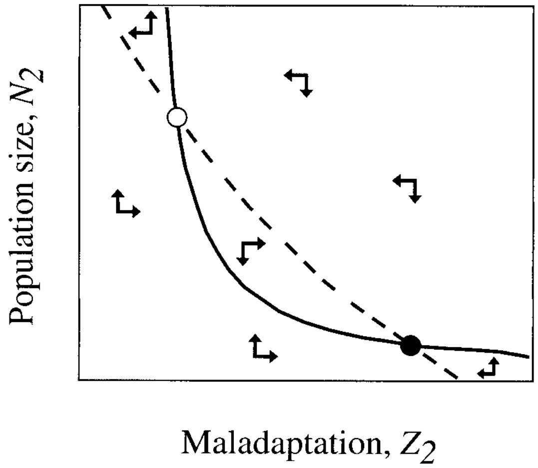

FIG. A1. Graphical stability of the asymmetric equilibrium in the case of low rates of movement between habitats. Populations are represented in the phase plan (Z_2, N_2), where N_2 is the population density in habitat 2 and Z_2 is the maladaptation in habitat 2. Only the positive quadrant of the phase plan is shown here. Dashed line represents the isocline of null variation for maladaptation (see eq. A6). Continuous line represents the isocline of null variation for population density (see eq. A7). Arrows indicate the initial direction of variation for N_2 and Z_2 starting from different initial conditions. White circle represents an unstable equilibrium. Black circle represents a stable equilibrium.

$$\hat{N}_2 = \frac{M(H - \hat{Z}_2)}{\Gamma \hat{Z}_2} \quad \text{and} \tag{A6}$$

$$\hat{N}_2 = \frac{2M}{2\Gamma H \hat{Z}_2 - \Gamma H^2 - 2}. \tag{A7}$$

Equations (A6) and (A7) respectively define sets of points (Z_2, N_2) for which maladaptation is at equilibrium and for which population size is at equilibrium (see Fig. A1). Such sets of points are called ''isoclines of null variation.'' A population initially above the isocline (A6) will evolve so that maladaptation decreases. Conversely, a population initially below the isocline (A6) will evolve so that maladaptation increases. Similarly, a population will increase or decrease in size depending on whether it is initially below or above the isocline (A7) (see Fig. A1). Both isoclines decrease monotonically with increasing maladaptation in the positive quadrant of the phase plane. Isocline (A6) intersects the x-axis when maladaptation equals H, whereas isocline (A7) approaches the x-axis asymptotically when maladaptation increases to infinity.

Intersections of the two isoclines define the equilibrium points. Solving equations (A6) and (A7) reveals that there are at most two equilibrium points. Those equilibria are real and positive only when

$$H > H_{\min} = 2 + \sqrt{\frac{2(1 + \Gamma)}{\Gamma}}. \tag{A8}$$

When there are two real and positive equilibria, Figure A1 shows that only the equilibrium with the smallest population size and the largest maladaptation is stable. This stable equilibrium is

$$\hat{Z}_2 \approx \frac{2 - 2\Gamma + 3\Gamma H^2 + \sqrt{(-2 + 2\Gamma + \Gamma H^2)^2 - 16H^2\Gamma^2}}{4H\Gamma} \tag{A9}$$

and

$$\hat{N}_2 \approx \frac{4M}{-2 - 2\Gamma + \Gamma H^2 + \sqrt{(-2 + 2\Gamma + \Gamma H^2)^2 - 16H^2\Gamma^2}}. \tag{A10}$$

Condition (A8) therefore guarantees the existence of a stable and viable asymmetric equilibrium.

APPENDIX 2

Stability of the Symmetric Equilibrium

We consider small perturbations around the symmetric equilibrium. The dynamics of those perturbations are given by the Jacobian matrix of the system of equations in (6), evaluated at the symmetric equilibrium defined by equation (7):

$$J = \begin{pmatrix} -M - \Gamma & -M & -\frac{M(H - 2\hat{Z}_1)}{\hat{N}_1} & \frac{M(H - 2\hat{Z}_1)}{\hat{N}_1} \\ -M & -M - \Gamma & \frac{M(H - 2\hat{Z}_1)}{\hat{N}_1} & -\frac{M(H - 2\hat{Z}_1)}{\hat{N}_1} \\ -\Gamma \hat{N}_1 \hat{Z}_1 & 0 & -\hat{N}_1 - M & M \\ 0 & -\Gamma \hat{N}_1 \hat{Z}_1 & M & -\hat{N}_1 - M \end{pmatrix}. \tag{A11}$$

The symmetric equilibrium is locally stable if all eigenvalues of the Jacobian have negative real parts. The eigenvalues of the Jacobian matrix in (A11) are

$$\lambda_1 = -2M - \Gamma, \tag{A12}$$

$$\lambda_2 = -\hat{N}_1, \tag{A13}$$

$$\lambda_3 = \frac{1}{2}\{-2M - \Gamma - \hat{N}_1 - \sqrt{(2M + \Gamma + \hat{N}_1)^2 - 4[\hat{N}_1 + 2M(1 - H\hat{Z}_1 + 2\hat{Z}_1^2)]}\}, \tag{A14}$$

and

$$\lambda_4 = \frac{1}{2}\{-2M - \Gamma - \hat{N}_1 + \sqrt{(2M + \Gamma + \hat{N}_1)^2 - 4[\hat{N}_1 + 2M(1 - H\hat{Z}_1 + 2\hat{Z}_1^2)]}\}. \tag{A15}$$

All four eigenvalues are real. The three first eigenvalues are all negative only if the symmetric equilibrium is viable (i.e., $\hat{N}_1 > 0$), which happens when

$$H < H_{\mathrm{v}} = \sqrt{2}\frac{(2M + \Gamma)}{M\sqrt{\Gamma}}. \tag{A16}$$

A necessary and sufficient condition for the fourth eigenvalue to be negative is that

$$H < H_{\max} = \frac{\sqrt{2M + 1}}{\sqrt{5}} H_{\mathrm{v}}. \tag{A17}$$

Therefore the symmetric equilibrium is stable and viable when $H < \min(H_{\max}, H_{\mathrm{v}})$. Note that when $M < 2$, then $H_{\max} < H_{\mathrm{v}}$ and the stability condition reduces to (A17). When $M > 2$, however, the stability condition reduces to the viability condition (A16).