

HABITAT SELECTION AND NICHE CONSERVATISM

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ABSTRACT

Niche conservatism is the phenomenon in which species or other phylogenetic lineages seem to exhibit much the same ecological niche over their geographical ranges or over evolutionary time scales. Previous studies have suggested that optimal habitat selection can constrain niche evolution (and thus may help explain niche conservatism), in effect by preventing populations from experiencing unfavorable sink environments with conditions outside the niche. This paper relaxes a key assumption in prior literature, by allowing habitat selection decisions to be conditional upon an individual's phenotype. We use individual-based simulations of evolution in source–sink landscapes to examine the consequences of phenotype-matching habitat selection. If each individual obeys a “perfect” habitat selection rule—moving to another habitat only if that movement increases the match between its phenotype and the habitat's optimum—then habitat selection can speed up the rate of adaptation to sink environments, and thus facilitate niche evolution. We also note that habitat selection can also indirectly influence the pool of variation available for selection, and thereby potentially alter to some degree this conclusion.

Keywords: habitat selection, source–sink, niche conservatism, niche evolution

INTRODUCTION

An evolutionary topic of growing interest these days is niche conservatism, which is basically the phenomenological observation that a species often has much the same ecological niche (defined as the range of environmental conditions, resources, etc., needed for population persistence) over its geographical range and substantial spans of its evolutionary history, even during geological epochs that have seen massive changes in environmental conditions around the Earth (Coope, 1979; Bradshaw, 1991; Holt and Gaines, 1992). Yet in some circumstances, niches can evolve rapidly (Kinnison and Hendry, 2001; Reznick and Ghalambor, 2001). Understanding the forces that govern when and where species remain relatively constant in their niches, versus when niches can evolve rapidly, is central to a wide range of basic and applied ecological and evolutionary issues—from understanding the determinants of species range limits, to gauging the threat of novel emerging diseases, to predicting species' responses to the looming

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Received 4 March 2008, accepted 16 July 2008.

threats of global climate change (Wiens and Graham, 2005). Explanations for niche conservatism involve the interplay of a very wide range of biological and ecological processes acting at many levels of organization, including fundamental constraints on genetic variation (Bradshaw, 1991; Blows and Hoffmann, 2005), organismal tradeoffs (Hansen and Houle, 2004), demographic constraints (Kawecki, 1995, 2000; Holt, 1996; Filin et al., 2008), strong interactions among species in a community context (Ackerly, 2003; Chase and Leibold, 2003; Case et al., 2005), and subtle but fundamental effects of habitat specialization upon the rate of adaptive evolution (Whitlock, 1996).

Adaptive habitat selection—the ability of organisms to move among environments in a way that tends to enhance their fitness—is believed to have profound consequences for many ecological and evolutionary processes, including population dynamics (Holt, 1985; Krivan, 2003), persistence in changing environments (Pease et al., 1989), the outcome of interspecific interactions (Rosenzweig, 1981, 1991; Schmidt et al., 2000), and even the likelihood of speciation (Maynard Smith, 1966; Diehl and Bush, 1989; Bush, 1994). Could the capacity of a species to exhibit habitat selection indirectly influence the likelihood it will also exhibit niche conservatism? Habitat selection is a particularly clear form of “niche construction,” where organisms selectively filter and modify their environments, which then helps define how natural selection will occur in a population (Odling-Smee et al., 2003). Holt (1985, 1987), Rosenzweig (1987), and Futuyma and Moreno (1988) have suggested that optimal habitat selection could lead to a greater tendency for habitat specialization, and in effect, via behavioral avoidance, indirectly cut off the opportunity for evolutionary responses to novel, initially unfavorable environments. If valid, their hypothesis is that habitat selection, in an evolutionary context, basically tends towards niche conservatism.

The basic reasoning went as follows. Consider a landscape where the spatial variance in fitness of a species is sufficiently great that in some habitats fitness is less than unity at all densities (“sink” habitats), while in others, fitness is greater than unity for some range of densities (“source” habitats). If “ideal free” assumptions are met (*sensu* Fretwell, 1972, so that there is no direct interference, and individuals can accurately assess fitness in each habitat and move without incurring fitness costs), then in a stable environment where a population is at demographic equilibrium, no individuals should reside in the sink habitats at all. This means that if an allele arises which could improve fitness in the sink habitat, its potential fitness advantage will not be expressed, and so it may be lost if it is neutral in the occupied habitat, or actively weeded out if it has a fitness cost there. Alleles that arise which improve fitness in the occupied habitat, at the expense of potential fitness elsewhere, will be positively selected, and alleles that are neutral in the occupied (source) habitat but deleterious outside can accumulate due to drift. Over time, these processes may lead a species that is already somewhat specialized in its habitat requirements to experience yet greater fitness costs in habitats it is not using, which further increases the fitness advantage of habitat selection. This positive feedback between habitat selection and local adaptation can promote increasingly tight habitat specialization.

This positive feedback can even arise when neither habitat is a sink, but there is a between-habitat tradeoff in performance leading to different local carrying capacities.

For instance, Holt (2003) examined evolution in such a two-habitat environment, assuming a tradeoff between habitats (so increasing performance in one came at a cost in the other) coupled with ideal free habitat selection. The models examined in that paper assumed that habitat selection and performance evolved in sequential evolutionary steps; after a round of evolution in habitat-specific adaptation, the habitat selection rules would readjust to an ideal free state, which could then pave the way for another evolutionary shift in adaptation. This study revealed that a species could initially be a generalist, adapted to both habitats, but gradually evolve towards greater specialization, because of the coevolution of habitat selection behavior and local performance. Basically, as population size declines in one environment, selection increasingly discounts this environment in determining the overall direction of selection, and so there is a positive feedback between density-dependent habitat selection and increasing specialization towards one habitat (usually, though not always, the habitat in which the species was initially more abundant). For this outcome not to occur, and habitat generalization to be maintained, fitness sets need to be strongly convex, so that adaptation to one habitat incurs little or no cost as measured in adaptation to the other (which maintains a rough demographic balance between the two habitats, as measured by carrying capacity).

In the models explored in Holt (2003), and indeed in most of the literature on evolution in source–sink environments, there was an implicit and critical assumption. Namely, when genetic mutants arise in a given habitat, their habitat selection or dispersal behavior is assumed to be that expected on average in the resident subpopulation in that habitat. So movement decisions impacting the fate of a rare allele are assumed to be made independent of the genotype an individual actually has at that moment. This is often reasonable. Many empirical studies have revealed a surprisingly poor relationship between habitat selection and individual performance, when performance differences have a genetic basis (Jaenike and Holt, 1991).

But what if individuals can detect their phenotypic state, and modify their movement propensities, so that they are more likely to move from habitat A to habitat B when their phenotype is somewhat more fit in the latter (compared to the modal phenotype in the population)? We will call this “phenotype-matching habitat selection” (Edelaar et al., 2008, use the term “matching habitat choice”). Pleiotropic genetic effects of this sort can have major evolutionary consequences. This has been addressed in the literature of evolutionary genetics. Jones (1980) reported a number of examples where individuals seem to match their phenotypes to their choice of habitats. For instance, in the Caribbean, *Anolis* lizards have a conspicuous polymorphism in body pattern, with a mixture of striped and unstriped individuals found in the same population. Unstriped lizards are largely on the ground, whereas striped individuals tend to live in bushes where they are better concealed (Schoener and Schoener 1976).

Theoretical models show that such habitat selection can help maintain adaptive genetic polymorphisms (Taylor, 1976; Maynard Smith, 1966; Hedrick, 1990; Ravigne et al., 2004). However, this is more likely if there is soft selection in each habitat (i.e., each habitat may be at its own carrying capacity, fixed independent of changes in gene frequency), than if there is hard selection, where the output of each habitat depends upon its

genetic composition (De Meeus et al., 1993). A source–sink system in a sense combines elements of hard and soft selection; selection in the source might not have much impact on population size there because of density dependence, but in the sink where densities are assumed low, if selection can increase fitness to exceed unity (so that the habitat is no longer a sink), population size will also be expected to increase.

Intuitively, it seemed to us that if individuals could assess their phenotypes (which would be an estimate of the genotype, modified by a random term due to, for instance, development accidents), and modify their movement rules so that movement becomes more likely the more their own phenotype matches that of the habitat toward which they move, then this bias in movement might facilitate evolution to a sink habitat, outside the original niche of the species. The reason was twofold. First, immigrants would tend to be a biased sample from the source population, where the bias would be in the direction of those individuals already to a degree “preadapted” to the conditions of the sink, more so than represented by a random sample from the source. Second, one reason why recurrent immigration tends to lead to persistent maladaptation is that maladapted individuals can move into a habitat and mate with more-adapted residents, lowering the reproductive success of the latter. Habitat selection should reduce the number of such maladapted individuals that appear in a sink habitat, and so make selection there more effective at honing local adaptation. So, phenotype-matching habitat selection should tend to facilitate niche evolution in sink environments.

What we will show in the following paragraphs is that this hunch appears to be correct. But our study will also reveal some subtle effects of habitat selection upon the evolutionary process, which will be mentioned briefly here, and explored more fully elsewhere. Whether or not phenotype-matching habitat selection facilitates niche evolution depends upon the accuracy of habitat selection decisions, and upon the indirect effects of habitat selection upon the pool of genetic variation available for selection.

To encompass many realistic aspects of the evolutionary process in sinks, such as mutation, drift, demographic stochasticity, density dependence, and the dynamics of genetic variation itself, in our prior work we have used individual-based simulation models that keep track of each individual and its genotype as evolution occurs in a heterogeneous landscape. We continue to use such models here, to show that adaptive habitat selection may lead to some evolutionary surprises. We first sketch the elements of the model we use here, summarize insights from our past studies, and then turn to how adaptive evolution in sinks is modified by phenotype-matching habitat selection.

AN INDIVIDUAL-BASED MODEL OF ADAPTIVE EVOLUTION TO A SINK WITH HABITAT SELECTION

The individual-based model tracks each individual and its genotype, and includes a reasonable amount of detail about demography and genetics. We consider a species experiencing spatial variation in a coarse-grained manner, such that the environment consists of two discrete habitats, one with conditions within the species’ niche, with a persistent population (a source), and the other initially outside (a sink). The environment is temporally constant. We describe the details of the model in the Appendix (adapted

from Holt et al., 2005; the genetic assumptions largely follow Burger and Lynch, 1995). Basically, we assume discrete generations with stabilizing selection on a juvenile quantitative trait (via survival), with different phenotypic optima in the source and sink, and keep track of each individual over its lifetime. The source is initially populated and the sink empty. Because of the difference in phenotypic optima, migrants from the source tend to be maladapted to the sink. The larger the difference in phenotypic optima, the greater this average maladaptation of immigrants; therefore, we refer to this difference as the sink maladaptation. A number of genetic loci (and a Gaussian environmental term) contribute additively to the trait (phenotype) under selection. Stabilizing selection depletes genetic variation, which is maintained by mutational input. Mutation is simulated by adding a Gaussian random variable to an allelic value, so that most mutants have a small effect upon the phenotype, but there is a nonzero probability of mutants of large effect appearing. There is “ceiling” density dependence, so that the number of breeding adults is capped at a carrying capacity, K . If individuals migrate at the adult stage, this density regulation occurs after dispersal. The simulations start with a long period of time during which the source habitat is closed, which allows it to reach its demographic and evolutionary equilibrium, with the mean trait of the population remaining very near the local optimum. Underlying this near-constancy at the phenotypic level, there is constant turnover of genetic alleles, due to a combination of mutation, drift, and selection. This implies a fresh supply of variation that can be “tested” against the conditions of the sink environment. The outcome of the simulations are presented as figures summarizing many thousands of models runs, showing the probability of adaptation to the sink over some time horizon (e.g., 1000 generations) as a function of (for instance) the difference in the phenotypic optima between source and sink habitats. In Holt et al. (2003), we calculated the probability of adaptation as a function of the time horizon (without habitat selection), and the results implied a nearly constant per-generation probability of adaptation. Therefore, it is reasonable to assume that a higher probability of adaptation implies a higher rate of adaptation.

EVOLUTION IN SINK ENVIRONMENTS: DISPERSAL WITHOUT HABITAT SELECTION

Clearly, if no individuals move from the source to the sink, then evolution cannot directly sculpt adaptation to the sink habitat, simply because no individuals occur there. To permit adaptation to a sink to occur in a stable environment, one must permit dispersal from the source to the sink. One way that such dispersal can occur is if species depend upon physical transport processes for movement even within their preferred habitat; some individuals are then likely to end up in the wrong place. Given a fixed rate of dispersal (either number of individuals, or per capita) from source habitats into sinks, a very general pattern that has emerged in previous studies is that the likelihood of adaptation over a given time horizon declines with increasing difference between source and sink phenotypic optima. Basically, groups of colonists plucked from the source and put into the sink, by definition face extinction. The harsher the environment is in the sink, the more rapidly extinction should occur there, precluding any further opportunity for selection to fashion adaptation. If the difference between the source and sink optima is

large, the sink may thus remain stuck in a state of maladaptation for a very long time period (Ronce and Kirkpatrick, 2001; Filin et al., 2008).

A further insight is that the effect of the rate of immigration on adaptation to the sink depends upon genetic details, as well as the overall pattern of movement, and the strength of density dependence. Analyses of single-locus models (Gomulkiewicz et al., 1999) demonstrate that when densities are low and density dependence is weak, increasing the rate of such immigration tends to facilitate adaptation to the sink because immigration increases the pool of variation made available for local selection. However, in models of quantitative trait evolution (Holt et al., 2004a), this positive effect of immigration via genetic variation is usually offset by the negative “swamping” effect of maladapted immigrants mating with residents. Negative density dependence in the sink tends to hamper adaptation there (Filin et al., 2008). Finally, a variety of complicated patterns emerge with bidirectional movement (Kawecki and Holt, 2002; Holt and Barfield, in prep.). Below, for simplicity we assume that movement is unidirectional, from source to sink. One rationale for this is that the source is initially occupied but the sink is not. Therefore, an individual whose phenotype matches the sink more closely than the source is better off moving. The same is not true for individuals in the sink while it is at low density because they will face competition for breeding sites in the source.

Examining one-way dispersal helps conceptually to clarify the processes at play in adaptation to a sink habitat. With bidirectional dispersal, several factors that are going on simultaneously must be considered. First, the appropriate measure of fitness for any allele is given by a complicated average over both habitats (Holt, 1996; Kawecki, 1995), where the averaging depends upon the pattern of movement. Kawecki (2000) found in a model with bidirectional movement but without habitat selection that the movement rate that made adaptation to a sink most likely depended upon whether or not one was concerned with alleles of small or large effect upon fitness. Second, adaptation in the sink will influence the gene pool present in the source (not just the mean genotypic value, but the entire shape of the genotypic distribution), which feeds back to influence evolution in the sink. This can lead to nonlinear relationships between the rate of movement and the rate of adaptation. With unidirectional dispersal, the source can be assumed to be at equilibrium. We will discuss bidirectional dispersal elsewhere (Holt and Barfield, in prep.), and the results presented here provide a useful stepping stone to these and other more complex scenarios.

PERFECT HABITAT SELECTION

First, assume that habitat selection is “perfect.” In standard habitat selection theory (Fretwell and Lucas, 1969; Fretwell, 1972; Holt, 1985), an individual compares its expected fitness in the habitat it currently occupies with its fitness in the other habitat. In purely ecological models, differences in individual fitness arise because of differences in ecological factors, such as intrinsic habitat quality or local density. But if there are genetic differences between individuals that influence fitness, and each individual can assess its genetic state and thus its likely habitat-specific fitness, within-population variability in habitat selection decisions may arise.

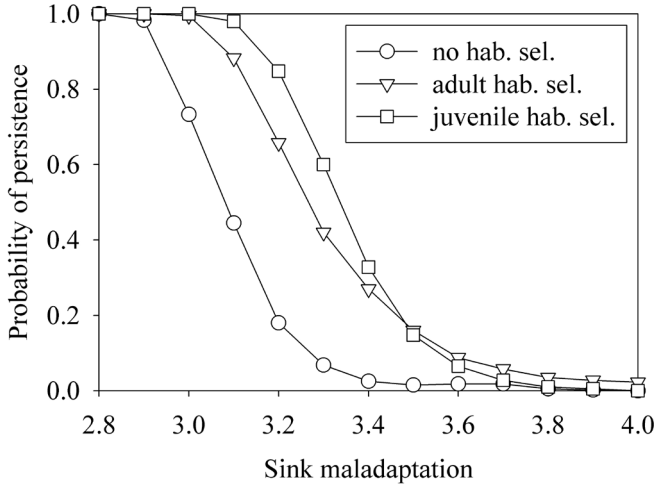


Fig. 1. Probability of adaptation (sink persistence after dispersal discontinued following 1000 generations of dispersal) with adult habitat selection (each source adult migrates if its phenotype is closer to the sink's optimum), and with no habitat selection and an equivalent average dispersal rate. The sink maladaptation is the difference in optimum phenotypes between source and sink. Probability of adaptation with habitat selection and juvenile dispersal is also shown. Carrying capacity $K = 256$, number of loci $n = 10$, fecundity $f = 4$, mutation rate per haplotype $n\mu = 0.01$, variance of mutational input $\alpha^2 = 0.05$, and strength of selection $\omega^2 = 1$.

In our previous individual-based simulations, we assumed that selection acts on survival, but adults disperse. To facilitate comparisons with those results, we here assume each individual can accurately assess its phenotype, and moves to the sink only if its phenotype is closer to the sink's phenotypic optimum than to the source's optimum. Since fitness decreases with an increasing difference between an individual's phenotype and a habitat's optimum, this means that for our phenotype-matching movement rule, the dispersing individual's fitness is expected to be higher in the sink than if it were to stay in the source. (Note that although adults have already been through selection, the offspring of adults with higher fitness in the sink will also tend to have higher fitness in the sink than would the offspring of the other adults.) We also present below results in which juveniles migrate before selection. Because most individuals in the source are expected to be more adapted to the source, they should not be expected to move to the sink.

Because mutation is assumed to occur independently of its effect upon an individual's fitness, a primary constraint upon adaptation to the sink is simply the rate at which appropriate novel variants arise via mutation in the source. Our assumption that most mutations have a small effect upon the phenotype implies that there may be a long waiting time before an individual appears whose phenotype is closer to the sink's optimum than that in its natal habitat. Figure 1 shows that the likelihood of adaptation over a number

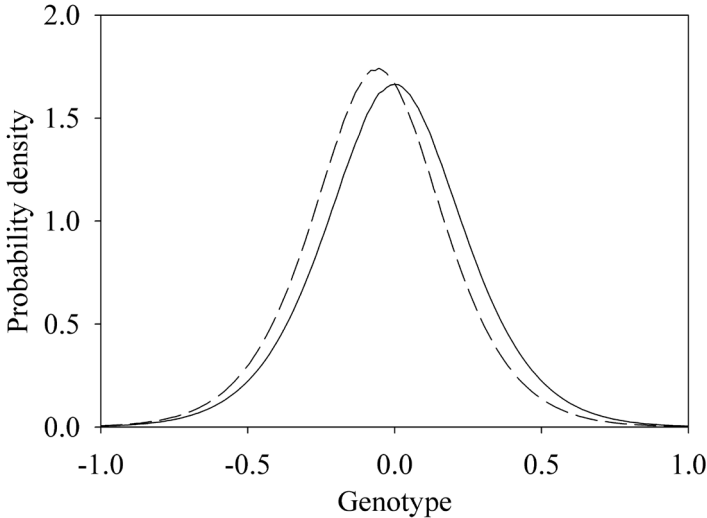


Fig. 2. Probability density functions (PDFs) of genotype with (dashed) and without (solid) habitat selection, with adult dispersal. Parameters as in Fig. 1 with sink maladaptation = 3, and with values pooled from 5,000 generations of each of 200 simulations. The effect of phenotype-matching habitat selection is to push the PDF away from the optimum in the sink.

of generations of dispersal (in the example shown, 1000 generations) is boosted, given “ideal” phenotype-matching habitat selection and adult dispersal, compared to the same rate of recurrent dispersal independent of phenotype. Dispersal is discontinued after 1000 generations, and the probability of adaptation is defined as the fraction of the sink populations that persist (other definitions of adaptation give similar results). The rate of dispersal for each sink maladaptation without habitat selection is set at the average rate of dispersal realized with habitat selection. This drops from about 2.5% at a maladaptation of 2.8, to about 0.3% at 4.0. With increasing sink maladaptation, there are fewer source individuals closer to the sink optimum, and those that are have lower average sink fitness than with a milder sink. Also shown in Fig. 1 is the probability of sink adaptation with habitat selection and juvenile dispersal, which is similar to habitat selection with adult dispersal, but generally a little higher. For the example shown, the increase in the likelihood of adaptation is particularly strong for intermediate differences in phenotypic optima between the source and sink habitats. The reason for this pattern is as follows.

To understand rates of evolution, in general, one must always consider two things: the determinants of genetic variation, and the force of natural selection. With stabilizing selection around a phenotypic optimum and recurrent mutation, populations can retain additive genetic variation. In any given snapshot of the population, there will be a larger pool of individuals varying to a small degree from the optimum than of individuals varying to a large degree. (Figure 2 shows the distribution of genotypes over many generations and populations.)

When there is only a small difference in phenotypic optima (on the left of the figure; i.e., the sink is mild), Fig. 1 shows that adaptation to the sink is relatively rapid even without habitat selection, and habitat selection has a minor effect upon the rate of evolution (as noted above, in a previous study we found that a higher probability of adaptation over a fixed time frame corresponds to a higher rate of adaptation). The balance between selection (and drift) weeding variation out, and mutation bringing it in, provides a relatively large pool of individuals with phenotypes modestly different from the source optimum. This means that even with random dispersal, there is a reasonable probability some migrants to the sink will by chance be preadapted there. Even in favorable environments, colonizing propagules that are small in number are likely to go extinct (MacArthur and Wilson, 1967). But as long as this chance is nonzero, with enough iterations of bouts of immigration, eventual successful colonization is inevitable (Holt et al., 2005). So with a small difference between the source and the sink, adaptation is likely, even without the boost provided by phenotype-matching habitat selection.

If, by contrast, there is a very large difference in phenotypic optima between the source and sink habitats (i.e., the sink is quite harsh), the rate of adaptation to the sink is very slow, with or without phenotype-matching habitat selection. The reason is that stabilizing selection in the source constrains variation there, and does so particularly effectively for phenotypes which deviate strongly from the local optimum. This makes it unlikely that individuals will be present with phenotypes that might be favored in the sink. Given a large difference in optima between source and sink, then even if an individual arises with a phenotype deviating in the direction of the optimum in the sink, although its fitness is less than the average fitness of residents in the source (which tends to be around unity because the source population is at demographic equilibrium), its fitness in the sink will likely be even less. So it should not change habitats.

But at intermediate levels of maladaptation in the sink, these same individuals may perceive that they would increase the fitness of their offspring by moving to the sink habitat. Moreover, the pool of potentially favorable variants available in the source should be larger (because they have smaller deviations from the local optimum, they are being less effectively removed by selection from the source). If individuals can accurately assess their individual phenotypes, and then use this assessment in making habitat selection decisions, there is a substantial increase in the rate of adaptation. So in some circumstances, ideal free habitat selection can speed up the rate of adaptation to novel, harsh environments, provided each individual can assess its expected fitness as a function of the habitat in which it resides, and make movement decisions accordingly.

There is a second, somewhat subtle, effect of phenotype-matching habitat selection upon evolution that can be potentially important. If individuals who are born with phenotypes differing in one direction from the source optimum leave, and neither they nor their descendents return, this in effect amounts to an additional force of directional selection acting in the source habitat. This component of selection pushes the mean phenotype of the source population farther away from the sink optimum. This could in principle make adaptive evolution to the sink less likely, since it reduces the pool of variants present that are likely to be preadapted to sink conditions. Figure 2 shows for our example that

the probability density function of source genotypes is shifted by phenotype-matching habitat selection, away from the sink optimum by a small amount. Quantitatively, this effect of habitat selection on the pool of genetic variation in our example is relatively minor. Basically, this is because with our assumption that each individual can perfectly assess its phenotype in making a decision to emigrate, relatively few individuals leave the source, and so the force of the emergent directional selection away from the sink is quantitatively small. However, this effect of habitat selection upon the pool of genetic variation can play a much more substantial role upon adaptive selection to sink habitats when phenotype-matching habitat selection rules are imperfect, and indeed such habitat selection may actively hamper adaptation to a sink environment. We plan to present these results in detail elsewhere, along with analyses of the consequences of bidirectional movement, where these effects of dispersal upon the pool of variation turn out to have important and sometimes surprising consequences (Holt and Barfield, in prep.).

A brief summary is as follows. Back movement (from sink to source) can affect the rate of adaptation in several ways. First, there is the demographic effect on the sink. Back migration leads to the loss of some sink individuals, which can reduce the probability of adaptation, especially if the sink population is low (which is more likely with adult movement). However, on average, individuals that leave the sink will be less well adapted to the sink than individuals that stay. This could help adaptation in the sink. Another effect is on the genetics of the source. Individuals that return to the source from the sink are probably on average genetically more suited to the sink than a random source individual, so this feedback will likely increase sink adaptation by perturbing the source gene pool a bit towards the sink optimum. For instance, with juvenile movement, back migrants are quite likely to survive selection in the source (because movement depends on the juvenile phenotype, on which selection acts), and so such movement will likely have an effect on the array of genotypes present in the next generation. Those with genotypes favorable in the sink are then more likely to move to the sink.

CONCLUSIONS

Habitat selection by individuals has consequences that resonate through nearly all the themes of population and community ecology, and such behavior has crucial implications for evolution as well. Habitat selection that is phenotype-independent may act as a powerful constraint on adaptive evolution, in effect because such behavior defines the spatial template against which genetic variants are tested (Brown and Pavlovic, 1992; Odling-Smee et al., 2003). An implicit assumption that these authors made, however, was that when novel genetic variants arose by mutation in an individual, it used the same movement rules as employed by other individuals not carrying that mutation. We have explored some of the implications of situations in which individuals can accurately gauge the fitness consequences of the phenotypes they carry, and make movement decisions accordingly. Our protocol has been to splice such rules into individual-based simulation models in which individuals and their genotypes are tracked over many generations. The examples we present suggest that phenotype-matching habitat selection

can facilitate adaptive evolution to sink environments. However, we also parenthetically have noted that such habitat selection can impact the nature of local gene pools, which in turn can indirectly influence the likelihood of niche evolution.

To apply these insights to natural systems requires that we understand when one might expect to see phenotype-matching habitat selection decision rules. Studies of oviposition behavior in insects have often revealed surprising discrepancies between genetically-based host plant preferences and oviposition behaviors (Jaenike and Holt, 1991), suggesting that phenotype-sensitivity is probably not universal. But in some circumstances, it is plausible that the mapping of genotype to phenotype could be used by organisms to provide cues as to likely fitness in various environments. For instance, for nocturnal moths, finding an appropriate substrate to hide against in the daytime may be critical to surviving bird predation. Moths might be able to visually match their own phenotypes against the visual environments of particular habitats, and move accordingly. A mutation that arose that changed wing color could then lead directly to changes in habitat selection decisions. We suggest that an important direction for future work will be to elucidate those situations in which novel mutants affecting fitness provide cues that can be directly used by organisms in making habitat choices, and those in which there is a decoupling of such genetic variation from the rules of habitat selection. In the former, habitat selection may facilitate niche evolution, but in the latter, habitat selection may lead to niche conservatism. Habitat selection may thus play a crucial role in the emerging framework for understanding the determinants of niche conservatism versus evolution.

ACKNOWLEDGMENTS

We thank the reviewers and Doug Morris for their helpful remarks, and University of Florida Foundation and the National Science Foundation for support.

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APPENDIX

INDIVIDUAL-BASED MODEL FOR ADAPTATION TO SINKS WITH RECURRENT DISPERSAL

Deterministic models can illuminate the interplay of population and evolutionary dynamics (see, e.g., Gomulkiewicz and Holt, 1995; Kawecki, 2000), but a full treatment of extinction requires one to incorporate stochasticity. When population sizes are low, discreteness and stochasticity of mutation, birth, death, and movement events become important. It is difficult to treat all these factors in analytic models. To provide insight into the consequences of this stochasticity, we have carried out simulations using individual-based models that monitor the fate of each individual (e.g., Holt et al., 2003). The model is based on the model of Burger and Lynch (1995), who examined adaptation to a continually changing environment, for a single character determined by genes at many loci. In the results discussed in the text, we examined adaptation to a sink habitat that experiences recurrent immigration of individuals from a source habitat.

Key assumptions in the simulations (see Holt et al., 2003) are:

- (A) Genetic assumptions—(1) there are n additive diploid loci, with no dominance or epistasis (each allele has a continuous numeric value, and an individual's phenotype is the sum of these values over all loci and a zero-mean, unit-variance Gaussian random value); (2) mutation maintains variation (the effect of mutation is to add to a current allelic value a number drawn from a zero-mean Gaussian distribution); (3) there is free recombination between all loci; (4) the initial source habitat is allowed to reach mutation–selection–drift balance before dispersal to the sink begins;
- (B) Life history assumptions—(1) discrete, non-overlapping generations; (2) hermaphroditic sexual system, with a random mating system allowing all individuals to mate at low densities; (3) with adult dispersal, the order of life history events is reproduction, selection, dispersal, density regulation, reproduction—and with juvenile dispersal, the order is reproduction, dispersal, selection, density regulation, reproduction;
- (C) Ecological assumptions—(1) each source adult has a probability of migrating which depends on its phenotype, for simulations with habitat selection, or has a fixed dispersal probability for simulations without habitat selection; (2) “ceiling” density dependence (i.e., a limit is placed on the number of mating adults); (3) a fixed number of offspring for each mating pair; (4) the probability of a juvenile surviving to adulthood is a Gaussian function of the difference between its phenotype and the habitat optimum phenotype;
- (D) Mating system assumptions—in each generation, individuals are selected at random without replacement from all adults (after dispersal if individuals migrate at the adult stage) to have the female role in a mating pair, up to the carrying capacity; in other words, below K all individuals mate as females, whereas above K , only K individuals do so. Each mating female then selects a random individual (with re-

placement) from all adults in the habitat (including possibly itself) to act as a male. This protocol eliminates the small Allee effect that arises in a monogamous mating system (with an odd number of adults below the carrying capacity, one individual remains unmated; this decreases average expected fecundity over all individuals, particularly when the number of adults is small). We have shown elsewhere (Holt et al., 2004b) that Allee effects can influence adaptation to sink habitats, so it is useful to eliminate this possibly confounding factor.

Our results using this model appear to be robust to changes in many of these assumptions. For instance, changes in the number of loci have a relatively minor effect on the probability of adaptation, as does eliminating recombination (Holt and Gomulkiewicz, 2004, and unpublished results).

In generation t , the number of adults is N_t . For adult dispersal, after the census, there is dispersal, followed by random mating. The number of mating sites is fixed at a value K (carrying capacity), which limits the number of mating adults. Individuals produce gametes with free recombination among all loci. Mutation occurs with a fixed probability on each gametic haplotype. If a haplotype is determined to have had a mutation, a random value is added to a randomly chosen allele on that haplotype. Each mated pair produces f offspring, each of which survives to adulthood with probability $s(z, i) = \exp[-(z - \theta_i)^2/2\omega^2]$, where z is its phenotype, θ_i is the optimum phenotype in habitat i , and ω^2 is inversely proportional to the strength of stabilizing selection. Selection is therefore on juvenile to adult survival. If the average z value is sufficiently far from the optimum, mean fitness is below one and the population tends to decline. Individuals surviving selection are the adults counted at the next census, N_{t+1} . With juvenile dispersal, dispersal occurs just after reproduction, and is followed by selection on survival to adulthood, and then mating.

At the start of each simulation, the source population is simulated for 1000 generations before dispersal begins, to allow it to reach selection–mutation–drift equilibrium. The sink habitat is unoccupied until dispersal begins. We should stress that in this individual-based model, stochasticity plays multiple roles. Mutation and dispersal are stochastic. Gametic combinations and the genetic composition of immigrants to the sink have multi-locus allelic combinations that vary due to random sampling. Finally, because survival is probabilistic, there is both genetic drift and chance variation in population size, due to demographic stochasticity.