

# MATCHING HABITAT CHOICE CAUSES DIRECTED GENE FLOW: A NEGLECTED DIMENSION IN EVOLUTION AND ECOLOGY

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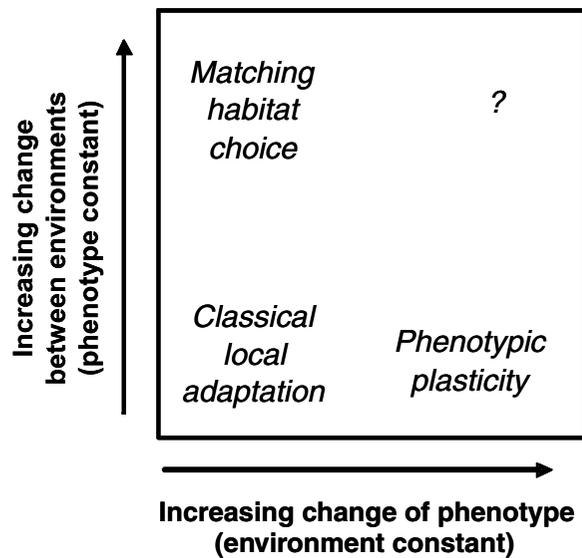
Gene flow among populations is typically thought to be antagonistic to population differentiation and local adaptation. However, this assumes that dispersing individuals disperse randomly with respect to their ability to use the environment. Yet dispersing individuals often sample and compare environments and settle in those environments that best match their phenotype, causing directed gene flow, which can in fact promote population differentiation and adaptation. We refer to this process as “matching habitat choice.” Although this process has been acknowledged by several researchers, no synthesis or perspective on its potentially widespread importance exists. Here we synthesize empirical and theoretical studies, and offer a new perspective that matching habitat choice can have significant effects on important and controversial topics. We discuss the potential implications of matching habitat choice for the degree and rate of local adaptation, the evolution of niche width, adaptive peak shifts, speciation in the presence of gene flow, and on our view and interpretation of measures of natural selection. Because of its potential importance for such a wide range of topics, we call for heightened empirical and theoretical attention for this neglected dimension in evolutionary and ecological studies.

**KEY WORDS:** Dispersal, gene flow, habitat choice, local adaptation, migration–selection balance, natural selection, population differentiation.

The evolutionary success of an individual depends to a large degree on the performance of its phenotype in a specific ecological context (Darwin 1859). Environments are seldom homogeneous in time and space, and individuals in these environments are rarely identical, thus the impact of this environmental heterogeneity

(e.g., local resources) on fitness may differ between individuals. Individuals therefore continually assess their environment, because evading the selective pressures against them is expected to increase their fitness. An individual finding that it suffers from a phenotypic mismatch with its current environment has but a few ways to deal with this (Fig. 1). First, it could make the best of it with its current, unchanged phenotype and environment. Given that individuals differ in their phenotypes, some phenotypes will

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**Figure 1.** Two dimensions of change classify mechanisms displayed by individuals that can increase the match between populations and their environments; that is, that can lead to local adaptation in the broad sense. In this article we only contrast extremes along each axis (as labeled), but real populations may and probably do occupy intermediate positions.

do better on average than others. Assuming this performance is based on heritable traits, after at least one generation natural selection causes increased classical local adaptation at the population level. (For the purposes of this article, we call this process that yields a pattern of evolved, genetically determined increased fit between local phenotypes and environments “classical local adaptation” because the other, more recently appreciated processes we discuss here [Fig. 1] also cause the general pattern of local individuals that are more adapted than foreign ones [see Kawecki and Ebert 2004], which we call local adaptation in the broad sense). Second, it may change its phenotype to better match local environmental pressures (i.e., various forms of phenotypic plasticity, such as physiological acclimation, behavioral adjustments, etc.). And logically, a third option exists: it keeps its phenotype unchanged but changes environments through dispersal. That is, it moves out of its current environment and searches for another one that is more suitable for its phenotype.

In the rest of this article, we will argue that this third path—for which we will use the term “matching habitat choice”—is a largely neglected dimension in evolution and ecology, that it may have important repercussions on a suite of phenomena, and hence deserves more attention. We begin by refining our definition of matching habitat choice and when and where the process is likely to occur, we then discuss potential implications of the process, outline criteria and approaches to test whether the process is operating, and finish with additional discussion of this process.

## *What Is Matching Habitat Choice and When and Where Is It Likely to Occur?*

With matching habitat choice, we envision a process of habitat choice that depends on the phenotypic traits of an individual, and where individuals with a given phenotype try to settle in the environment that best matches its capacities to use this environment. For example, because intake rate is highest when seeds fit well in a bird’s bill during processing, a large-billed bird searches for habitat patches in which large seeds are present, whereas a small-billed bird searches for patches with small seeds. In other words: individuals bias their movements to climb spatial fitness gradients (Armsworth and Roughgarden 2005a,b). Here habitat choice does not need to have a heritable genetic basis (cf. Jaenike and Holt 1991). Rather, matching habitat choice is an indirect effect of ecological traits (phenotypic traits that are important in the interactions between an organism and its environment, e.g., a birds’ bill size affects aspects of food uptake). Matching habitat choice is orthogonal to phenotypic plasticity (Fig. 1). Although in both processes the fitness-enhancing effect stems from an increase in the match between phenotype and environment, plasticity changes the phenotype to fit the environment, whereas with matching habitat choice the individual moves to an environment that fits its fixed phenotype. Obviously, both phenotypic plasticity and habitat choice can operate simultaneously to increase an individual’s fitness, but their distinction has important conceptual and empirical ramifications.

A crucial difference exists between matching habitat choice and other kinds of phenotype-dependent dispersal/habitat choice, such as dispersal affected by characteristics like age, size, sex, dominance rank, condition/state, which have already been extensively discussed elsewhere (e.g., Clobert et al. 2001, 2004). With matching habitat choice, individuals with different phenotypes rank environments differently, even in the absence of any competition, because the environment/resources that are optimal for one phenotype (e.g., large seeds for birds with large bills) will be suboptimal for another (e.g., large seeds for birds with small bills). In other words: phenotypic differences generate a trade-off in performance along environmental gradients, and when individuals differ in ecological traits this will lead to a phenotype  $\times$  environment interaction in their habitat preference and ideal free distribution (Fretwell and Lucas 1970). Based on this preference (but potentially contingent upon additional effects of density- and frequency-dependent competition), individuals on average settle in those habitats in which their fitness prospects are higher than in other habitats. In the case of a genetic basis for these phenotypic differences, the process of matching habitat choice also results in a genotype  $\times$  environment covariance. That is, individuals of similar genotype are found in

similar environments more often than expected from a random distribution.

The process we describe here has repeatedly been introduced or discussed, but no consistent terminology is used, which we suspect has caused fragmentation of attention for the process. The phrases “phenotypic sorting” (Siepielski and Benkman 2005), “phenotype-dependent dispersal” (Garant et al. 2005), “phenotype-sensitive dispersal” (Holt and Barfield, in press), “phenotype-specific habitat selection” (Holt and Barfield, in press), “genotype-specific microhabitat partitioning” (Harris and Jones 1995), “genotype-specific habitat selection” (Shine et al. 1998), “adaptive or refined habitat selection” (Fretwell 1969), “matching habitat choice” (Ravigné et al. 2004), “phenotype-matching habitat selection” (Holt and Barfield, in press), “fitness-dependent dispersal” (Armsworth and Roughgarden 2005a), “directed movement” (Armsworth and Roughgarden 2005a,b), and possibly others we have not found have all been used to describe the process we describe here. It also shares similarities with “fitness-driven dispersal” or “conditional movement” (Ruxton and Rohani 1999), “fitness-associated dispersal” (Hadany et al. 2004) and the “colonization-effect” (Hanski and Singer 2001). This varying terminology, for very similar processes, indicates that several workers have independently realized the importance of the phenomenon, but that subsequent workers have failed to use their ideas in later work. Here we use the term “matching habitat choice” because it modifies the widely understood term “habitat choice” to highlight that the aim of the process is an increased match between the individual and the environment to increase fitness. We suggest as a formal definition for matching habitat choice: the process that increases the correlation between individual ecological traits and environmental characteristics after dispersal, due to preferential settlement in those environments that better match individuals’ capacities to use them to increase fitness, and independent of the effects of competitive exclusion, phenotypic plasticity, natural selection, and genetic variation in habitat choice.

In a perfect world with no costs and limits to dispersal, matching habitat choice would be adaptive for any organism that experiences relevant spatial variability in environments. However, costs and limits to dispersal are a biological reality. Thus, we suspect that matching habitat choice may be more prevalent or important among organisms with high mobility relative to spatial variation in environments. That is, where dispersal distances are relatively large, and the organisms have control over where they settle (we invite plant biologists to consider this as well, see Bazzaz 1991). Organisms need not be capable of covering large geographic distances (e.g., snails, fruit flies), only that individuals are readily capable of sampling different habitats within their dispersal range. Thus, we suspect it may be more important in study systems when barriers to dispersal are low and in environments

with much temporal and spatial heterogeneity. Because dispersal often has fitness costs, matching habitat choice may only pay off when organisms are subject to sufficiently strong trade-offs in resource use (e.g., when traits and/or resources are quite variable), such that the expected fitness benefits in the new environment are greater than the expected dispersal costs. This requirement may be easiest to fulfill in those organisms with obligatory dispersal or very low dispersal costs. Alternatively, settling individuals may not choose among environments, but simply adapt to wherever they end up by phenotypic plasticity. Perfect plasticity without costs and limits obviously removes any need for matching habitat choice, so matching habitat choice is expected for those species and traits in which plasticity is constrained or too costly (DeWitt et al. 1998).

We suspect that it should be straightforward for an organism to assess the match between its ecological traits and environmental characteristics, via its performance. Most mobile organisms exhibit some sort of habitat selection, because habitat patches within acceptable (e.g., genetically programmed) environments often vary in quality due to abiotic factors or the abundance of resources, competitors, predators, and diseases, etc. The field of behavioral ecology has provided ample evidence that individuals can be exceedingly responsive to such differences, behave adaptively when deciding over their location, and that this is not restricted to species with large cognitive capacities. In fact, it is to be expected that organisms will continuously monitor some aspects of their well-being as part of their daily routines, for example through assessing body temperature, food intake rate, energy stores, and other elements of overall condition (Houston and McNamara 1999). Such commonplace adaptive behavior to deal with normal environmental variation suggests that it should also be affected by variation in individual ecological traits, and that it should potentially be easily generalizable to novel environments without having to evolve *de novo*.

## *Implications of Matching Habitat Choice*

Matching habitat choice can have important effects from the individual level up to the community level, and can play a role on both short and long time scales. Below we outline for a number of prominent topics why the concept of matching habitat choice is potentially important.

### **RATE AND DEGREE OF LOCAL ADAPTATION**

Currently, most biologists view the evolution and degree of local adaptation as an antagonism between local selection for adaptive genotypes, and the entry of novel, potentially maladapted genotypes into the local population through mutation, recombination and migration (Slatkin 1987; Hendry et al. 2001; Lenormand

2002; Kawecki and Ebert 2004). This view is, however, changing (e.g., Räsänen and Hendry 2008). First, immigration can promote local adaptation via the infusion of genetic variation (reviewed in Garant et al. 2007). Second, when there is migration, there can be matching habitat choice. We outline here how in some cases immigration/dispersal combined with matching habitat choice can in fact promote, rather than constrain, local adaptation.

Local adaptation by matching habitat choice occurs when organisms choose among different environments, such that individuals with similar ecological traits cluster together through directed (not random) gene flow. However, exactly in those situations of highly mobile organisms, researchers typically do not consider the possibility of quantitative genetic population structure emerging because of the expected homogenizing effect of gene flow. Sometimes an observed lack of neutral genetic differentiation is even used to argue that populations are genetically identical and thus ecologically undifferentiated. Yet, neutral genetic markers and ecological traits are not necessarily correlated and can structure quite differently (Merilä and Crnokrak 2001; McKay and Latta 2002; Leinonen et al. 2007). In contrast to the common view of fairly slow local adaptation across several generations due to differential reproduction, matching habitat choice can lead to rapid local adaptation (Armsworth and Roughgarden 2005a, Holt and Barfield, in press) and can happen within the time-span of a generation or even “instantaneously” if environments change rapidly but individuals also respond rapidly. For example, as insects disappear at the end of summer, many bird species switch to feed on seeds. If, unlike the insects, these seeds have a patchy distribution (e.g., due to different plant species growing at different ambient conditions), a genetic population structure could emerge over, say, the course of a couple of weeks (the length of time the birds make the transition from insects to seeds). Hence, local adaptation and population differentiation in adaptive genetic traits are occurring on the time scale of most empirical studies, when changes in the genetic composition of study populations are often assumed to remain constant (Slobodkin 1961).

It might be worth pointing out here that we do not define population boundaries by the spatial arena delimited by the mating pool, as many population geneticists might, but by the spatial arena defined by environmental characteristics (including points along an environmental gradient, as done by Kawecki and Ebert 2004). This is because spatially and ecologically distinct clusters of individuals might have increased performance in their habitats at a given time (i.e., function as locally adapted populations), even when fully mixed at other times or when showing random mating. It seems a missed opportunity not to explore the possible evolutionary and ecological consequences of such spatial clustering of phenotypically similar individuals, and to deny the strong parallels with local adaptation as caused by selection within restricted mating pools.

To the extent that individuals have perfect knowledge of the available habitats, and that there are no barriers to choosing and moving to the one habitat that fits their phenotype best (cf. ideal free distribution, Fretwell and Lucas 1970), local adaptation by matching habitat choice may not only be achieved rapidly, but initially also to a higher degree than by differential reproduction alone, as in classical local adaptation. This is because a small decrease in reproductive success of maladapted individuals does not prevent the occurrence of maladaptive offspring in the next generation, whereas in the extreme, facing the same small loss may be enough of an incentive for all maladapted individuals to leave and not reproduce at all locally.

#### PEAK SHIFT AND NICHE WIDTH

Fitness surfaces, composed of peaks of high fitness and valleys of low fitness in relation to phenotypic traits, have proven to be a useful heuristic for understanding adaptive evolution, particularly adaptive radiations (Schluter 2000; Benkman 2003). However, the move by a population from their current adaptive peak to an unoccupied or higher adaptive peak poses a basic problem—namely that selection (by definition) would resist the initial move down the current peak and through the valley before the other peak can be climbed, because this would reduce population fitness. Schluter (2000) reviews two ways adaptive peaks shifts can occur. In the first, adaptive valleys are crossed via selection when, for example, the valley temporarily disappears, or the valley only appears after differentiation has already begun. In the second, from a genotypic perspective (e.g., the adaptive landscape) Wright (1931) formulated a theoretical process whereby populations could move from a low fitness peak in the adaptive landscape across a valley of even lower fitness to a peak of higher fitness: the shifting balance. This process of peak shift involves random genetic drift in small local populations causing them to move down the peak, followed by selection-driven climbing of the new peak, and subsequent dispersal back to the population(s) of the ancestral type, which thereby also moves to the new peak. Its realism has been heavily debated and its occurrence seems restricted to a narrow range of parameter values (Coyne et al. 2000). We suggest that matching habitat choice is an alternative mechanism that can allow populations to ford fitness valleys. Peak shifts via matching habitat choice simply occur when individuals originating from one peak disperse, choose among different environments (i.e., essentially different adaptive peaks), most preferring the old peak but—given a sufficiently large phenotypic variance relative to the distance between alternative peaks—some finding themselves particularly suited to an alternative peak, and settle on it. Here again, rather than viewing dispersers to new environments as a random subset of the population, those individuals moving and settling in the environment representing a new adaptive peak are those that are essentially preadapted, thus obviating the need

for drift or selection to move a population through a fitness valley. In fact, the theoretical problem of crossing adaptive valleys is based on population fitness, whereas in our view of peak shift by matching habitat choice the important element is the fitness of individuals with a particular phenotype as a function of habitat or resource characteristics. To date empirical fitness surfaces (fitness as a function of phenotypic traits) for sympatric populations have been constructed assuming that populations use the resource they are best suited to (with the behavioral mechanism determining use unspecified); that is, they involve several resources simultaneously available to all individuals (Schluter and Grant 1984; Benkman 2003). Now, if not only populations but also individuals are assumed to be able to choose their resource by estimating their own fitness for each resource/habitat and to settle where fitness is higher, then no population as a whole needs to cross an adaptive valley. Rather, the nonrandom subset that does move to a new peak only climbed upwards their own fitness gradient, so never experienced an adaptive valley. Yet the result of our scenario would be the same as those discussed by Schluter (2000): a phenotypically variable species utilizing several peaks in an adaptive landscape. Our suggestion that matching habitat choice can favor adaptive peak shift is supported by the results of Holt and Barfield (in press). Using individual-based simulations of evolution in source-sink landscapes, they found that matching habitat selection can speed up the rate of adaptation to sink environments, and thus facilitate niche evolution.

With adaptive peak shift by matching habitat choice, niche width at the individual level may decrease (individuals become more specialist), but niche width at the species level increases (species as a whole becomes more generalist; see also Bolnick et al. 2007). Matching habitat choice may be perhaps the easiest way by which populations can avoid the problem of having to evolve through a fitness valley if they are to occupy a new adaptive peak (see also Rosenzweig 1978, 1995). Additionally, the outcome of matching habitat choice need not be a variable population utilizing several adaptive peaks. It is possible that the subpopulation with the highest fitness swamps other subpopulations with crowded-out surplus dispersing offspring so that the population as a whole evolves to occupy the peak with the highest fitness, similar to phase three of the peak shift as described by Wright (1931).

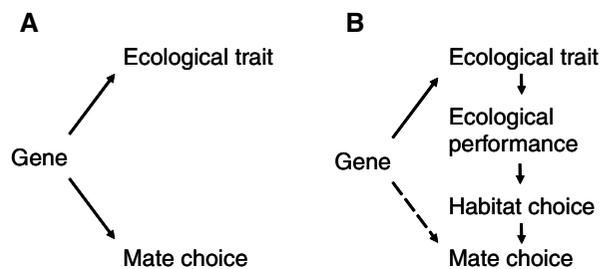
#### LIKELIHOOD OF SPECIATION-WITH-GENE FLOW

Speciation in the presence of gene flow (e.g., sympatric or parapatric speciation, speciation by reinforcement) is a vigorously debated arena of evolutionary biology, because gene flow is expected to cause remixing of any evolving population structure and to cause the formation of intermediate (hybrid) offspring. This is especially destructive if ecological and mate choice traits have a separate genetic basis and recombination destroys any linkage

disequilibrium between these traits, preventing the formation of reproductively isolated species (Felsenstein 1981).

Theoreticians outlined early on that divergence is indeed possible if the divergently selected ecological trait automatically results in assortative mating (Maynard-Smith 1966; Gavrillets 2003). These traits have been termed “no-gene” mating traits (Coyne and Orr 2004) or even “magic traits” (Gavrillets 2003), suggesting such pleiotropic effects are unrealistic. We suggest that the process of matching habitat choice in effect enables ecological traits to act as such magic traits in the following way (see also Maynard-Smith 1966; Garcia-Dorado 1986; Jaenike and Holt 1991; Ravigné et al. 2004).

Consider a population in the process of occupying different adaptive peaks through matching habitat choice; for example, a founder population of birds colonizing an island with a mosaic of discrete resource patches (i.e., plants with small and large seeds). As a first (and not at all unimportant) effect, if population densities are regulated mostly within habitat types (soft selection) then the occupying of different peaks will lead to the preservation of genetic variation, or even polymorphism, in the species. In addition, when mating partners are encountered within the near surroundings of feeding individuals (e.g., same habitat, same social group), then mating will by default be assortative with respect to the ecological trait through indirect pleiotropy (Fig. 2), because despite dispersal at every generation, individuals with similar ecological traits are found in patches of the same habitat. In this simple scenario, there is no need for the theoretically complicated fixation of different alleles for habitat choice, mating signals, and mating preferences. Hence, there is no potential for recombination to break down linkage disequilibrium, because there is no linkage disequilibrium as only ecological traits diverge (initially) between



**Figure 2.** (A) Pleiotropy is direct when a gene influences the expression of several traits, but where its effect on one trait has no effect on its effect on the other trait. (B) Pleiotropy is indirect when a gene influences the expression of several traits because its effect on one trait influences the expression of another trait. For example, a gene that increases bill size of a bird also increases its intake rate on large seeds, which increases its preference to feed in patches with large seeds, which increases its probability to mate with another large-billed individual also feeding in the same habitat.

populations. (We note that unlike some of the other processes we discuss, this process would require a heritable genetic basis of the ecological traits.) This process by itself may cause sympatric speciation, or it could kick-start the process with later support by other mechanisms that can evolve after initial divergence is large enough (Rice and Hostert 1993). As such, this simple model resembles a “theoretician’s nightmare” (Rice and Hostert 1993): it can be deduced from empirical results, it is simple, and it is obvious.

However, testing this simple model is also an empiricist’s challenge. The few experimental studies of sympatric speciation involving habitat choice have focused on divergent selection for genetically determined habitat choice only (Rice and Salt 1990), which suffers from the potential of breakdown of habitat selection and reproductive isolation when experimental selection is lifted because there is no divergence in ecological performance. Hence, the simplest models with the greatest potential for stable sympatric speciation have never been tested experimentally. Current research efforts in the field of speciation-with-gene-flow are largely restricted to development of (increasingly fragmented) theory (Kirkpatrick and Ravigné 2002; Gavrillets 2003) and interpretation of (molecular) patterns in nature. We suggest that some empiricists refocus on experimental testing of the key elements of those early and simple models that suggest that sympatric spe-

ciation is possible, and urge that matching habitat choice is a key element that has been overlooked for decades. Studies that have addressed matching habitat choice (Table 1) could test for a heterozygote deficiency due to assortative mating, but so far, this has hardly been done.

We also expect that habitat shifts and contractions through matching habitat choice increase reproductive isolation in secondary sympatry, and hence act to favor ecological speciation, because individuals potentially capable of producing fertile hybrid offspring would not encounter each other if partner choice or mating occurs in their preferred habitat. It might also promote reinforcement by reducing gene flow among diversified populations for long enough until other reproductive isolating mechanisms have evolved. These effects of matching habitat choice do not seem to have been modeled nor tested (but see Armsworth and Roughgarden 2005b for related matter).

#### INTERPRETATION OF NATURAL SELECTION AND MEASURES OF SELECTION

The comparison of population differentiation in neutral markers ( $F_{ST}$ ) and its equivalent for quantitative traits ( $Q_{ST}$ ) has recently been promoted to measure the force and direction of natural selection ( $Q_{ST}$ -method: Merilä and Crnokrak 2001; McKay and Latta 2002; Leinonen et al. 2007). However, because matching habitat

**Table 1.** Empirical tests for matching habitat choice are more convincing if they are shown to meet a number of criteria. Below we list for a sample of studies chosen to cover a wide taxonomic range of animal groups to what extent each criterion has been met: +, met; –, not met; ?, unclear or not investigated. Numbered criteria in header, (1) individuals differ in ecological traits (ecological traits in parentheses), (2) ecological traits and habitat traits are correlated (habitat or resource variable in parentheses), (3) habitat choice is repeatable and differs between individuals, (4) individuals have a higher expected fitness following habitat choice, (5) differential habitat choice is not (only) caused by genetic polymorphism in habitat choice alleles or imprinting, (6) differential habitat choice is not (only) caused by competitive exclusion by others, (7) differential habitat choice is not (only) caused by selective mortality and reproduction, (8) differential habitat choice is not (only) caused by phenotypic plasticity.

Taxon	1	2	3	4	5	6	7	8	Reference
Land snail	+(banded/unbanded shell)	+(exposure to sunlight)	+	?	?	?	+	+	Jones 1982
Fruit fly ( <i>simulans</i> )	+(eye colour)	+(dim or bright places)	+	–	+	+	+	+	Jones and Probert 1980
Fruit fly ( <i>pseudoobscura</i> )	+(strain/genotype)	+(larval food substrate)	+	+	?	+	+	+	Taylor and Condra 1983
Pumpkinseed sunfish	+(morphology)	+(benthic/limnetic)	?	+	?	?	?	+	Robinson et al. 1996
Lizard ( <i>Anolis sagrei</i> )	+(striped/unstriped)	+(perch width)	?	?	?	?	?	?	Schoener and Schoener 1976
Blood python	+(skin colour, size)	+(habitat/diet)	?	?	?	?	?	?	Shine et al. 1998
Crossbill	+(bill depth)	+(conifer/cone type)	?	?	?	?	?	?	Summers et al. 1996
Great tit	+(body mass)	+(study areas/density)	+	?	+	?	?	+	Garant et al. 2005
Citril finch	+(wing/tarsus length)	+(breeding habitat)	+	?	?	?	?	+	Senar et al. 2005
Finches and sparrows	+(tarsus length)	+(wintering habitat)	?	?	?	?	?	+	Fretwell 1969
Medium ground finch	+(bill size)	+(breeding habitat)	?	+	?	?	?	+	Price 1987
Oystercatcher	+(bill length)	+(prey type/feeding area)	+	+	?	+	+	+	Swennen et al. 1983
Deer mice	+(tail/foot length)	+(degree arboreal feeding)	+	?	?	?	?	?	Smartt and Lemen 1980
Polecat	+(coat colour, size)	+(type of forest)	?	?	?	?	?	+	Lodé 2001

choice leads to directed gene flow and thus to larger  $Q_{ST}$  values of ecological traits, the same pattern of larger quantitative than neutral genetic divergence can be found even when natural selection has not caused any differential survival and reproduction. If environments fluctuate and matching habitat choice is rapid, measures of  $Q_{ST}$  may even vary within a generation in the complete absence of any mortality and reproduction. This does not imply that the  $Q_{ST}$  method is flawed, but we suggest that interpretation for observed patterns must recognize matching habitat choice as an alternative explanation.

Several studies showing pronounced differentiation in adaptive traits in the presence of gene flow have interpreted this as evidence that strong selection against maladapted individuals can overcome the homogenizing effect of gene flow (e.g., Schneider et al. 1999; Storz 2002). We caution that without additional evidence, an alternative or at least additional interpretation of such studies should be that matching habitat choice leading to adaptation by directed gene flow has occurred. Instead of a homogenizing effect of dispersal (gene flow) on population structure in ecological traits, dispersal and habitat choice may create such population structure, with more dispersal during sampling even enabling a better choice and resulting in more structure after settlement. For example, Garant et al. (2005) show that there is spatial variation in selection on Great tit (*Parus major*) nestling body mass, and that nonrandom dispersal (e.g., in effect matching habitat choice) acts to reinforce the pattern of body mass differentiation.

### Testing for Matching Habitat Choice

How does one recognize and show that matching habitat choice occurs in nature? The most convincing tests for matching habitat choice should show the following elements: (1) individuals differ in ecological traits, (2) ecological traits and habitat traits are correlated (phenotype  $\times$  environment covariance), (3) habitat choice is repeatable and related to an individual's ecological trait, (4) individuals have a higher expected fitness following habitat choice, (5) habitat choice is not directly determined by genetic polymorphism in habitat choice alleles nor by imprinting (i.e., there is no "heritability" of habitat choice other than through inherited ecological traits), (6) habitat choice is not (only) caused by direct exclusion by other individuals (of the same or different species), (7) the observed match between phenotypes and environment is not (only) caused by selective mortality and reproduction, (8) the observed match between phenotypes and environment is not (only) caused by phenotypic plasticity.

The central prediction of matching habitat choice is the correlation between phenotype and environment. Unfortunately, this pattern is shared with classical local adaptation and phenotypic plasticity. Hence, the first four criteria act to establish whether

key elements of matching habitat choice are present, whereas the last four act to distinguish matching habitat choice from classical local adaptation and phenotypic plasticity (or to unravel their relative effects if several occur simultaneously). If individuals differ in ecological traits due only to nongenetic reasons (maternal effects, growth conditions, etc.), matching habitat choice can still occur, so we have not included heritability of ecological traits as a criterion. In fact, change of preferred habitat after phenotypic manipulation of these traits would provide a strong test of the process. We note that if the relevant variation in ecological traits has no genetic basis then the implications of matching habitat choice will be mainly restricted to ecological effects (see Discussion).

The relevant data to address these criteria could be collected in a number of ways; some providing stronger tests than others could. By following individuals whose ecologically important traits have been measured, we could test if departure and settlement decisions of individuals evaluating the same set of environments are correlated with their phenotype (cf. Stamps 2001; Garant et al. 2005). More convincing, experimental studies could manipulate environments to see how this affects the decision of phenotypically different individuals to leave or settle in each of the different offered environments (cf. Jones and Probert 1980). Although less easy to perform, phenotypic manipulation of the hypothesized relevant ecological trait is a very powerful way to uncouple any direct genetic determination of habitat choice from performance-determined habitat choice; however, there seem to be no published studies that have attempted this. Because size is often the main axis of variation in functional traits within (and between) populations, manipulation of growth conditions (food, hormones) comes to mind as a way to test how the preference for certain habitats or resources depends on the functional traits of adults with the same genetic background. Such a manipulative test of course assumes that any other traits that could be affected by the manipulation are unimportant enough as not to erase the signature of matching habitat choice based on size. One would also want to equalize as much as possible condition or any other potentially confounding effects after the growth manipulation and prior to the test of habitat choice.

Natural experiments could also provide support. For example, when populations encounter new niches or competitors, or as existing environments change or new ones are created (naturally or anthropogenically), or as competing species enter or leave the community (extinctions, introductions) we could determine if the individuals that leave or settle in the focal environment are a nonrandom subset of the population with respect to their ecological traits. In these situations in which we can compare patterns in time or space in a historical context, matching habitat choice may be more readily detectable.

For all of these descriptive and experimental studies, it is crucial that we can exclude phenotypic plasticity and differential

survival and reproduction as the principal explanations for observed matches between phenotypes and environments, for example, when plasticity and differential survival and reproduction are random or insufficiently strong with respect to the traits of interest. This is, of course, no easy task. In addition, interpretation is strengthened if we understand why certain phenotypes function best under certain environmental characteristics, i.e. if we have a functional understanding of how the ecological traits better enable their bearer to use particular habitats and resources.

In Table 1, we list a (not exhaustive) number of studies in which matching habitat choice might have occurred. All listed studies demonstrated a correlation between ecological traits and habitat use—the basic outcome of matching habitat choice. Several studies noted that the correlation between ecological traits and habitat use observed within species mimicked the pattern across species, which provides comparative support that this correlation has some adaptive explanation. This latter pattern also hints at the possibility that it may promote assortative mating and speciation. However, none of these examples has provided positive support for all of the criteria listed above, so future studies should focus on doing so. Some earlier putative cases of matching habitat choice are not included in Table 1 because differential mortality was ultimately implicated as the cause for the observed correlations between phenotypes and environments. For example, wild-caught dark butterflies preferred to settle on dark surfaces for increased crypsis, but their captive offspring showed no preference, suggesting that visual predators had eaten dark individuals preferring pale surfaces prior to capture and testing (Jaenike and Holt 1991).

## Discussion

We have distinguished three main ways whereby individual responses to environmental heterogeneity affect local adaptation in the broad sense (Fig. 1). We did not discuss an individual's response to actively change the characteristics of their environment through niche construction, even though Laland and Sterelny (2006) essentially view matching habitat choice as a form of niche construction. Of these three ways, matching habitat choice has received the least attention by far, even though it may be common. Habitat selection is common, and has a profound influence on key phenomena such as population regulation, species interactions, the assembly of ecological communities, and the origin and maintenance of biodiversity (Morris 2003). Determining the presence, magnitude, and impact of phenotype-dependency of habitat selection should thus be highly relevant. Although there is an increased interest to study dispersal syndromes (dispersing individuals are characterized by a suite of particular life-history traits, e.g., Dingemanse et al. 2003; Ronce and Olivieri 2004; Cote and Clobert 2007), there seems to be a relative scarcity of theoretical studies of population- and community-dynamics that

consider phenotypic effects on habitat selection (Armsworth and Roughgarden 2005a). Studies on the effects of habitat selection of interacting species on population dynamics and species coexistence may provide a good basis to construct similar models incorporating intraspecific matching habitat choice. Likewise, theory and application of population- and quantitative genetics depend heavily on the assumption that dispersers are random members of the population. There seems to be ample opportunity for conceptual improvement here.

Besides the above treated evolutionary effects of matching habitat choice, there are also a number of potentially major ecological effects that may occur. A higher degree of local adaptation caused by matching habitat choice often implies that populations can reach higher densities (e.g., Siepielski and Benkman 2005; but see Holt 1985), and consume more resources. These indirect effects may not be trivial, because densities of conspecifics, prey and predators are often important determinants of the structure and dynamics of populations and communities (Tilman 1982; Begon et al. 1996; Turchin 2003; Morris 2003). Even when knowledge of the available habitat is imperfect (which it almost certainly is), and individuals only compare local expected fitness to some threshold value when deciding to disperse or settle, population dynamics may be drastically simplified and stabilized (cf. Ruxton and Rohani 1999). This would occur because some individuals would climb the spatial fitness gradient and level out population dynamical extremes, including local extinctions in meta-populations.

The direct adaptive effects of matching habitat choice can also influence population dynamics and community structure. For example, *Daphnia* run the risk of being eaten by visually hunting fish, so larger, more conspicuous individuals often reside at a greater, darker water depth. Thus, as an individual grows its optimal habitat changes. DeMeester et al. (1995) observed that an unusual *Daphnia* strain that did not adjust its habitat choice depending on individual size went extinct after predatory fish were introduced, whereas two other co-occurring strains that did show a match between size and habitat survived. Besides showing the strong effect of habitat choice on population/community dynamics, this example also suggests that matching habitat choice itself can be favored by natural selection. In another example, Jones and Probert (1980) observed that in exclusively light or dark conditions a mutant white-eyed fruit fly was out-competed by the wild-type. However, because the white-eyed fly preferred dark conditions whereas the wild-type preferred normal, light conditions, and population densities were mostly regulated within each habitat (soft selection), the white-eyed fly did persist when both habitats were available and flies could choose between habitats. Hence this experiment showed that phenotype-dependent habitat choice can maintain genetic/community diversity.

The long-term evolutionary effects of matching habitat choice are also of potential importance. We already suggested

that matching habitat choice might increase the level of local adaptation, might stabilize population dynamics, might conserve genetic variation, or even produce a genetically variable species utilizing several resources—all effects that should enhance the survival of local populations. As such, matching habitat choice is not only of value to the individual, but also to those taxa that have evolved it, because matching habitat choice promotes their long-term existence. Thus, matching habitat choice could influence macro-evolutionary patterns. We even suggested that matching habitat choice could lead to speciation, leaving additional marks on long-term evolution. In this context, it is also of interest to address a more speculative way matching habitat choice might play a role at the species/macroevolutionary level. If a species is subjected to a change in the environment, classical evolutionary theory would suggest that natural selection would favor those individuals that are best adapted and that, given heritable variation in traits, genetic change in the population would promote its long-term existence: the species adapts by genetically changing its traits (i.e., by evolving). However, it has also been suggested (e.g., Holt 1990; Björklund and Merilä 1993) that another solution to environmental change would be to look for environments that are more suitable given the traits of the species as they are: the species adapts by changing to another environment, not by changing its traits. The outcome of the latter process would be more long-term stasis in species traits, but more variable habitat use. There is some evidence in line with this hypothesis (Huntley et al. 1989; Björklund and Merilä 1993; Peterson et al. 1999), and further tests using the fossil record of traits of both species and environments might be possible. A somewhat relevant contemporary event is that global climate change seems to have a larger impact on global distributions (e.g., species expanding to poleward habitats) than on locally evolving traits, something that is mirrored in patterns from recent glaciations (Parmesan 2006). However, it remains to be tested to what extent such distributional change is due to mobile individuals testing environments prior to settling, that is, matching habitat choice (C. Both, pers. comm.) or whether this is solely driven by local extinctions away from the poles and local establishment toward the poles (i.e., differential reproduction of random dispersers).

Because matching habitat choice can introduce adaptive genotypes through directed gene flow into local populations and increases the rate and perhaps the degree at which populations reach their adaptive peak, as well as maximum population density, taking matching habitat choice into account could yield altered conclusions and predictions for any model that includes effects of population dynamics (density and frequency of genotypes) (see Bolnick et al. 2003 for discussion of related topics). In fact, the evolution of dispersal itself is probably strongly affected by matching habitat choice (Armsworth and Roughgarden 2005b). Despite the fact that we know of only a few theoretical papers that

are relevant to the process of matching habitat choice (see citations above), in this article we have only outlined verbally what several of its theoretical implications might be. Although these may make sense to most people and may even be convincing to some of them, we hope that our suggestions stimulate more thorough theoretical studies into the various assumptions and predictions of the process. One might even want to go as far as to study the dynamics and evolution of matching habitat choice when phenotypic plasticity and classical local adaptation are co-occurring or are allowed to evolve, because it is not clear how each performs relative to the others under particular circumstances, and whether any important interactive effects may occur.

Empiricists have always appreciated that dispersal among populations occurs, but mostly viewed dispersers as randomly chosen individuals or as low-quality individuals forced out of populations by competition/dominance. There is now ample evidence that dispersers are not a random subset of the individuals within a population with respect to morphology, physiology, or behavior (Clobert et al. 2004). However, the extent to which dispersal represents individual decisions as to direction and location of final settlement depending on each individual's ecological performance across the habitats available and visited remains to be more thoroughly investigated; the same is true for the consequences of the process of matching habitat choice. With accumulating evidence, we will gain better insight into the relative occurrence of matching habitat choice, its necessary conditions, and its impacts on evolutionary and ecological processes. For both classical local adaptation and phenotypic plasticity, the costs and limits at the individual and population level are increasingly well understood. It is time that these are also identified for matching habitat choice, to obtain a more complete understanding of the mechanisms creating and maintaining biological diversity.

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