ADAPTATION TO MARGINAL HABITATS

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■ **Abstract** The ability to adapt to marginal habitats, in which survival and reproduction are initially poor,
plays a crucial role in the evolution of ecological niches and species ranges. Adaptation to marginal
habitats may be limited by genetic, developmental, and functional constraints, but also by consequences of
demographic characteristics of marginal populations. Marginal populations are often sparse, fragmented,
prone to local extinctions, or are demographic sinks subject to high immigration from high quality core
habitats. This makes them demographically and genetically dependent on core habitats and prone to gene
flow counteracting local selection. Theoretical and empirical research in the past decade has advanced our
understanding of conditions that favor adaptation to marginal habitats despite those limitations. This
review is an attempt at synthesis of those developments and of the emerging conceptual framework.

INTRODUCTION

Virtually all species are confronted with variation in habitat quality, where the
habitat is defined as a particular set of resources and conditions (abiotic and biotic)
relevant from the viewpoint of survival and reproduction of individuals.
Hutchinson's concept of ecological niche (Hutchinson 1961, Pulliam 2000) divides
the multidimensional parameter space of habitat variation in two regions. The
habitats where the intrinsic rate of population growth is positive, thus in principle
permitting a population to persist without immigration, by definition fall within the
ecological niche of the species. Those where the intrinsic rate of increase is negative
are outside the niche.

A simplistic prediction would be that populations should thrive in habitats that
belong to the ecological niche of the species and be absent from those that do not,
but the species distributions often do not conform to this prediction (Pulliam 2000).
In particular, a stable population may be maintained by immigration in habitats
outside the niche, where births can never compensate for deaths. Other habitats may
satisfy the niche requirements most of the time, but with little "safety margin," so
that the local populations are vulnerable to extinction owing to temporal variation,
demographic stochasticity, or edge effects. Some low-quality habitats may be able to
sustain a sparse population but be subject to high immigration. Finally, a local
population may be sufficiently locally adapted to a particular low-quality habitat to

persist, but other populations, living in good (core) habitats, would lack this adaptation and would not be able to survive if transplanted into the poor habitat. Rather than a sharp line, it is thus more realistic to regard the boundary of the ecological niche as a fuzzy transition zone between suitable core habitats, where the species can thrive, and completely unsuitable habitats. Habitats in this transition zone are occupied at least part of the time and some reproduction occurs in them, but their importance from the viewpoint of the demography of the entire species is marginal. Adaptation to such marginal habitats is the focus of this paper.

Even though marginal habitats may be of little ecological importance, they are important from the evolutionary perspective. The ecological niche of a species reflects traits of the individuals, and so the niche can evolve. As a result of an evolutionary change, the survival and reproduction in an initially marginal habitat may become high enough for the habitat not to be considered marginal any more. Conversely, evolution of habitat specialization implies loss of adaptation to some habitats---habitats that were previously suitable become marginal and eventually unsuitable. Thus, adaptive evolution in marginal habitats drives the evolutionary dynamics of ecological niches.

The ability of a species to adapt to marginal habitats also plays a major role in the evolution of species ranges. Although some limits to species ranges are imposed by barriers to dispersal or sharp environmental transitions, others occur on ecological gradients. As the habitats along the gradient become increasingly less suitable (i.e., increasingly marginal), survival and reproduction decline, and so do the population density and habitat occupancy. The species range tapers off, often with no clear border. Thus, habitats marginal from the perspective of the ecological niche will also often be marginal (peripheral) from the spatial perspective of the species' range. Range expansion over evolutionary time requires that the peripheral populations become better adapted to their habitats, so that their abundance and persistence increase, population fragmentation is reduced, and enough offspring are produced for those previously marginal habitats to become the source of individuals colonizing farther outlying areas along the gradient.

If natural selection had been all-powerful, the marginal habitats would have been a transient phenomenon---with time, species would have well adapted to all encountered habitats. This seems not the case; few species distributions are limited solely by barriers to dispersal, and many species are narrow habitat specialists. The width of the ecological niche and the size of the geographic range sometimes differ dramatically between closely related species. Spectacular cases of adaptive radiations such as that of Hawaiian honeycreepers or cichlids in the African great lakes certify to a great potential for ecological niches to evolve given the right circumstances. Yet, some other taxa, e.g., thrushes in Hawaii (Freed et al. 1987), or squeaker catfishes in African great lakes (Koblmuller et al. 2006), conserved their ecological niche in the very same environments and did not radiate. The degree to which ecological niches are evolutionarily conserved versus malleable has important consequences for a number of ecological and evolutionary phenomena, including speciation, community structure, patterns of species richness, invasiveness of

introduced species, responses to human-induced environmental changes, and species conservation (Wiens & Graham 2005).

Understanding adaptation to marginal habitats has direct consequences for human welfare: pesticide-treated crops or drug-treated patients are initially marginal habitats for pests and pathogens as they evolve resistance. It is also relevant for the evolution of pathogen virulence, either because humans are a marginal host for the pathogen, or because virulence results from invasion of, and adaptation to, particular "habitats" in the host body that, from the viewpoint of the pathogen transmission, may be marginal (Sokurenko et al. 2006).

Rather than on the consequences, this review focuses on the processes and factors involved in evolutionary adaptation to marginal habitats. I begin by arguing that, because of several demographic features, adaptation to marginal habitats requires its own conceptual framework rather than being just another case of adaptation in general. Subsequently, I summarize evidence for the processes thought to limit adaptation to marginal habitats: genetic, developmental, and functional constraints; genetic make-up of marginal populations; and asymmetric gene flow. A major section reviews the insights from mathematical models and the factors predicted to facilitate or hinder adaptation to marginal habitats, followed by a summary of the few experimental tests of those predictions. The final section discusses the explanations for the often observed prevalence of parthenogenesis and hybridization in marginal habitats and their potential role in adaptation.

DEMOGRAPHY OF MARGINAL POPULATIONS

Populations in marginal habitats tend to differ systematically from those in core habitats in several demographic characteristics. First, populations in marginal habitats will usually have low density relative to core habitats. A simplistic version of this prediction---that species abundance should decline monotonically from the center of distribution to the edges---is not generally supported (Sagarin et al. 2006). This is not surprising, given that the there is no reason for habitat quality to be highest at the geometric center of species range. However, where marginal habitats were identified based on their quality, they were usually found to harbor less dense populations (reviewed in Sagarin et al. 2006, Vucetich & Waite 2003).

Second, populations in high-quality (core) habitats usually produce more offspring (i.e., more potential dispersers) per unit area than those in marginal habitats. Thus, as long as the propensity to disperse is similar for offspring born in each habitat, dispersal will be asymmetric in absolute terms: more individuals will disperse from the core to marginal habitats than the other way round. In other words, marginal populations are often **demographic sink**s (**Figure 1**): They receive an excess of immigrants (Dias 1996, Kawecki 2004, Pulliam 1988). In particular, net immigration from core habitats can maintain permanent populations in habitats where the intrinsic population growth rate is negative and so births can never compensate for deaths (**Figure 1c**); such habitats are referred to as absolute sinks (Kawecki 2004). But even if a marginal habitat is able to sustain a population without immigration, it may still be a (relative) sink: The net immigration will keep

the local population above the local carrying capacity so the local death rate will in the long run be greater than the local birth rate (**Figure 1b**). The excess of immigrants will come from source populations in core habitats; these populations will show an excess of births over deaths. Individuals in a sink habitat have on average lower reproductive value: their expected contribution to the future gene pool is smaller than that in a source, which renders natural selection in the sink less effective (Kawecki 2004). The sink nature of marginal habitats has been directly demonstrated in a number of species, at various spatial scales (e.g., Blondel et al. 2006, Boughton 1999, Breininger & Carter 2003, Manier & Arnold 2005, Stanton & Galen 1997, Sulkava et al. 2007, Thingstad et al. 2006).
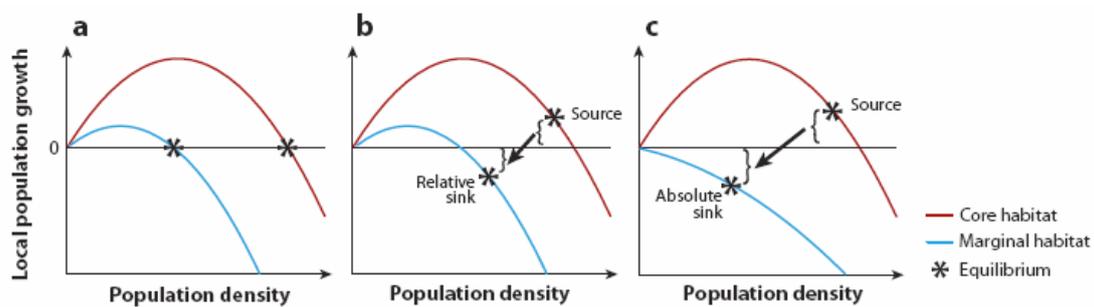
Figure 1. Dispersal between habitats of different quality creates source-sink population structure. The lines show the local population growth (births minus deaths) as a function of local density for a high-quality core habitat (*red*) and a marginal habitat (*blue*); the asterisks indicate equilibria. (*a*) In the absence of dispersal, each local population equilibrates around density at which the local population growth is zero. (*b*) With random dispersal the difference in density is reduced; at the equilibrium the core habitat is a source with a surplus of births over deaths (*brace*) compensated by a net emigration to the marginal habitat (*arrow*); the marginal habitat is a (relative) sink with net immigration (*brace*) and a negative local growth. (*c*) Immigration can maintain a stable population in a marginal habitat in which local growth is negative at any density (absolute sink).

Third, in marginal habitats even small changes in conditions in space and time may have a large impact on the persistence of local populations, especially if dispersal is too low to sustain them demographically. As a consequence marginal populations are often more fragmented and more prone to local extinctions owing to environmental fluctuations, demographic stochasticity and edge effects (e.g., Gonzalez-Megias et al. 2005, Manier & Arnold 2005, Tossas & Thomlinson 2007). If those extinctions are uncorrelated across patches of the marginal habitat, the vacated patches may be recolonized by dispersers from other marginal patches. However, if the extinctions are due to an environmental event that affects the entire region, all marginal populations go extinct simultaneously. The marginal habitat can then only be recolonized by dispersers from core habitats. This is metapopulation-level source-sink dynamics: even though in a short term marginal habitats may be demographically independent, they would be recurrently seeded by core populations and would not persist long enough to adapt.

To summarize, populations in marginal habitats are demographically and genetically linked with those in core habitats, and these links are typically highly asymmetric: The core populations have a much greater impact on the demography and gene pool of marginal populations than vice versa. Theoretical and empirical research discussed in this review shows that taking these links and asymmetries into account is essential for understanding of evolution in marginal habitats.

GENETIC, FUNCTIONAL, AND DEVELOPMENTAL CONSTRAINTS

Most species harbor large amounts of genetic variation detectable at both molecular and phenotypic levels. Furthermore, countless experiments demonstrated that almost all quantitative traits readily respond to artificial selection (Brakefield 2003, Partridge & Barton 2000). Thus, though available genetic variation has been recognized as a limiting factor for evolution of novel traits, the prevailing view has been that evolutionary changes in existing quantitative traits are not limited by the lack of **additive genetic variation**. However, this view has been challenged; a recent review (Blows & Hoffmann 2005) reports numerous cases where an ecologically relevant trait has failed to respond to strong experimental selection even though the population showed heritable variation for other traits. Some of those examples are relevant for adaptation to marginal habitats, e.g., neither marginal nor core populations of *Drosophila birchii* seem to have the genetic potential to evolve greater desiccation (dehydration) resistance, even though desiccation resistance in this species is considerably lower than in sympatric congeners. This may explain why the species remains restricted to rainforests (Hoffmann et al. 2003, Kellermann et al. 2006).

One reason for the apparent lack of additive genetic variation for traits adaptive in marginal habitats could be that the right mutations have not (yet) happened, so alleles that would convey the adaptation are absent from the gene pool. Selection would also be ineffective if the alleles were present, but were rare and recessive and/or interacted epistatically, so that the combination of alleles needed to produce the favored phenotype occurred only extremely rarely. In such cases, the adaptation would in principle be a question of time until the mutations occur and the alleles drift to high enough frequencies, although in reality the time needed might exceed the lifetime of the species. For example, in spite of widespread application of organophosphate insecticides to control mosquitoes, resistant mutants arose in few populations; the other populations only evolved resistance when the resistant alleles were brought in by gene flow (Raymond et al. 2001). In a similar vein, several cases of niche expansion were apparently mediated by **introgression** from another species, the focal species apparently lacking the relevant alleles in its own gene pool (see section on Asexuality and Hybridization).

Alternatively, absence of genetic variation for particular phenotypes may reflect developmental or functional constraints that make these phenotypes either difficult to express or too costly. It has been postulated that over evolutionary history many organisms become increasingly phenotypically integrated---their traits become molecularly, physiologically, developmentally, and functionally increasingly

interdependent. Complex patterns of **pleiotropy** and **epistasis** evolve, making it impossible to change one trait without changing many others, and thus leaving evolution fewer degrees of freedom (Brakefield 2006, Pigliucci 2003, Stearns 1994). Such patterns of pleiotropy could lead to trade-offs that would prevent adaptation to a marginal habitat even if all relevant traits were genetically variable. This constraint on the response to simultaneous selection on multiple traits can be quantified by comparing the orientation of the main axes of variation of the genetic variance-covariance matrix with the vector of multivariate selection (Blows et al. 2004, Blows & Hoffmann 2005). Such a constraint has been invoked in climatic adaptation of a prairie legume plant (Etterson & Shaw 2001). However, in several experiments in the butterfly *Bicyclus anynana*, bivariate selection succeeded in producing evolutionary changes in wing pattern traits in directions which, based on the genetic correlations in the base population, should have been strongly constrained (Brakefield 2006). This would suggest that such constraints can be overcome, but it is difficult to generalize these results to other types of traits. Furthermore, the constraints are predicted to become stronger as the number of traits increases (Blows & Hoffmann 2005, Pease & Bull 1988). Thus, though many species undoubtedly do have the genetic potential to adapt to marginal habitats, a few (like *Drosophila birchii*) apparently do not.

POPULATION GENETICS OF MARGINAL POPULATIONS

Origin of Adaptive Alleles

For adaptation to a marginal habitat it does not suffice that the gene pool of the species harbors genetic variation for relevant traits---this variation must be present in the marginal habitats, where the relevant natural selection acts. Yet, most new mutations will occur in core habitats, simply because more offspring are produced there. Thus, most new alleles conveying adaptation to marginal habitats will have been brought there by gene flow. Consistent with this prediction, local populations of the grass *Agrostis capillaris* only evolved local adaptation to small patches of zinc-contaminated habitat where the large population in uncontaminated habitat already contained alleles for zinc tolerance (Al-Hiyaly et al. 1993). The genetic potential to adapt may be particularly dependent on gene flow where the adaptation requires changes in specific single genes.

Are Marginal Populations Genetically Depauperate?

Even if gene flow imports new alleles, genetic variation in a marginal population could be lost to genetic drift. Demographic characteristics of many marginal populations---low and fluctuating size, greater fragmentation, extinction-colonization dynamics---reduce the effective population size and so should make them more prone to loss of allelic diversity (Glemin et al. 2003, Whitlock 2004). In agreement with this prediction, marginal populations of many plant and animal species show lower genetic diversity of molecular markers than conspecific core populations (e.g., Hoffman & Blouin 2004, Holtken et al. 2003, Michalski & Durka

2007, Tsumura et al. 2007, Van Rossum et al. 2004), although this is not a universal pattern (e.g., Garner et al. 2004, Jacquemyn et al. 2007).

However, the relationship between marker diversity and heritable variation for quantitative traits is in general not very robust (Reed & Frankham 2001), so the low marker diversity of marginal populations does not imply a low potential to respond to selection on quantitative traits. Studies comparing genetic variation for quantitative traits between core and marginal populations are scarce, e.g., marginal populations of *Drosophila robusta* showed a slower response to selection on locomotor activity than core populations (Carson 1959); similarly, marginal populations of *Drosophila serrata* had a lower **heritability** of desiccation resistance (Blows & Hoffmann 1993). Nonetheless, in both cases the marginal populations did respond to artificial selection. Furthermore, the same marginal populations of *D. serrata* did not differ with respect to genetic variation for cold resistance and morphological traits (Jenkins & Hoffmann 1999 2000). Similarly, a recent review found no consistent relationship between quantitative genetic variation and local population size (Willi et al. 2006). One reason might be that drift may lead to an increase in additive genetic variance for quantitative traits, especially if the underlying loci interact epistatically (Whitlock et al. 1993). Thus, though a general conclusion would be premature, it seems that many marginal populations are not genetically depauperate for variation in ecologically relevant traits.

Inbreeding Load

Finally, even if marginal populations harbor enough genetic variation for the traits relevant for adaptation, they may suffer from **inbreeding load**. In accordance with this prediction, a meta-analysis suggested that among conspecific plant populations fitness is positively correlated with population size (Leimu et al. 2006). However, to show that fitness differences are due to inbreeding rather than other reasons requires comparing the fitness of within- and between-population crosses. One study using this approach demonstrated a negative correlation between inbreeding load and local population size of an alpine gentian; in particular populations smaller than about 200 individuals suffered owing to fixation of mildly deleterious mutations (Paland & Schmid 2003). The relationship between habitat quality and inbreeding load was not directly tested in these studies, but their conclusions can presumably be extrapolated to marginal populations of similar or smaller size. Inbreeding would make marginal populations demographically weaker, so they would become more prone to extinction (Nieminen et al. 2001) or more dependent on immigration. Association with deleterious mutations could also nullify the fitness advantage of locally adapted genotypes over immigrant ones (Ebert et al. 2002). Thus, even if there is enough genetic variation for the focal traits, adaptation to marginal habitats would be facilitated by a large local effective population size.

GENE FLOW VERSUS LOCAL ADAPTATION

As argued above, populations in marginal habitats will often be subject to high immigration from core habitats. The immigrants will bring with them alleles representative of the core populations, which will tend to counteract the effect of

natural selection on the local gene pool. This also applies to migrants from marginal to core habitats, but because core populations are usually much larger, the impact of gene flow from marginal habitats on their gene pool will often be negligible. For this reason, gene flow from core habitats has long been recognized as a major, if not the main, factor limiting adaptation to marginal habitats. Nonetheless, although asymmetric gene flow can be relatively easily documented through the analysis of genetic markers (e.g., Manier & Arnold 2005), its impact on adaptation to marginal habitats has only rarely investigated in detail.

One of the best examples comes from a long-term study of blue tit populations inhabiting a mosaic of deciduous and evergreen habitat patches in southern France (Blondel et al. 2006). These two habitats differ crucially in the phenology of the food supply for the birds: The peak of caterpillar abundance occurs in the deciduous habitat one month earlier than in the evergreen habitat. Synchronization of breeding with food supply is important for the breeding success, and the tits in the deciduous habitat indeed lay their eggs right in time to match the maximum demand for food for the young with the peak caterpillar abundance. However, birds in the evergreen habitat in the same region do not breed one month later to match their habitat's phenology. Instead, they lay their eggs only a few days after the birds in the deciduous habitat, and so miss the peak of food supply by more than three weeks. As a result, they have low breeding success despite working twice as hard to feed the young as the birds in the deciduous habitat. An analysis of genetic markers and demographic patterns shows that the evergreen habitat is a sink, with net immigration from the deciduous source habitat. The breeding date is, to a large degree, genetically determined and has the potential to evolve to match the phenology of the evergreen habitat, as demonstrated by a well-adapted population of the same species in Corsica. Thus, one can argue convincingly that adaptation to the evergreen habitat, which has all the hallmarks of being marginal for blue tits in southern France, is hampered by asymmetric gene flow from the deciduous source habitat (Blondel et al. 2006).

Asymmetric gene flow has been invoked to explain maladaptive traits of marginal populations in a number of other cases (reviewed in Bridle & Vines 2007, Kawecki 2004). Yet, some marginal populations become locally adapted despite gene flow. A spectacular example is the repeated evolution of heavy metal tolerance by numerous plant species that colonized abandoned heavy metal mining sites and zinc-polluted areas around electricity pylons (Al-Hiyaly et al. 1993, Macnair 1993). Initially, these sites must have formed small pockets of a marginal habitat surrounded by large patches of core habitat. Yet, the local populations were able to adapt rapidly to the toxic habitat despite continuous gene flow. The following section reviews theoretical developments that address the conditions that facilitate adaptation to marginal habitats. Because of the demographic asymmetries between core and marginal habitats, I concentrate on models that account for both genetic and demographic aspects of dispersal.

THEORY OF ADAPTATION TO MARGINAL HABITAT

Niche Conservatism and Alternative Equilibria

Evolutionary models that incorporate the demographic effects of dispersal confirm that under a broad range of conditions evolution tends to maintain or improve adaptation in core (source) habitats, where the population is already well adapted, and be ineffective in improving adaptation to marginal (sink) habitats (reviewed in Kawecki 2004, Lenormand 2002). This may occur even if all the habitat-specific parameters are symmetric, i.e., all habitats have the same productivity and patch size, equal genetic potential to adapt is assumed, and per capita dispersal rates are symmetric. In such a case the marginal status of a habitat is entirely the result of the genetic composition of the species, with no inherent differences in habitat quality. Such a situation implies alternative equilibria/**attractor**s: Depending on the initial conditions, the system may evolve to a state where habitat A becomes a source, with a well-adapted local population and habitat B becomes a sink, or vice versa (Kirkpatrick & Barton 1997, Ronce & Kirkpatrick 2001). In addition to those "specialist" outcomes, a "generalist" attractor, with local populations equally adapted to each habitat, often exists for the same set of parameters. Alternative "specialist" and "generalist" attractors also often exist when the habitats do differ in quality, size, or dispersal rate, although the "generalist" attractor will then be somewhat biased toward better adaptation to one habitat (Holt et al. 2003, Kimbrell & Holt 2007). A species may even remain "trapped" at a "specialist" attractor centered on a relatively low-productivity habitat and be unable to adapt to a high-quality habitat in which, if well-adapted, it could eventually perform much better (Ronce & Kirkpatrick 2001). By studying those attractors, and in particular the conditions under which a generalist attractor is reached even if the species is initially a habitat specialist, one can use the models to predict which factors should facilitate adaptation to marginal habitats. Such predictions are discussed in the rest of this section.

Manifold Consequences of Dispersal

As discussed above, dispersal can affect adaptation to marginal habitats in multiple ways. It results in asymmetric gene flow, pushing allele frequencies in marginal habitats toward those typical for core habitats, and so "swamping" the effects of local selection. It brings in new alleles that originated in the core habitat and replenishes local genetic variation. It may also carry alleles selected in the marginal habitat back to the core habitat, which may be important for their fate (see below). It sustains marginal populations demographically, increasing the number of individuals exposed to selection in marginal habitats and maintaining populations in habitats where the intrinsic population growth is negative ("absolute sinks"). Conversely, dispersal from marginal to totally unsuitable habitats imposes a drain that the marginal populations may be unable to sustain. Finally, immigrants may compete with the locals for resources and mates. No single mathematical model has taken into account all those consequences of dispersal, but even accounting for some of them reveals that adaptation to marginal habitats depends on complex interactions

between dispersal, habitat quality, form and strength of selection, and genetic architecture of underlying traits.

This complexity already becomes apparent in the simple model of a "black hole sink": a marginal habitat that receives a constant number of immigrants I from a core habitat, with no dispersal back to the core habitat. A simple mainland-island population genetic model predicts that a rare allele that improves fitness in the marginal habitat and is absent from the core habitat will increase in frequency if

$$W_1 / W_0 > 1/(1-m) \,, \qquad 1$$

where W_0 and W_1 stand for the absolute fitness (**lifetime reproductive success**) of the homozygotes for the common allele and heterozygous carriers of the rare allele, respectively, and m is the relative immigration rate (Holt & Gomulkiewicz 1997). The immigration rate $m = I/N$, i.e., the proportion of fresh immigrants in the local population, so it would seem that a greater number of immigrants makes the conditions for the spread of the rare alleles more stringent. But this reasoning neglects the effect of immigration on the local population size. The change in the local population size from one generation to the next can be described as $N(t + 1) = N(t)W_0 + I$ (because the carriers of the rare allele are rare, their impact on population growth can be neglected). At a demographic equilibrium $N(t + 1) = N(t)$, so the equilibrium population size equals $N = I/(1 - W_0)$. Note that this equilibrium will only exist if $W_0 < 1$, either owing to intrinsic maladaptation of the common genotype, or owing to density-dependence. Thus, at the demographic equilibrium,

$$m = \frac{I}{I/(1-W_0)} = 1 - W_0, \quad 2$$

i.e., the immigration rate is independent of the number of immigrants and instead depends on the absolute fitness of the common genotype. This counterintuitive conclusion is a consequence of the demographic effect of immigration on local population size. With this taken into account by substituting **Equation 2** into the inequality **1**, the condition for the rare allele to increase becomes simply $W_1 > 1$ (Holt & Gomulkiewicz 1997).In other words, irrespective of the number of immigrants and the fitness of the common allele, the rare allele will only increase in frequency if the average lifetime reproductive success of its carriers is greater than one. Note, however, that more immigrants mean higher equilibrium population density, so the number of immigrants will still indirectly affect the fate of the rare allele if W_1 is density-dependent (Gomulkiewicz et al. 1999). Thus, accounting for the demographic effects of dispersal into a black hole sink habitat qualitatively changes the conclusions about the conditions that permit a rare allele to increase in frequency.

Considering adaptation based on polygenic traits and allowing for stochastic effects changes the outcome: individual-based models predict that adaptation to a "black hole" sink is more likely with a greater number of immigrants (Holt et al. 2003, Kimbrell & Holt 2007). This leads to a paradoxical conclusion that, even though gene flow "swamps" local adaptation and immigrants compete with the

locals, the positive effects of dispersal may often be more important in promoting adaptation to marginal habitats.
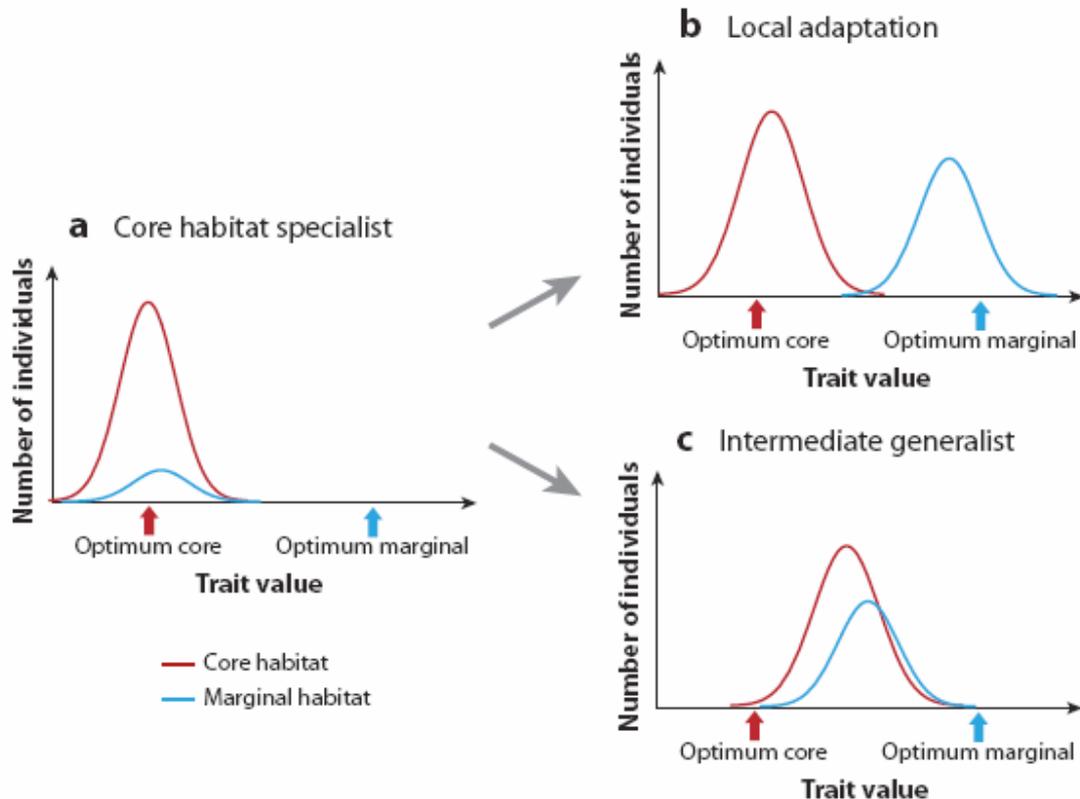
Figure 2 Two ways of adapting to a marginal habitat. Fitness is assumed to depend on a quantitative trait with different optima in the two habitats (*arrows*); lines show the distribution of trait values in the core (*red*) and marginal (*blue*) habitat, scaled in absolute numbers of individuals. (*a*) Initially the population is well adapted to the core; a small maladapted population is maintained in the marginal habitat by immigration from the core. (*b*) If the trait is affected by loci with large effects and dispersal is low, the marginal population can differentiate in allele frequencies from the core population, adapt locally and become independent of immigration. (*c*) If the trait is affected by many loci with small effects and dispersal rate is high, gene flow prevents substantial differentiation between the populations. Adaptation to the marginal habitat can only occur by both marginal and core population evolving intermediate mean trait value, which may be associated with substantial fitness cost in the core habitat.

If, as is more realistic, some dispersal back from the marginal to the core habitats is allowed, conditions for adaptation to the main habitat become less stringent. Even if the alleles favored in the marginal habitat are mildly deleterious in the core habitat, this "return" gene flow will establish a low frequency of those alleles in the adjacent areas of the core habitat. Thus, some of the immigrants into the marginal habitat will now carry the locally favored alleles (Kawecki & Holt 2002, Lenormand 2002). Deterministic two-patch models predict in such a case that the effect of dispersal rate on adaptation depends on the magnitude of the fitness effects of underlying alleles (**Figure 2**). If the adaptation is mediated by few alleles with large

effects, low dispersal allows local adaptation: The allele frequencies will increase locally in the marginal habitat much more than in the core habitat (**Figure 2b**). But if many alleles with small effects are involved, even low gene flow prevents differentiation of allele frequencies, and so local adaptation is not possible. In this case, adaptation to the marginal habitat can only occur if the alleles also increase in frequency in the core habitat, and so both marginal and core populations become more adapted to the marginal habitat (and so less adapted to the core habitat; **Figure 2c**). This process is promoted by a high dispersal rate, which exposes a greater fraction of the entire regional population to the marginal habitat, and by phenotypic plasticity that allows the same genotype to express different phenotypes in the two habitats. For a range of intermediate cases, a U-shaped relationship between dispersal rate and adaptation to a marginal habitat is predicted, with intermediate dispersal being least favorable (Kawecki 2000, 2004; Ronce & Kirkpatrick 2001).

In contrast to models assuming two discrete habitat types, models of adaptation on an environmental gradient typically predict low dispersal rates to be more favorable to adaptation to marginal habitats and thus range expansion along the gradient, even if many loci with small effects are involved (Bridle & Vines 2007, Kirkpatrick & Barton 1997, Taper & Case 2000). The dynamics of adaptation along a spatially explicit gradient is likely to be quite different from a two-patch system, and more analysis is needed to see how robust this conclusion is.

Life Cycle

The prospects of adaptation to a marginal habitat are likely to be affected by the order of dispersal, natural selection, and mating. If dispersal occurs at a juvenile stage, immigrants are subject to natural selection before their genes can recombine with the local gene pool. In contrast, if dispersal occurs at the adult stage, followed by mating, even individuals that would be unable to survive to adulthood in the marginal habitat can contribute to gene flow. Intuitively, one may expect that zygote dispersal would be more favorable to adaptation to marginal habitats than (sex-unbiased) adult dispersal followed by mating. This has indeed been predicted by Ronce & Kirkpatrick (2001), but, surprisingly, the opposite prediction has been obtained by Holt et al. (2003). One possible reason for this discrepancy is the stochastic nature of the latter model, where adaptation to marginal habitat may be limited by loss of genetic variation in a small marginal population; with dispersal just before mating the effective population size is greater.

Sex-Biased Dispersal

Although gene flow occurs through both sexes, in most species only female immigrants contribute to local population growth. Strongly female-biased dispersal is therefore predicted to be most favorable, and strongly male biased dispersal least favorable, for adaptation to marginal habitats (Kawecki 2003). An extreme case of the latter is pollen dispersal, which especially in wind-pollinated trees can result in long-distance gene flow (Savolainen et al. 2007), but it will only affect the demography of local populations if they are pollen limited.

Environmental Fluctuations

As discussed above, adaptation to a marginal habitat may involve a shift between two alternative equilibria. Such a shift might be mediated by drift and mutation pressure (Holt et al. 2003, Kimbrell & Holt 2007), but this may require that the local populations are small. However, such shifts can also be mediated by temporal changes in the environment. A series of particularly good years can allow the marginal population to flourish; the temporary increase in the local population size makes local selection more effective relative to gene flow. This may allow the locally adapted alleles to increase in frequency sufficiently for the system to reach the domain of attraction of a "generalist" equilibrium (Holt et al. 2004). Conversely, a series of particularly bad years can depress the size of a locally adapted marginal population so much that its gene pool becomes swamped by immigrant alleles and the adaptation is lost (migrational meltdown; Ronce & Kirkpatrick 2001). A spectacular example of such a shift between alternative source-sink equilibria has been reported in a butterfly (Boughton 1999). Below I discuss how environmental fluctuations can combine with genetic drift and extinction colonization dynamics to facilitate niche shifts in a metapopulation setting.

Ecological Opportunity and Coevolution

As Darwin's finches and other cases of radiation following colonization of species-poor habitats suggest, adaptation to marginal habitats is probably easier when interspecific competition and the pressure of natural enemies are reduced. At a first approximation, these aspects of biotic environment can be accounted for by changes in demographic parameters within a single-species model. However, interacting species mutually affect each other's demography and evolution. These interactions have been addressed in a model of coevolution of ranges of competing species on continuous environmental gradients (Taper & Case 2000). It shows that, where the ranges of species meet, competition creates a positive feedback---local densities become reduced, gene flow becomes more asymmetric, and frequency-dependent selection in addition to drift acts to keep the population away from the optimum. Thus, the species ranges along the gradient evolve to be narrower than in a single-species model. Furthermore, the threshold steepness of the gradient below which the species continues to expand its range indefinitely is much lower with than without competition.

Because of the complex spatial and temporal patterns they can create even in uniform environments (e.g., Gandon & Michalakis 2002, Nuismer 2006), host-parasite interaction are likely to have idiosyncratic effects on adaptation of both hosts and parasites to marginal habitats. Quite often distribution of specialist parasites is more restricted than that of their hosts. In particular, marginal populations may be less affected by specialist parasites---their lower density makes parasite transmission more difficult, and the parasite can only colonize a habitat patch after the host has arrived there. This reduced parasite pressure may help marginal populations to persist, and thus facilitate their local adaptation, which, alas, may require evolving resistance to locally occurring opportunistic parasites absent in the core habitat. In some situations, the time window between colonization of a

marginal habitat and the arrival of specialist parasites may be crucial for the chance that the host population adapts well enough to persist even with the parasite pressure.

For a parasite, adaptation to a novel host species is essentially adaptation to a novel, initially marginal habitat, but the outcome can be complicated by the evolutionary responses of the host. In particular, in addition to increased gene flow, greater dispersal of the parasite between the host species (i.e., greater cross-infection) leads to higher parasite prevalence on the marginal host, thus exerting stronger selection on the host. As a result, the host may evolve greater resistance, possibly nullifying the effect of parasite adaptation (Nuismer & Kirkpatrick 2003). The effects of interspecific interactions and coevolution on adaptation to marginal habitats need to be further explored, but given their complexity one should not expect simple general predictions.

Genetic Architecture of Adaptation

It is usually assumed that adaptation to marginal habitats trades off with fitness in core habitats. This may not necessarily be the case, but gene flow can hinder adaptation only if it is; otherwise adaptation to the marginal habitat can occur as a byproduct of adaptation to the core habitat. It is not surprising that the stronger the trade-off (i.e., the greater the loss of fitness in the core habitat for a given fitness increase in the marginal habitat), the more difficult it is to adapt to a marginal habitat (e.g., Holt & Gaines 1992; Kawecki 2000, 2003; Ronce & Kirkpatrick 2001). However, for the same strength of the trade-off (e.g., for the same distance between the optima for a quantitative trait mediating adaptation), few loci with large effects are more favorable for adaptation to marginal habitats than many loci with small effects, especially when the dispersal rates are low (Kawecki 2000, 2004). With the same gene flow, greater effects of individual loci enable a greater degree of local adaptation, and rare alleles with a large effect are less likely to be lost to genetic drift.

Drift is also more likely to eliminate rare advantageous alleles if they are recessive. Furthermore, selection in favor of a recessive allele is less effective against gene flow bringing in a dominant allele than vice versa. For those reasons, adaptation to marginal habitats is more likely if nonrecessive alleles are involved (Lenormand 2002).

Adaptation to marginal habitats will also be facilitated by linkage between the loci involved. Selection will create positive **linkage disequilibrium** between alleles favored in the marginal habitat; this linkage disequilibrium inflates the genetic variation and thus makes selection more effective. Closer linkage between the loci will maintain greater linkage disequilibrium (Lenormand 2002). Close linkage is likely to be particularly important where the adaptation is mediated by specific allele combination.

Most models of adaptation to marginal habitats assume a simple genetic architecture (single locus or multiple loci with additive effects); the role of epistasis has been little investigated. One exception is a recent model where adaptation to the

marginal habitat is mediated by a change in a phenotype determined by the output of gene regulatory network (Kimbrell & Holt 2007). In addition to selection for different final output, the network is selected for "developmental stability," i.e., fast convergence to a stable state within a generation. In this model, the probability of adapting to the marginal habitat is predicted to decrease steeply with increasing network complexity. The reason is that, as a byproduct of selection for developmental stability, the gene networks evolve robustness to mutation (genetic canalization, Flatt 2005), and more complex networks become more canalized. Because canalization reduces the expression of genetic variation, it hinders the response to selection, and thus makes adaptation to marginal habitats more difficult. Where adaptation to the marginal habitat occurs, it is preceded by a breakdown of canalization and developmental stability, which allows the expression of hidden genetic variation. After the marginal population evolves locally adapted network output, the network again evolves a high developmental and mutational stability (Kimbrell & Holt 2007). This model suggest that where adaptation to marginal habitats involves a complex genetic architecture, the population may first need to cross an "adaptive valley" where the old genetic architecture breaks down and phenotypes become mutationally and developmentally unstable. The next subsection describes a scenario how demographic properties of marginal habitats may facilitate crossing such an adaptive valley.

Peak Shifts

Adaptation to a novel habitat may require a particular combination of alleles at several loci, such that each allele individually reduces fitness, and only an individual carrying all of them enjoys higher fitness. When these alleles are rare, they will occur together only very rarely, and so selection will act against them. Thus, using Sewall Wright's classic metaphor, the population will be stuck on a lower "adaptive peak," unable to reach the higher "peak" by selection alone (Wade & Goodnight 1998). Wright's shifting balance theory postulates that a shift to the higher peak would be possible in a metapopulation setting (Peck & Welch 2004, Wade & Goodnight 1998). In the first phase of the process, the frequencies of the focal alleles increase in one of the local populations owing to genetic drift, e.g., caused by a population bottleneck. This brings this population across the adaptive valley into the domain of attraction of the higher peak, so natural selection will now act to bring the alleles to fixation within the local population (phase two). In the third phase, the newly evolved genotypes are supposed to spread across the metapopulation in the process referred to as interdemic selection (Wade & Goodnight 1998). However, for this third phase to work as envisioned by Wright, the local populations where the shift to the higher peak occurred must start producing massive numbers of migrants, essentially swamping the other local populations. This is biologically unrealistic, and so shifting balance has been dismissed as biologically unimportant (Coyne et al. 1997, 2000). However, a recent theoretical analysis suggests that the conditions for the third phase of shifting balance are much less stringent in a metapopulation in a marginal habitat at the border of the species range (Peck & Welch 2004). According to this scenario, in the process of range expansion a species colonizes a series of rather isolated patches of a marginal habitat. Following the bottleneck associated

with the colonization, some populations go through the first two phases of the shifting balance, reaching the higher adaptive peak. Subsequently, general conditions in the area temporarily deteriorate, so that most populations in the marginal area go extinct; however, those that have reached the higher peak have a greater chance to persist owing to their higher mean fitness. When the conditions again improve, those populations recover and become the source of migrants colonizing habitat patches emptied through extinctions (Peck & Welch 2004). The marginal nature of the habitat assumed in this scenario magnifies the effects of small differences in mean fitness among populations---if the conditions for the population to persist are barely satisfied, a small difference in survival or reproduction may have a large impact on the chances of a population making it through hard times. Although this scenario does not assume that the benefits of peak shift are habitat specific, it is particularly attractive as a potential explanation of how evolutionary niche shifts involving complex genetic architectures might occur.

Behavior

Adaptation to a marginal habitat may involve changes in specific behavioral traits with habitat-specific effects on fitness. There are, however, several ways in which behavior may influence adaptation mediated by other traits. For example, males that have locally adapted genotypes might be able to invest more in ornamental traits preferred by females, and thus enjoy a higher mating success. This favors adaptation to marginal habitats (Proulx 2002), but only under juvenile dispersal, where males competing for mating will all have developed in the local habitat. If dispersal occurs just before mating, males arriving from core habitats may show greater ornaments by virtue of having developed under better conditions, and thus be preferred over local males.

Furthermore, though virtually all models cited above treat dispersal rates as given parameters, in reality they are an outcome of behavioral and other traits. Because fitness in marginal habitats is typically lower than in core habitats, and more individuals disperse from core to marginal habitats than in the opposite direction, spatial heterogeneity in habitat quality is predicted to favor reduced dispersal (Holt 1985, Kawecki 2004). However, in a more complex world, factors like temporal variability, inbreeding avoidance, and sib competition will favor some level of dispersal despite costs and risks (Ronce 2007). In actively dispersing organisms, dispersal is affected by habitat preference. With ideal information and unconstrained and cost-free movement, marginal habitats, especially those outside the niche, should be avoided (Holt 1997). However, in reality information is limited, and movement is costly and constrained. So individuals settling in a marginal habitat may be making the best of a bad situation, e.g., because they cannot afford the time or energy to look for a better place, or they cannot gain a breeding territory in the core habitat. In the latter case, they are likely to be phenotypically inferior, which may further reduce their breeding success in the marginal habitat. Alternatively, individuals choosing a marginal habitat may be simply making a mistake.

Conservative habitat preferences may also act to constrain the use of, and so adaptation to, habitats that are of sufficiently high quality to support a population. In

particular, in herbivorous insects it has been repeatedly shown that ovipositing adults avoid potential host plants that would be perfectly suitable for the larvae (Thompson 1988).

Finally, most animals are to some degree capable of learning, which may allow them to compensate for inadequacies of their genotype, explore new resources, or learn to avoid local predators---all within a generation. Such behavioral flexibility may help a species to establish and persist in marginal habitats before natural selection can produce genetically-based adaptations. Furthermore, by changing the relationship between genotype and fitness, learning may also affect the response to natural selection. Genetically maladapted individuals will often benefit from learning more (in terms of fitness) then genetically fit ones; in such a case learning will reduce the fitness variation among genotypes and thus render natural selection less effective. However, if all individuals are rather maladapted, learning may magnify small genotypic differences in fitness and thus make the response to selection more effective, a phenomenon known as the Baldwin effect. That learning can accelerate evolutionary change has been demonstrated in an evolutionary experiment (Mery & Kawecki 2004), and the general conditions under which this can happen have recently been addressed by mathematical models (Borenstein et al. 2006, Paenke et al. 2007).

EXPERIMENTAL ADAPTATION TO MARGINAL HABITATS

Studies of natural populations adapting---or failing to adapt---to marginal habitats can provide circumstantial evidence in support of particular hypotheses. For example, differences in the degree of phenological adaptation in different marginal populations of blue tits correlate with differences in dispersal distance and patch size (Blondel et al. 2006). Nonetheless, inference from such data is limited owing to confounding variables, limited information, and often lack of replication. Hypotheses about factors affecting adaptation to marginal habitats can be more directly tested with controlled evolutionary experiments. Numerous evolutionary experiments demonstrated the genetic potential of many species to adapt to various novel habitats. However, few mimicked the setting envisioned in this review, i.e., different habitats with large initial difference in fitness, connected by dispersal in a way that not only affects the gene pool but also the demography of the local populations. Several such experiments demonstrated that some degree of adaptation to marginal habitats, such as a salty larval medium in *Drosophila* (Verdonck 1987) or a dark environment in *Chlamydomonas* (Bell & Reboud 1997), can occur despite very high levels of gene flow. Another study showed that interspecific competition limited to one of two available host species can cause an initially generalist beetle species to become more specialized on the other host, with the first host becoming more marginal (Taper 1990).

It is, however, only recently that the role of specific factors, in particular dispersal rate, has been explicitly addressed with experimental evolution in microbial systems. One such study with *Pseudomonas* simulated a black hole sink habitat containing antibiotics and showed that the likelihood and degree of adaptation to this marginal

habitat increase with increasing immigration from an antibiotic-free source (Perron et al. 2007). This result, consistent across five different antibiotic regimes, conforms to the predictions of Holt et al. (2003). In a similar black hole sink habitat defined by the presence of a phage, the local bacterial host population became best adapted (i.e., most phage-resistant) under low-intermediate dispersal rate from a phage-free source habitat (Brockhurst et al. 2007). Possible reasons for the difference between these experiments include the coevolutionary character of the latter and different genetic architecture of antibiotic versus phage resistance.

High levels of dispersal were also unfavorable for adaptation of *Pseudomonas* to a marginal habitat defined by a novel energy source (xylose), which the bacteria could not use efficiently. However, the bacteria did adapt to using xylose when the contribution of the marginal habitat to the pool of dispersers was increased, effectively making the per capita dispersal rate from the marginal to the core habitat much greater than in the other direction (Jasmin & Kassen 2007). This is consistent with a prediction by Kawecki & Holt (2002).

These studies illustrate how evolutionary experiments can contribute to our understanding of evolution in marginal habitats. However, they use asexually reproducing microbes and start from a single clone, i.e., evolution is limited by new mutations. Extrapolation to sexually reproducing plant or animal species may be risky: Their evolution at least in the short term relies on standing genetic variation and is affected by recombination. This underscores the need for similar experiments in sexual outcrossing systems.

ASEXUALITY AND HYBRIDIZATION

Where sexual and clonal (parthenogenetic, apomictic) forms of reproduction coexist within a species, the clonal forms are often prevalent in marginal habitats, in particular those whose marginal nature is due to abiotic factors. This pattern has been observed in organisms as diverse as algae, flowering plants, flatworms, crustaceans, insects, mollusks, fishes, and reptiles (Glesener & Tilman 1978, Haag & Ebert 2004, Horandl 2006, Kearney 2003, Lively et al. 1990, Tatarenkov et al. 2005). Even though this pattern is also observed on a local scale (e.g., O'Connell & Eckert 2001, Verduijn et al. 2004), it is often called geographic parthenogenesis. Several hypotheses have been proposed to explain it. First, asexuality eliminates the risk of not finding a sexual partner in low-density marginal populations and makes it possible for a single individual to colonize an empty habitat patch. Second, according to the Red Queen hypothesis, sexual reproduction is favored because it helps the population to coevolve with specialist parasites and pathogens. Because of their lower density and therefore lower opportunity for parasite transmission, populations in marginal habitats are thought to be less affected by specialist parasites (Glesener & Tilman 1978, Lively et al. 1990), reducing the advantage of sex. Third, asexuality allows a genotype that happens to be locally well adapted to breed true (Peck et al. 1998). Fourth, marginal populations are often small and subject to frequent bottleneck, and thus prone to inbreeding; clonal reproduction preserves the original heterozygosity (Haag & Ebert 2004). There is some support

for each of these hypotheses but none can by itself fully explain the pattern (Haag & Ebert 2004, Horandl 2006, Kearney 2005).

Most asexual forms in both plants and animals are polyploid or of hybrid origin, or both; in particular all vertebrate asexuals are hybrids (Horandl 2006, Kearney 2005, Simon et al. 2003). Hybridization and polyploidy may be mechanistically involved in the origin of asexuality (Horandl 2006, Simon et al. 2003), and have usually not been regarded as causally involved in geographic parthenogenesis. However, recent evaluation of evidence suggests that hybrid origin may be crucial for the success of asexuals in marginal habitats, presumably owing to the resulting high heterozygosity. According to this view, asexual reproduction and polyploidy would play a secondary role in protecting the hybrid genotypes from loss of heterozygosity, preventing recombination with locally maladapted immigrants and escaping problems with meiosis (Horandl 2006, Kearney 2005). Polyploidy might also only be a mechanistic byproduct of hybridization (Ramsey & Schemske 1998).

Whatever the reason for their short-term success in marginal habitats, the lack of recombination limits the evolutionary potential of asexual lineages and makes them prone to accumulate deleterious mutations. Their genetic diversity is generated through recurrent origin of asexual clones from the parental species rather than diversification of existing asexual lineages. Asexual forms also do not contribute to the genetic pool of the parental species, so from the viewpoint of the latter they are an evolutionary dead end. Moreover, competition with the asexuals makes it even more difficult for sexual populations to establish in, and adapt to, marginal habitats. Thus, far from being a stepping stone to an expansion of the ecological niche of the species, the prevalence of asexuals in marginal habitats likely acts to conserve the ecological niche and geographic distribution of the species over evolutionary time.

In contrast, hybridization not associated with asexuality or polyploidy may enrich the genetic pool through introgression of alleles from a related species. Molecular data gathered in the past two decades reveal that such introgressive hybridization is much more common than previously thought (Arnold 2004, Dowling & Secor 1997, Mallet 2005, Willis et al. 2006). Through hybridization a species may acquire a specific adaptation from a relative that already has it, and recombination of hybrid genotypes creates a large amount of genetic variation, often exceeding the range of variation in the parental species (Rieseberg et al. 1999). Both should increase the potential to adapt to novel habitats (Anderson & Stebbins 1954). In the first putative example of this phenomenon (Lewontin & Birch 1966), introgression of alleles from a related species apparently allowed an Australian tephritid fly to extend its geographical and host range, a conclusion upheld by more recent molecular studies (Pike et al. 2003). In another well-studied example, introgression of herbivore resistance alleles from a local congener allowed a sunflower to adapt to expand its range in an originally marginal habitat (Rieseberg et al. 2007). Finally, heritable variation for phenological traits that allowed the tephritid fly *Rhagoletis* to broaden its host range may have originated by introgression of chromosomal inversions from a formerly allopatric population (Xie et al. 2007). Similar cases have been reported in an alpine sedge (Choler et al. 2004), mosquitoes, and trypanosomes (Arnold 2004). Horizontal gene transfer, though involving different mechanisms, is in some

ways an analogous phenomenon, playing an important role in the evolution of ecological niches of prokaryotes (Koonin et al. 2001).

Occasionally, hybridization-assisted adaptation to a marginal habitat is accompanied by the evolution of reproductive isolation, leading to the origin of new species (recombinational or homoploid hybrid speciation). A spectacular case has been reported in sunflowers, where independent hybridization events between two parental species gave origin to three specialist species adapted to three extreme environments (sand dunes, salt marsh, and desert flats; Rieseberg et al. 2007). Although recombinational speciation is probably rare (Mallet 2005), introgressive hybridization emerges as an important factor in adaptation to marginal habitats, and so deserves to be integrated into the theory of niche evolution (e.g., Bridle & Vines 2007, Godfree et al. 2007).

CONCLUSION

Starting with the seminal papers by Holt & Gaines (1992) and Hoffmann & Blows (1994), the past 15 years witnessed a growing interest in adaptation to marginal habitats as a mechanism driving the evolution of ecological niches and species ranges. Although we are still far from a comprehensive theory for the evolution of species ranges and ecological niches, we are beginning to formulate testable predictions and understand how specific assumptions affect the predictions. These theoretical developments stimulate empirical studies of source-sink structure, asymmetric gene flow, and genetic variation in marginal habitats and, most recently, evolutionary experiments testing the predictions of the theory in microbial systems. Thus, studying adaptation to marginal habitats has come of age as a subfield of evolutionary biology.

FUTURE ISSUES

1. Integration of two-patch models and gradient models would lead to understanding why they have provided contrasting predictions about the effect of dispersal rate on adaptation.

2. Applying experimental evolution to study adaptation to marginal habitats in sexual model systems would help us understand how adaptations to marginal habitats evolve in the presence of recombination.

3. Uncovering genetic architecture of adaptation to marginal habitats would lead to a greater genetic realism of the theory.

4. Multiple independent patches of marginal habitat, differing in dispersal parameters and environmental variables, could be found at the range limits of some species. In-depth studies of such replicated natural systems would offer an opportunity to see how inferences from theory and laboratory experiments extrapolate to more complex natural settings.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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TERMS/DEFINITIONS

Additive genetic variation: the heritable component of phenotypic variation, underlying the response to natural and artificial selection

Attractor: a state to which a dynamical system tends after a sufficiently long time; a generalization of the concept of equilibrium

Demographic sink: a habitat in which immigration on average exceeds emigration and the number of deaths exceeds the number of births

Epistasis: nonadditive effect of alleles at different loci on a phenotype or fitness

Heritability: the proportion of phenotypic variance in a quantitative trait which is due to additive genetic variance

Inbreeding load: reduction in mean fitness of a population due to increased homozygosity

Introgression: hybridization-mediated transfer of alleles between gene pools of different species or highly divergent populations

Lifetime reproductive success: the expected number of zygotes at generation t + 1 descended from a zygote present at generation t, in sexual organisms divided by 2 to account for meiosis

Linkage disequilibrium: nonrandom statistical association of alleles at different genetic loci in a gene pool

Pleiotropy: occurs when a difference in the genotype at a particular locus affects multiple traits