10

Theories of Niche Conservatism and Evolution

COULD EXOTIC SPECIES BE POTENTIAL TESTS?

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The niche of an invading species determines the range of environments in which it is initially expected to increase when rare, versus facing extinction. Given genetic variation, evolution by natural selection can lead to evolution in a species' niche. Recent theoretical studies have helped clarify when one would expect to see niche evolution, as opposed to niche conservatism or "stasis." This chapter synthesizes insights from theoretical and simulation models of coupled demographic and evolutionary change for species introduced into novel environments. Propagule pressure plays a key role in invasion "outside the niche" because the number of individuals per propagule, and the number of attempted invasions, influences the demographic opportunity and genetic potential for adaptive evolution. Infrequent colonization with propagules at low initial abundance should rarely succeed in habitats outside the ancestral niche. In spatially heterogeneous environments, after successful establishment in one habitat, evolution can either promote or impede a species' spread into other habitats. Many aspects of the basic biology and ecology of a species can influence its likelihood of niche evolution, including mating systems and temporal variation in the environment. Empirical studies of invasions potentially provide fruitful tests of this body of theory, but crucial data are often lacking because there are few records of failed invasions. Examples of lags in invasion

are consistent with evolutionary adjustment to novel environments; if this is indeed the case, the magnitude of the lag should be related to the degree of difference between the novel and ancestral environments.

Introduction

Invasions by exotic species occur when organisms are transported (typically by human agency) from an original ancestral range, across dispersal barriers, to new regions where populations can then become established, persist, and potentially spread over wide areas; we refer to such species interchangeably as exotic or invading species. Because of their enormous practical importance, exotic species have received a large and growing amount of attention (Vitousek et al. 1997; Crooks and Soulé 1999; Mack et al. 2000; Olden et al. 2004). Yet, as D'Antonio et al. (2001) note, our "ability to predict establishment success and impact of nonindigenous species remains limited." There are, of course, many purely ecological reasons for this apparent failure of prediction, but beyond these, another obvious general reason why the establishment and effects of exotic species are difficult to predict might be that these species are moving targets, whose genetic and phenotypic properties change due to evolution in the novel environments in which they find themselves.

There is now a growing body of work on the genetics of exotic species. Sakai et al. (2001) and Lambrinos (2004) provide excellent overviews of empirical studies of population and evolutionary processes in exotic species, and the recent book by Cox (2004) provides numerous examples of evolution in invasions. A useful review of the evolutionary genetics of exotic species by Lee (2002) emphasizes the importance of genetic architecture for understanding the evolutionary dimension of invasions. In this chapter, we discuss exotic species from the complementary perspective of recent general theoretical studies of niche conservatism and evolution. There is a rapidly growing body of literature exploring the coevolution of demography, fitness, and species' geographic and habitat ranges that is broadly pertinent to exotic species (e.g., Holt and Gaines 1992; Kirkpatrick and Barton 1997; Ronce and Kirkpatrick 2001; Antonovics et al. 2001; Kawecki 1995, 2000, 2004; Garcia-Ramos and Rodriguez 2002; Case et al. 2005). These studies highlight the importance of the interplay of demography, landscape structure, and temporal variation as both facilitators of and constraints on adaptive evolution. We do not attempt a comprehensive literature review here, but rather provide examples from our own work and some new results. The models in question tend to be rather abstract compared with those required to address concrete management or control problems. But we suggest that these relatively simple models lead to general, qualitative insights that carry over to more complex, realistic scenarios. Moreover, we suggest that exotic species may provide fertile ground for testing and refining this body of evolutionary theory.

A particularly interesting issue is how evolution influences the likelihood of invasion in spatially heterogeneous environments. Lyford et al. (2003) note that most ecological theories that have been applied to invasions focus on the processes of dispersal, establishment, and population growth in environments that implicitly are homogeneous in space and time. Yet, in reality, invasions typically occur on landscapes with complex spatial structures and in environments that are temporally variable and often nonstationary. Sax and Brown (2000) observe that spatial variation can help explain why many introductions of potentially successful invaders actually fail. As we will see, spatial and temporal heterogeneity may also be profoundly important in governing the evolution of exotic species.

Two factors that seem to have power for predicting the success of deliberate introductions within a region (e.g., as in game bird releases) are the number of individuals per attempted introduction and the number of introduction attempts (Veltman et al. 1996; Duncan 1997; Green 1997). Levine (2000) experimentally showed that the abundance of the initial propagule had a strong influence on initial establishment (see also Byers and Goldwasser 2001; Brown and Peet 2003). D'Antonio et al. (2001; see also Lonsdale 1999) highlight the importance of propagule pressure; they suggest that the presence of a sustained source of propagules (e.g., from garden populations) also appears to facilitate the eventual spread of exotics to broader landscapes. Successful invasions are often correlated with multiple attempts at deliberate introduction (Barrett and Husband 1990); a natural analogue of this may arise when a species becomes established in one habitat patch, from which it can send repeated propagules into other habitats in the surrounding landscape. There are, of course, purely ecological reasons to expect propagule pressure (reflecting both the numbers of individuals introduced per invasion episode and the number of repeated invasion attempts observed over time) to matter in determining the likelihood of successful establishment. The evolutionary theories sketched below suggest complementary reasons for increased invasion success with increased propagule pressure.

Before discussing this body of theory, it is useful to briefly sketch some reasons why an evolutionary perspective on invasions seems almost inescapable, and in particular, how invasions are (or should be) related to analyses of species' niches. We then present theoretical results having to do with how evolution can influence invasion into homogeneous environments. With these results in hand, we turn our attention to evolution by exotic species in spatially and temporally heterogeneous landscapes.

Ecological Niches and Initial Establishment

For the purposes of this chapter, the "niche" of a species refers simply to that suite of environmental conditions within which populations of that species are expected to persist deterministically, without recurrent immigration (Hutchinson 1978; Holt and Gaines 1992). Broadly speaking, those "conditions" can include abiotic factors as well as resource availabilities and abundances of interacting species such as competitors and predators. This use of the term "niche" goes back to Grinnell (1917), who invoked the concept to characterize the factors delimiting a species' distribution. Hutchinson (1957) formalized the concept in his famous "*n*-dimensional hypervolume," which emphasized the multidimensional nature of organisms' interactions with their environments. The "fundamental niche" describes the requirements of a species for persistence when one discounts the negative effects of predators and competitors. Maguire (1973) later demonstrated that it could be fruitful to characterize a niche as a response surface, where the response variable was the growth rate of a species when it was rare. In effect, the niche is a mapping of deterministic population dynamics onto an abstract environmental space.

The most fundamental feature of population dynamics is extinction versus persistence, and the niche describes how this fundamental feature depends on the environment. If the niche requirements of a species are met at a given site, we expect that, on average, births should exceed deaths when the species is rare, and so introductions at that site should have a chance of becoming established, leading to populations that persist over reasonable time horizons (which can be very long if the local carrying capacity is large and the environment is constant). By contrast, if the site has conditions outside the niche, then births are fewer than deaths, and extinction is certain.

Figure 10.1A schematically depicts a simple example of a species' niche, characterized as a response surface to two abiotic factors. We assume that the combination of abiotic factors for which growth rate equals zero (the inner circle) circumscribes the fundamental niche of a species, both at the site of orig-

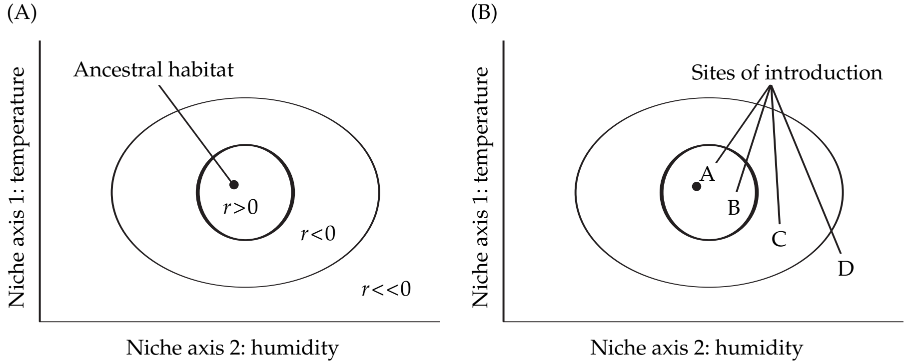

Figure 10.1 (A) A schematic representation of an ecological niche response surface. The inner circle demarcates the fundamental niche—a set of conditions that permit deterministic persistence. The outer ellipse schematically separates areas of niche space that imply gradual population decline as opposed to rapid population decline. In the optimal environment (represented by the dot), the species has a high growth rate; outside the fundamental niche, its numbers decline slowly (near the niche) or rapidly (far from the niche). (B) Different sites of introduction are likely to match a species' niche requirements to varying degrees. A and B are sites with conditions inside the niche; C and D have conditions outside the niche.

ination and at the sites where introduction occurs (at least initially), and, for the purpose of illustration, that the effects of the two abiotic factors shown outweigh those of other factors. There are, of course, many complexities in characterizing niches, most of which go beyond the intended scope of this chapter (Chase and Leibold 2003). For instance, in general, invasion is expected to depend strongly on interactions with resident resources and species, and these are likely to differ in many ways from the web of interactions within which the species evolved (Shea and Chesson 2002). The absence of coevolved natural enemies or competitors, for example, may permit a species to invade successfully into a wider range of abiotic conditions in the novel environment than in the ancestral range.

The Evolutionary Potential of Invading Species

It is likely that the environments faced by an introduced species will differ in many respects (often quite radically) from the environment harboring its ancestor. Species that leave behind their specialist natural enemies (e.g., predators, parasitoids, pathogens) (Keane and Crawley 2002) may be able to persist over a different set of abiotic conditions than that which characterizes their native range. Selection will often differ for many aspects of the phenotype relevant to coping with and utilizing the novel biotic and abiotic environment (Lewontin 1965). In a review of empirical studies of rapid adaptive evolution, Reznick and Ghalambor (2001) found that many examples involved a combination of directional selection and at least a short-term opportunity for population growth. They suggest that an opportunity for population growth may be a key attribute of rapid evolution, because otherwise directional selection might lead to population decline and even local extinction. Successful invaders, by definition, experience periods of sustained population growth, and so should be candidates for rapid evolution. Indeed, some of the clearest examples of rapid evolution come from introduced species (e.g., Quinn et al. 2000). One possible indication of evolution is that in many successful invasions there is a lag phase of very slow growth, followed by an accelerated clip of advance across space. A potential explanation for this lag is that it reflects a lag in adaptation of the exotic species to the novel environment (Crooks and Soulé 1999).

But it should not be automatically assumed that evolutionary dynamics are essential components of invasion dynamics. Indeed, an intriguing dichotomy—almost a form of schizophrenia—has arisen in the field of ecology and evolutionary biology in the last few years. On one hand, as just noted, there is a mounting body of evidence from studies of microevolution that adaptive evolution is rapid, can be readily observed (well within human life spans), and has important applied consequences for resource management, conservation, and the control of undesirable species (Hendry and Kinnison 1999; Ashley et al. 2003; Rice and Emery 2003; Stockwell et al. 2003). Stockwell and Ashley (2004) suggest that in altered environments, “rapid adaptation is the norm rather than the exception." Ashley et al. (2003) show that many instances of rapid evolution come from introduced species. Rapid evolution might appear to be the default assumption in studies of exotic species.

On the other hand, there is considerable evidence from biogeography, phylogenetics, and paleobiology that species' niches can be relatively conservative. There is a sense among many scientists that niche conservatism is ubiquitous and poorly understood (Hansen and Houle 2004). Some examples of conservatism can be found at microevolutionary time scales. Bradshaw (1991, p. 303) reviews a number of case studies in which there appears to be no evolution, despite ongoing selection, and remarks: "For a century we have been mesmerized by the successes of evolution. It is time now that we paid equal attention to its failures." Merila et al. (2001) also discuss a wide range of systems in which selection appears to be ongoing over short time scales, but stasis is observed instead of evolutionary responses. Other instances of conservatism in species' niches become apparent when species or clades are examined over broad sweeps of evolutionary history: "The presence of strong constraints on alterations in the ecological posture of species is seen in their response to long-term environmental change during the Quaternary" (Levin 2003). Many paleobiologists have commented on the prevalence of conservatism in evolutionary history (Schopf 1996). For instance, the paleobotanist Huntley (1991) argues that when climate changes, species typically migrate (or go extinct), rather than shift their niche requirements (see also Coope 1979). Indeed, some authors have argued that phylogenetic niche conservatism appears to be the norm, rather than the exception, in evolution (Peterson et al. 1999; Ackerly 2003; Peterson 2003).

A reconciliation of these two disparate perspectives may come, we suggest, from a close consideration of the demographic context in which evolution necessarily occurs. Niche conservatism is not really a species (or clade) property, but rather a reflection of the interaction of species' properties, environmental contexts, and demographic responses to environmental conditions. In the next few paragraphs, we view the problem of invasion by exotic species through the lens of evolutionary niche theory, focusing in particular on the issue of when evolution by natural selection is a necessary ingredient in successful invasion. Conversely, we expect that in the future, exotic species could provide testing grounds for assessing theories of niche conservatism and evolution. Below, we will sketch some desiderata for such tests.

As noted above, the niche of a species strongly affects the initial likelihood that a propagule will become established, leading to a potential invasion. As a simple hypothetical example (see Figure 10.1B), assume that the focal species has the fundamental niche shown in Figure 10.1A, and that the invading propagule originated in a habitat with optimal conditions like those at the dot (which we will call the ancestral habitat), and is introduced into a variety of sites (denoted by letters A, B, C, and D in Figure 10.1B) with varying local conditions. Assume for the sake of simplicity that the species is at its evolutionary optimum in its site of origination. Site A has conditions essentially similar to optimal conditions in the ancestral habitat; the species will thus face only minor differences in the selective environment, and should have a relatively high growth rate when introduced here. At site B, it is expected to become established and persist, although it will grow rather slowly; this implies that it may stay at low numbers, at which it is vulnerable to extinction due to demographic stochasticity and other factors, for a long time. Finally, at C and D, the species is predicted to decline to extinction, albeit at different rates. Thus, a first-order prediction about establishment success comes from matching a species' niche requirements against environmental conditions at the site of introduction.

This basic logic underlies the entire protocol of "climate matching" as a tool for predicting the potential success of invading species. For instance, artificial intelligence techniques are being used to develop ecological niche models in the native distributions of species, which then permit projections about the likely initial success and ultimate spatial extent of invasions by those species (Peterson 2003). However, such predictions assume that species' niches stay reasonably constant from initial establishment through the later stages of invasion.

In the region of origin, the stability of species' range boundaries and habitat distributions over evolutionary time scales is likely to reflect niche stasis. Such stasis is assumed whenever one uses a niche model developed in a site of origin to make predictions about establishment. For instance, Levin and Clay (1984) describe an experimental study of the niche conditions defining the success of introduced populations of an annual plant species, *Phlox drummondii*. In natural environments, this species inhabits sites with loose sandy loam. Levin and Clay planted seeds in adjacent habitats with denser soil. The number of seeds produced was much less than the number planted (hence, in all the introduced populations, $r < 0$, in the terms of Figure 10.1), and all the populations ultimately went extinct. A niche model with an axis of soil density would identify a soil density above which establishment is predicted to be prevented, provided the species were to remain unchanged. The best-performing population was the one placed in soil with properties closest to the soil of the ancestral environment. The theoretical results discussed below suggest that niche evolution, if it occurs at all, is most likely for that population which was not initially all that far removed from the bounds of its niche requirements.

Sites C and D in Figure 10.1B might be called "sink habitats," where conditions are outside a species' fundamental niche; by contrast, sites A and B are "source habitats." Evolution may influence a species' persistence and invasion potential in sites A and B, but is not *necessary* for invasion to occur. By contrast, if the niche itself does not evolve, invasions into sites C and D will inevitably fail. Thus, a basic question we can ask is when niche evolution can occur, converting a sink habitat into a source habitat. The issue of whether or not successful invasion into sink habitats is possible is intimately related to the potential for niche evolution.

Evolution can influence the course of establishment in several distinct ways, as shown in Figure 10.2, which plots dynamics in local population size following establishment for sites A–D in Figure 10.1B. At site A, initial growth rates are rapid, and (by assumption) the selective environment is similar to that of

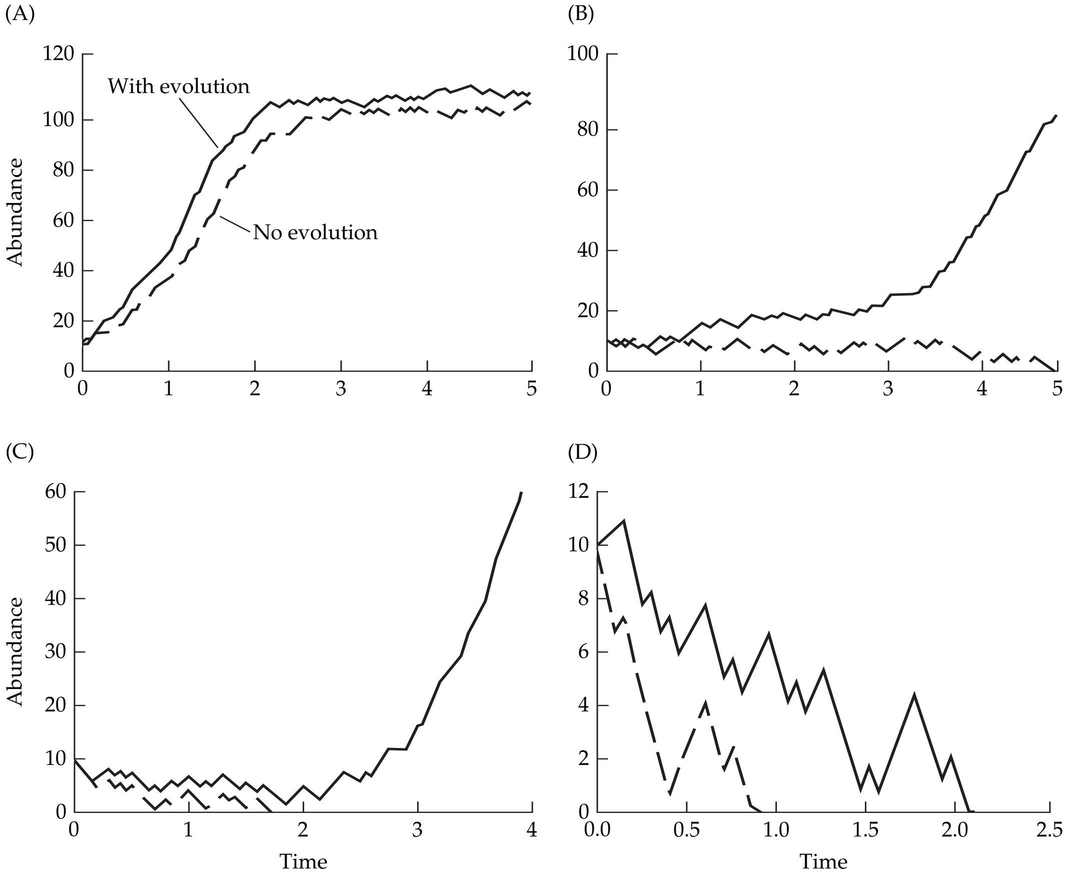

Figure 10.2 Population dynamics expected for species introduced at the niche positions shown in Figure 10.1B. A simple model was used to derive these figures for illustrative purposes. The population change was governed by $dN/dt = rN(1 - N/K)$. Evolution is simulated by linearly increasing r and K with time. In all cases with evolution, K starts at 100 and increases at a rate of 1 per time unit. Random gain or loss of one individual every 0.05 time units has been added to simulate demographic stochasticity. (A) Evolution is not needed for persistence, but can affect abundance. The initial r is 2, and it evolves at a rate of 0.5. (B) Evolution may increase growth rates, and so facilitate persistence in the face of possible extinction due to demographic stochasticity. The initial r is 0.05, and it evolves at a rate of 0.3. (C) Evolution rescues this population from extinction. The initial r is –1, and it evolves at a rate of 1. (D) Evolution occurs, but cannot save this population. The initial r is –1.5, and it evolves at a rate of 0.5. Similar patterns emerge in more complex, realistic models (see text).

the ancestral habitat. Evolution should not matter greatly in initial establishment (though there could be minor effects if selection leads to a modest acceleration of the initial rate of increase). As the population grows, density dependence should begin to limit growth. If density-dependent factors operate differently than in the ancestral environment, evolution could also subsequently act to alter population size. In the example shown, it is assumed that density-dependent selection occurs, so that as the introduced population evolves, its numbers increase. The magnitude of the change in population size depends on the local selective environment, the nature of density-dependent feedbacks, and the amount of genetic variation available for selection (either introduced in the original propagule or originating via in situ mutation). Such evolution could matter greatly in governing the transition from initial, local establishment to widespread invasion because propagule pressure across the landscape should scale with local abundance. However, this kind of evolution, though interesting and potentially important in invasion dynamics, may not greatly influence the probability of initial establishment *per se*.

Site B also has conditions within the ancestral niche, but much nearer the niche boundary. This implies that population growth rates should be lower, and hence that a population introduced at low numbers should remain at low densities for much longer than a similar introduction at site A. The population would thus face an enhanced extinction risk due to both ecological factors (e.g., demographic stochasticity, Allee effects) and genetic factors (inbreeding, mutational meltdown) (Lande 1998). Many introductions into sites with conditions just within a niche boundary should fail. If evolution could increase the initial growth rate for such introductions, it could reduce the time the population is exposed to elevated extinction risks and thus increase the probability of establishment.

The initial stages of evolution following introduction will depend on the amount of genetic variation brought in with the initial propagule (unless there is hybridization with native species: Lee 2002), which can be viewed as a "bottleneck" in the original population. In general, the rate of population growth following a bottleneck is a crucial determinant of the amount of genetic variation that is lost (Nei et al. 1975; Gaggiotti 2003). If the growth rate is rapid (as in site A), little variation will be lost. But if growth rate is slow (as in site B), considerable variation may be lost. Moreover, because numbers are low, inbreeding is likely. There is some evidence that when conditions are stressful (as is likely near the edge of the niche), inbreeding depression is more severe (Gaggiotti 2003). Saccheri et al. (1998) argue that inbreeding increased extinction risk in small populations of a butterfly, the Glanville fritillary (*Melitaea cinxia*).

Another potential cause of elevated extinction risk for a species introduced near the edge of its niche, where numbers stay low longer, is the accumulation of slightly but unconditionally deleterious mutations (Lynch et al. 1995). Natural selection is less effective at weeding out mildly deleterious mutations in small populations than in large populations. The genetic load of mutations should thus be greater for populations near the edge of a species' niche (Kawecki et al. 1997). This is a somewhat controversial prediction (Gaggiotti 2003; Whitlock et al. 2003), but the controversy has to do with the exact magnitude of the effect, rather than with its existence.

Site C has conditions just outside the ancestral niche. In the absence of evolution, the introduction will surely fail. However, if evolution can increase the growth rate of the species sufficiently rapidly, it is possible that the species will, in effect, evolve "out of the niche." If evolution can rescue a population from extinction, it will be because there has been a change in the niche of the population itself. The dynamics of such a "rescued" population, initially occupying an environment outside its niche, should usually exhibit a U-shaped trajectory (Gomulkiewicz and Holt 1995; and see below).

Site D is like site C, but considerably worse; here the population declines so rapidly that even if appropriate genetic variation is present and evolution occurs, it is insufficient to rescue the population from extinction. In effect, there is a race between a demographic process, a decline in numbers driving the introduced species to extinction, and an evolutionary process, increasing fitness in the local environment. In the example shown, evolution loses.

In both C and D, the invading propagule faces an environment much harsher than that experienced in the ancestral habitat. There is now a substantial theoretical literature on evolution in changing environments. Many papers consider environments with systematic temporal trends (due to climate change for instance), with a linear trend in a phenotypic optimum (e.g., Pease et al. 1989; Burger and Lynch 1995; Lande and Shannon 1996). Several authors have considered an alternative scenario in which there is an abrupt transition between two environmental states (e.g., Gomulkiewicz and Holt 1995). The latter models should apply equally well to analyzing the fate of a colonizing propagule plucked from an environment where its ancestors evolved in the face of one set of selective challenges and then placed in a novel environment with quite different selective challenges. In the next few paragraphs, we highlight general insights from these models, which help identify circumstances in which one might observe invasion "outside the niche."

Gomulkiewicz and Holt (1995; see also Holt and Gomulkiewicz 1997b) employed a heuristic device to examine the joint effect of population dynamics and evolution on population persistence in an environment experiencing abrupt change. Conservation biologists have suggested that there is a population size (a "critical number") below which extinction is risked for a whole suite of reasons (e.g., demographic stochasticity, Allee effects, and inbreeding). If the initial state of a population has an absolute fitness of less than 1, then without evolution, that population will certainly decline toward this critical number and face likely extinction (as at sites C and D in Figure 10.1B; see Figure 10.2C,D for numerical examples). With evolution, provided that selection can lead to a population with a positive growth rate, numbers will eventually rebound. This requires that the population have sufficient genetic variation (or can accumulate such variation rapidly) to at least persist in the novel environment. Selection in each generation increases average fitness, provided that the assumptions of Fisher's fundamental theorem approximately hold (Fisher 1958; Burt 1995). But if a population starts at low numbers, and if evolution by natural selection is slow, so that average fitness stays low for a sufficiently long time, then the population may reach low critical numbers at which it is vulnerable to extinction.

There are several qualitative messages that emerge from such models linking changes in population size with evolved changes in phenotypes (Gomulkiewicz and Holt 1995; Holt and Gomulkiewicz 2004):

- If the initial propagule number is small, then extinction is by far the most likely outcome of introduction into environments outside the niche. Upon reflection, this is not very surprising. After all, small population sizes can lead to extinction even in favorable environments, so propagules with a small number of individuals face elevated extinction risks in any case. If numbers tend to decline because niche requirements are not met, then even with appropriate genetic variation, the population is not likely to be able to evolve sufficiently rapidly to shift its niche requirements before suffering extinction.
- One effect of a large initial propagule number is to make it more likely that a species can invade environments outside its ancestral niche, because a greater number of individuals increases the demographic window of opportunity for selection to operate.
- Nonetheless, even for initial propagules with a large number of individuals, evolution is unlikely to rescue populations introduced into environments where conditions are much outside the species' ancestral niche requirements. If initial fitness is very low, the population is likely to decline rapidly and go extinct before it can adapt and grow.
- Finally, increasing genetic variability (heritability) does make evolutionary rescue more likely, but even populations with abundant genetic variability are not likely to persist in environments where initial propagule numbers and/or growth rates are very low.

To go beyond these heuristic conclusions, one needs models that describe the probability of actual extinction. Analytically describing the probability of extinction for populations evolving in tandem with changes in abundance is challenging. One approach we (Holt et al. 2003; Holt and Gomulkiewicz 2004) and others (e.g., Boulding and Hay 2001) have taken is to develop individual-based simulation models in which individuals and their genotypes are tracked and extinction probabilities calculated as a function of initial population size, initial fitnesses (reflecting the match between the local environment and a species' niche requirements), and genetic parameters. Box 10.1 describes one such model. In short, individuals are assumed to be diploid, and fitness is assumed to depend on a single quantitative trait (e.g., body size) genetically determined by n unlinked loci (in the examples shown, $n = 10$) plus an environmental effect. Genetic variation in the source population arises from a balance between mutation introducing novel variation and selection and drift weeding it out. Immigrants are drawn at random from the source population. In the introduced population, mating is random, and mutation occurs after segregation. The fitness function has a Gaussian shape, whose peak (and therefore the optimum phenotype) differs between the presumed source habitat of the population and the novel habitat, so that the initial population at the time of introduction is maladapted to the novel habitat.

BOX 10.1 *An Individual-Based Model for Analyzing Niche Evolution*

Deterministic models can illuminate the interplay of population and evolutionary dynamics (see, e.g., Gomulkiewicz and Holt 1995; Holt and Gomulkiewicz 2004; Holt et al. 2003, 2004), but a full treatment of extinction requires the incorporation of stochasticity. When populations are low in abundance, accounting for individual discreteness due to stochastic processes of mutation, birth, death, and movement becomes important. Realistic models accounting for these processes present many analytic challenges. To provide insight into the consequences of this stochasticity, we have carried out studies using individual-based simulations in which the fate of each individual is tracked (e.g., Holt et al. 2003). These simulations utilize the same basic assumptions as those of Burger and Lynch (1995), who examined adaptation to a continually changing environment for a single multilocus character. We examined both evolution in populations established by single colonizing episodes following abrupt environmental change and adaptive evolution in spatially discrete scenarios in which species successfully invaded stable source habitats in a heterogeneous landscape that were coupled by migration to sink habitats. The simulations were predicated on several key assumptions (see Holt et al. 2003).

Genetic assumptions

1. There are *n* additive loci, with no dominance or epistasis (each allele contributes a fixed amount to the phenotypic value, and an individual's phenotype is the sum of this quantity over *n* loci, plus a random term, which has a zero-mean, unit-variance normal distribution)
2. Mutational input maintains variation (the "continuum-of-alleles" model, in which mutational effects are drawn from a continuous, normal distribution)
3. There is free recombination
4. In the model for a heterogeneous landscape, the initial source habitat reaches mutation-selection-drift balance, which then determines the immigrant pool available for colonizing the sink habitats

Life history assumptions

1. Discrete, nonoverlapping generations
2. A dioecious and hermaphroditic sexual system

Ecological assumptions

1. A constant number of immigrants per generation (in spatial model)
2. "Ceiling" density dependence (i.e., density-independent growth below *K*)
3. A constant fecundity per mated pair
4. Offspring survival probability is a Gaussian function of phenotype

Two different mating systems assumed

1. The monogamous mating system has monogamous mating pairs (randomly formed from all adults), as in Burger and Lynch (1995) and Holt et al. (2003). This mating system has a small Allee effect (with *n* individuals, if *n* is an odd number, one individual remains unmated; this depresses average expected fecundity over all individuals, particularly when *n* is small).
2. The random mating system ensures that there is no Allee effect. In each generation, individuals in their female capacity are selected at random without replacement, up to the carrying capacity; in other words, below *K*, all individuals are chosen to be reproductive, whereas above *K*, only *K* individuals get to mate. For mating to occur, each individual selects a random individual (with replacement) from the entire population to act as a male. This protocol

BOX 10.1 *(continued)*

eliminates the small Allee effect that arises in the monogamous mating system.

We have shown elsewhere (Holt et al. 2004b) that Allee effects can influence adaptive evolution in sink habitats, so it is useful to examine scenarios in which no Allee effects exist, especially when comparing different immigration rates (or propagule sizes). With the monogamous mating system, if there are *N* adults, there are at most *N*/2 mating pairs, while with the random mating system, there are *N* pairs (each individual mates as a female, and, on average, once again as a male), unless limited by the carrying capacity. Therefore, to compare the two systems, there should be twice as many offspring per pair with monogamous mating to give the same average fecundity. For the simulations discussed in the text, we used four offspring per pair for the random mating system and eight offspring per pair for the monogamous mating system.

The qualitative findings reported in the text and figures appear to be robust to changes in many of these assumptions. For instance, changes in the number of loci have a relatively minor effect on the probability of adaptation (Holt and Gomulkiewicz 2004; R. D. Holt and R. Gomulkiewicz, unpublished data).

Adults were counted in each generation (N_t). After the census, in the spatial model, there is immigration, followed by random mating. The mating population is not allowed to exceed *K* (the carrying capacity). Individuals produce gametes with free recombination among *n* loci. Mutation occurs on gametes, with a stochastic mutational input per genome (distributed randomly over all *n* loci). Each mated pair produces *f* offspring, surviving to adulthood with probability

$$s(z,i) = \exp\left[\frac{-(z-\theta_i)^2}{2\omega^2}\right]$$

where *z* is the realized phenotype of a given offspring, θ_i is the optimum phenotype in habitat *i*, and ω^2 is inversely proportional to the strength of stabilizing selection. This is the life stage that experiences selection. If the average *z* value is sufficiently far from the optimum, mean fitness is below 1, and the population tends to decline. Individuals surviving mortality are the adults counted at the next census, N_{t+1}.

At the start of the simulation, the source population (either in the ancestral habitat or in a suitable habitat patch in a heterogeneous landscape) is allowed to reach selection-mutation-drift equilibrium. Immigrants then migrate into a sink habitat that initially has zero abundance. We should stress that in this individual-based model, stochasticity plays multiple roles. Mutation is stochastic. Gametic combinations and the genetic composition of immigrants to the sink (in the spatial model) have multilocus allelic combinations that vary due to random sampling. Finally, because survival is probabilistic, there is both genetic drift and chance variation in population size due to demographic stochasticity.

The same broad conclusions emerge from this model (illustrated in Figure 10.3) as suggested by the heuristic model of Figure 10.2. Figures 10.3A and 10.3B depict a number of population trajectories for introduced propagules drawn from similar source populations. For those populations that persist, a clear U-shaped trajectory in numbers occurs (Fig. 10.3A). The solid lines in Fig-

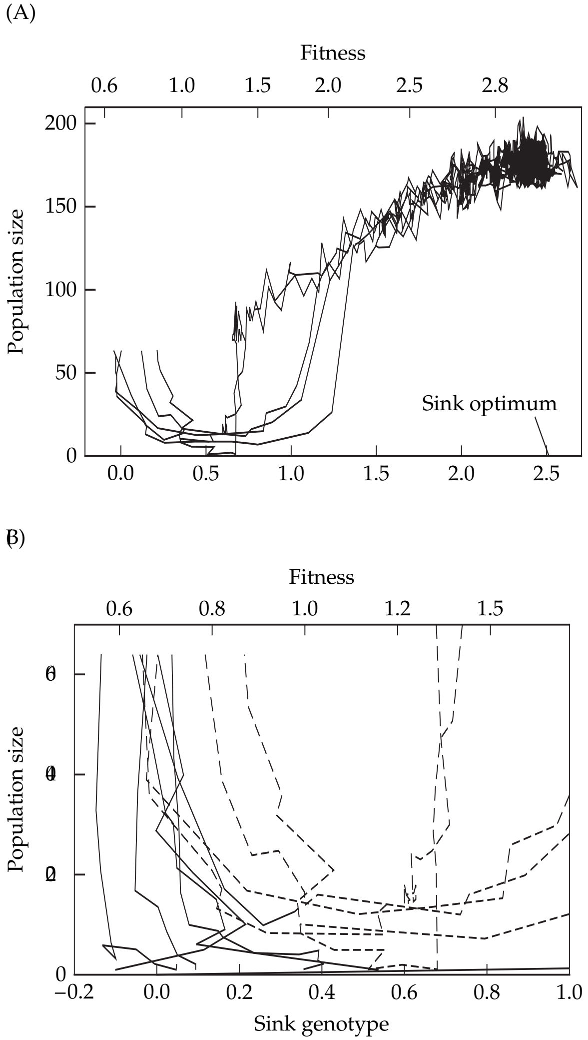

Figure 10.3 Sample trajectories for population size and mean genotypic state for populations introduced into a sink habitat, from a simulation using the individual-based model described in Box 10.1 and the text. (A) The trajectories for populations that adapt and persist in the novel environment. Initially, all populations shown decline in abundance, but these particular populations rebound as they adapt to the environment (a U-shaped trajectory in numbers). (B) Trajectories for populations that go extinct (solid lines) and the initial portions of trajectories for those that persist (dashed lines; the same examples as shown in part A). $K = 64$, mutational rate per haplotype = 0.01, mutational variance $\alpha^2 = 0.05$, strength of selection $\upsilon^2 = 1$, propagule number = 64; 4 births per pair. Random mating is assumed. The optimal genotype in the source scales at a phenotypic value of zero, while the sink optimum is at 2.5. Propagules are drawn at random from the source population (which is at a mutation-drift-selection equilibrium); all propagules have 64 individuals in generation 1.

ure 10.3B are the trajectories of populations that go extinct, while the dashed lines are the trajectories of the populations shown in Figure 10.3A, which have adapted to the novel environment and are persisting. Surviving populations typically evolve more rapidly than do those that go extinct (Figure 10.3B). Often (though not always), evolutionary rescue is facilitated because, by chance, the initial propagule has a mean genotype somewhat closer to the sink habitat optimum (Figure 10.4). Once the population adapts sufficiently to persist, it then shows a period of increasing adaptation and rising population size.

A demographic signature of invasion "outside the niche" is that population numbers have a U-shaped trajectory. If the rate of initial decline is only slightly below zero and censuses are noisy (or the environment temporally variable),

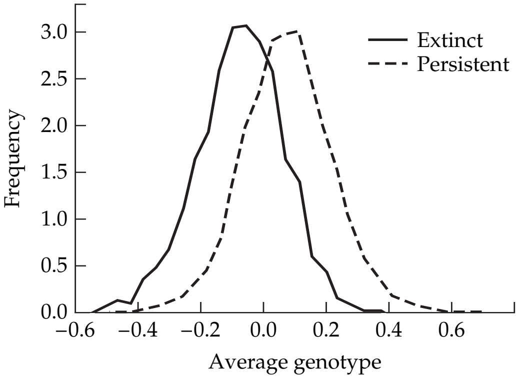

Figure 10.4 Relative frequencies of the mean genotypic state of propagules drawn from the source population (where the phenotypic optimum is assumed to be zero). Each propagule consists of 4 immigrants that were placed into a sink habitat with a phenotypic optimum of 2.5. On average, introductions that were successful (dashed line) had colonizing propagules that were somewhat closer to the new sink habitat optimum than those that went extinct (solid line). However, there is a broad overlap in the distributions. Other parameters are as in Figure 10.3. The figure illustrates the inherent uncertainty of colonization dependent on evolution in a species' niche.

then numbers may be approximately constant and then begin rising rapidly. Lags in population growth rate following introduction may be indirect indicators of periods of evolution in species' niches.

Figure 10.4 describes the initial genotypic state of propagules used in colonization attempts that either failed or succeeded (as in the examples of Figure 10.3B). In these examples, the optimal character value in the site of origination is scaled at zero, and the optimal character value in the site of introduction is a positive value (in this example, it happens to be 2.5). On average, successful introductions have a genetic composition that by chance is somewhat better adapted to the local environment. This means that they enjoy a greater demographic window during which selection can increase population fitness; they initially decline more slowly and require less evolutionary modification to enjoy a positive expected growth rate. However, note that there is a great deal of overlap in the distributions describing successful and failed invasions. Some propagules that seem to be moderately preadapted to the novel environment nonetheless fail. Conversely, some propagules that are more maladapted than the average in the source population nonetheless succeed. These results imply that there is a great deal of inherent unpredictability that arises whenever invasion depends on evolution of traits that influence a species' niche. Many invasion biologists lament the fact that it is difficult to predict invasion success. We suggest that if evolution is involved in the initial establishment of a species in a novel environment, one should not be surprised to observe a substantial degree of unpredictability in invasion success, arising from the interwoven stochastic vicissitudes of demography and evolutionary shifts.

Another issue (not addressed in the figures shown) is that the likelihood of successful invasion increases with the amount of genetic variability present in the source population from which the colonizing propagule is drawn. Novak and Mack (this volume) note that one can greatly inflate the genetic variation of a propagule by using an admixture of individuals plucked from different local populations in the ancestral range, as compared with the same number of individuals drawn from a single local population. Phylogeographic studies may be able to retrospectively identify such admixtures of source populations and identify candidate cases of rapid niche evolution in the initial stages of invasion (see Wares et al., this volume). It would be ideal to compare a number of introductions, including failures as well as successes, differing in the number of source populations included in the original immigrant gene pool. It may be difficult to achieve this ideal in practice, however, at least in retrospective analyses of accidental introductions, as generally we become aware of only those invasions that were successful.

Figure 10.5 summarizes the results of a large number of simulations using the individual-based model described in Box 10.1, which collectively document how the probability of persistence (which is also the probability of adaptation and niche evolution) varies as a function of the degree of both maladaptation and initial propagule abundance (using random mating and monogamous mating systems). These results broadly match the conclusions we drew from the heuristic model of Gomulkiewicz and Holt (1995). Overall, the more maladapted the initial propagule is in the novel environment, the less probable it is that evolution will rescue the population from extinction. Evolutionary modifications of the niche are more likely if they require only modest changes in the phenotype. Moreover, if propagules have smaller initial abundances, successful, persistent invasions into habitats outside the ancestral niche become less probable. When propagule numbers are small, the probability of successful invasion can be low even in environments within the niche; in environments with conditions outside the niche, the opportunity for evolutionary rescue is very short because extinction is expected to be rapid. In addition, note that there is a greater probability of population survival with the random mating system than with the monogamous mating system, and that the difference is greater for the smaller propagule size. This difference is probably due to the Allee effect seen with monogamous mating. The Allee

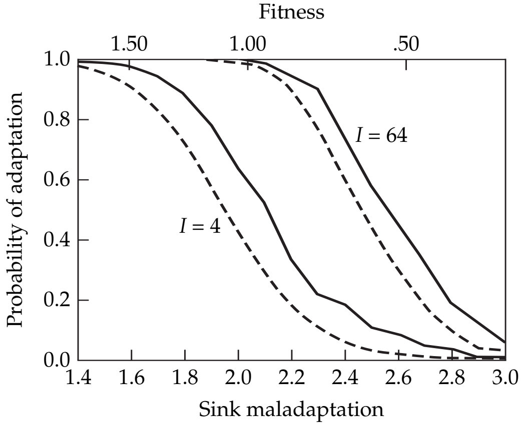

Figure 10.5 The probability of persistence and adaptation as a function of degree of initial maladaptation to the sink habitat for two different abundances of an initial colonizing propagule (*I*) and two mating systems. Other parameters are as in Figure 10.3, except that we assume eight births per pair for the monogamous mating system. Propagules with large abundance have a higher probability than propagules with small abundance of adapting to and thus persisting in habitats where they are initially sufficiently maladapted that extinction is expected in the absence of evolution. In addition, the random mating system (solid lines) gives a higher probability of adaptation than the monogamous mating system (dashed lines) because the latter has a small Allee effect.

effect is quite small for a population size of 64, but, as shown in Figure 10.3, a population with this initial size can fall to much lower levels (at which the Allee effect will be more significant) before it adapts.

These theoretical exercises provide a partial justification for attempts to develop predictive niche models for assessing where invading species may gain a foothold, based on characterizations of their preexisting niches in their ancestral environments (e.g., Peterson 2003). If niches were completely plastic and could evolve very rapidly, then such models would be useless for predicting establishment. If propagule number is typically small, establishment is expected to be quite difficult (per colonizing episode) outside the ancestral niche requirements. Invasion "outside the niche" should require propagules that are larger, and should be more likely if the invading population is not too maladapted to the novel environment, so that its initial growth rate is not too far below replacement.

However, even if static models assuming no evolution can adequately characterize initial invasion success, for reasons discussed below, they should often prove less adequate in predicting the final spatial scope of widespread invasions. Such "failures" could be viewed in a positive light, as potential indicators of rapid niche evolution (e.g., as suggested for some species of New World jays: Peterson and Holt 2003). A future task will be to carefully analyze failures in predicting invasion in the light of potential evolutionary modifications in the very first stages of invasion. Again, it would be desirable to characterize failed invasions as well as successful ones, but this is rarely possible (or even attempted) for many species. In some cases, however, introductions occur quite deliberately, as in game bird or fish stocking and biological control programs. Careful comparisons of successes versus failures for such systems could reveal occasional mismatches between invasion success and predictions based on niche requirements evaluated in the sites of origination. Such mismatches could provide presumptive cases of rapid niche evolution during establishment.

To use an invading species as a crisp "test" of theories of niche conservatism versus evolution requires that one have a handle on a number of things, many of which may be absent for particular systems. Ideally, one would know (1) the site of origin of the initial propagule, (2) the degree of genetic variability in the initial propagule for ecologically relevant traits, (3) the number of individuals contained in the original propagule, and (4) the magnitude of the difference in niche requirements between the ancestral environment and the site of invasion. It is plausible that such data could be gathered for systems in which invasions are deliberate, as in biological control efforts. For accidental introductions, one must make inferences on the basis of limited information for each of these desiderata, which makes testing theory more challenging.

Another complication is that a full characterization of the conditions for evolutionary rescue via niche evolution requires that one be able to specify the genetic architecture of the traits that are under selection and can influence absolute fitness. This warrants much more study, both theoretically and empirically. For instance, there does not appear to be a consistent effect on heritability of exposure to novel environments (Hoffmann and Merila 1999). We recognize the importance of characterizing the detailed genetic underpinnings of niche traits (e.g., major vs. minor genes; genetic correlations and epistasis among distinct niche traits), but it goes beyond the scope of this chapter to treat this issue beyond this bare mention.

Evolution and Rate of Spread in Homogeneous Landscapes

Given that a population becomes established, it may then begin to spread. In a homogeneous environment, and with random movement, a general rule for spread is that the edge of the invading species' range will move across space with a velocity equal to $v = c(rD)^{1/2}$, where r is the intrinsic rate of increase when a population is rare (a mean absolute fitness), D is the root-mean-squared distance of movement (a diffusion coefficient) (Okubo and Levin 2001), and c is a proportionality constant. According to Fisher's fundamental theorem, mean fitness should increase at a rate that is proportional to the variance in fitness, or $dr/dt = \sigma^2{}_r$ (for simplicity, assuming a simple clonal model; Crow and Kimura 1970, p. 10).

We can use these equations to make a prediction about evolution and how it accelerates the rate of invasion: the instantaneous acceleration in invasion due to evolution by natural selection is

$$dv/dt = q(r)^{-1/2}\sigma_r^2$$

where q is a proportionality constant. The acceleration in invasion is directly proportional to variance in fitness. Moreover, the acceleration is particularly pronounced when the initial rate of increase is low. Hence, the lag observed in many empirical studies of invasion (which is tantamount to an acceleration in the rate of invasion) could well reflect the fine-tuning of adaptation to novel environments.

Anthropogenic forces can lead to directional changes in environments. Theoretical studies by Lande and Lynch (e.g., Lynch and Lande 1993) suggest that there are maximal rates of environmental change outside of which it is difficult for evolution to permit species persistence. This general point is as pertinent to invading species as to resident natives. If invasion is occurring into environments undergoing anthropogenic change, an ability to evolve rapidly may determine whether or not the invasion is ultimately successful.

The Evolutionary Ecology of Invasion into Heterogeneous Landscapes

Most invading species enter landscapes that are spatially heterogeneous, including some habitats with conditions within their niche and others with conditions outside it (With 2002). The spatial configuration of these habitats within the landscape, and how they are coupled via dispersal, potentially have very important influences on the eventual spread of the invading species (Shigesado and Kawasaki 1997). Garcia-Ramos and Rodriguez (2002) recently described a model of invasion by a species into an environment with a smooth environmental gradient, which incorporated population dynamics along with adaptation to a clinally varying phenotypic optimum. Here, we discuss complementary models that focus on invasion into landscapes with discrete and distinctly different habitats.

A species that becomes established in a source habitat with conditions well within its ancestral niche may then have the opportunity to send out a recurrent rain of propagules into other habitats that are initially not within its niche. There may be many more sites available outside the niche than within it. If the species can adapt to these sites so that it persists at one of them, it can then spread among them all. What are the constraints on adaptive evolution in these sink habitats, and how is adaptation there influenced by immigration from the source habitat? It is of particular interest to compare adaptation when sinks are mild with adaptation when they are harsh.

Theoretical studies in recent years have clarified the diverse ecological and genetic influences of dispersal on local adaptation and niche evolution in sink habitats (Holt and Gaines 1992; Hedrick 1995; Kawecki 1995, 2000, 2003; Holt 1996; Holt and Gomulkiewicz 1997a,b; Kirkpatrick and Barton 1997; Gomulkiewicz et al. 1999; Case and Taper 2000; Ronce and Kirkpatrick 2001; Tufto 2001; Kawecki and Holt 2002; Lenormand 2002; Holt et al. 2003, 2004a,b). It is now recognized that there are four distinct mechanisms involved when considering the evolutionary implications of dispersal and immigration in heterogeneous landscapes: (1) opportunities for exposure to alternative environments without risking overall extinction; (2) the provisioning of genetic variation on which natural selection can act; (3) the swamping of gene flow by recurrent immigration; and (4) shifts in population size, which can affect selection if fitnesses are density-dependent. Here we consider each of these mechanisms in turn as they pertain to invasion by an exotic species.

Testing the waters

If an exotic species can persist in one site, then emigrants from that site can repeatedly "test" alternative sites by sending out colonizing propagules. Imagine that emigration from the source habitat is sporadic. If p is the probability per colonization bout that a given propagule will persist and adapt in a particular sink habitat patch, then if there are n independent colonizing events, the probability that at least one of them will be an evolutionary and ecological success is

$$1 - (1 - p)^n$$

Figure 10.6 shows a theoretical example of the probability of eventual adaptation and invasion as a function of the initial degree of maladaptation to the sink habitat for four different numbers of independent colonizing events (n) for immigrants drawn from a specific established source population. The n =

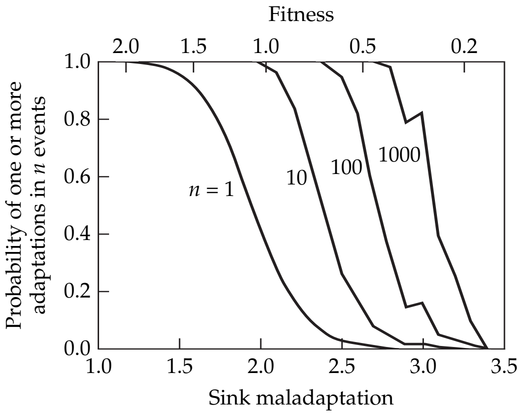

Figure 10.6 Propagule pressure facilitates persistence and adaptation in sink habitats. The graph shows the probability of persistence and adaptation in one or more colonizing episodes (for $n = 1$ to 1000) as a function of degree of maladaptation to the sink habitat. Other parameters are as in Figure 10.3, except that the monogamous mating system was used, assuming eight births per pair. The harsher the sink, the less likely one is to see adaptation over a long time period (1000 generations in this case). However, for more moderate sink habitats, recurrent invasion attempts can permit niche evolution to occur, leading to successful establishment in the initially unfavorable habitat. [At high values of n, the curves are close to 1 unless p is very small, which means that the initial maladaptation is very severe. Since p was determined by simulating a number of populations (up to 11,000) and dividing the number that persisted by the number simulated, there is some random variation in p, especially for small p (since in these cases very few populations persisted). This variation in p translates into a much greater variation in $1 - (1 - p)^n$ for large n. This accounts for the kinks in the $n = 100$ and $n = 1000$ curves (and to a much lesser extent in the other two curves). All result from the fact that there were slightly more populations persisting at a maladaptation of 3.0 than at 2.9 (19 versus 17 out of 11,000), going against the decreasing trend. However, the difference in these numbers is less than half the expected standard deviation of each.]

1 curve was obtained using the individual-based model to calculate the probability of adaptation and survival for a single colonizing event (giving p). The other curves were calculated using these p values and the formula for successful adaptation and establishment after n colonization attempts, $1 - (1 - p)^n$. The basic insight of this figure is that if an exotic species establishes a foothold in one habitat, it can then repeatedly send out propagules into other habitats, in effect providing repeated evolutionary "trials" in the novel environment.

Some plausible empirical examples of this phenomenon are provided by Harrison et al. (2001), who demonstrate that invasion of non-native plants into patches of serpentine soil is greatest in small patches; these authors provide suggestive evidence that the non-native species in these small patches show signs of incipient local adaptation. They argue that this enhancement of local adaptation in smaller patches reflects the greater potential rate of input of seeds from external sources into smaller patches, which in effect are "all edge." These observations could also reflect the following mechanism.

Gene flow provides adaptive genetic variation

Recurrent immigration can facilitate adaptive evolution by an invading species to a novel environment via the infusion of novel variation. Grant et al. (2001) describe how on the Galápagos island of Daphne Major, a population of the large ground finch (*Geospiza magnirostris*) was established by a single pair of individuals. Despite the extreme bottleneck at the time of establishment, heterozygosity remained roughly constant over the next 15 years, and allelic diversity doubled. Grant et al. (2001) suggest that the reason genetic variation was retained was that after its founding, the population continued to receive immigrants at a low rate from several other islands. This infusion of variation may have permitted an observed evolutionary step-function shift in beak shape due to selection. Similarly, Keller et al. (2001) described a population bottleneck in an insular population of song sparrows (*Melospiza melodia*), in which they found that genetic diversity rapidly regained pre-bottleneck levels within a few years after the crash due to a low level of immigration (about one bird every generation or two—a level of immigration that in less intensely studied populations would be almost impossible to detect). Gomulkiewicz et al. (1999) provide a model of single-locus evolution that formalizes this idea. In general, in low-density populations, immigration (which can draw on the variation maintained in abundant populations) provides a much more potent mechanism for providing variation than does mutational input.

Gene flow can hamper selection

A familiar idea in evolutionary biology is that gene flow can swamp local selection (Antonovics 1976; Hedrick 1985). For instance, Kirkpatrick and Barton (1999) analyzed a model of selection on a quantitative character along a cline in a phenotypic optimum in which local fitness determines population size. Gene flow from well-adapted, abundant populations into poorly adapted, scarce populations impedes selection in the latter and could lead to a stable distributional limit along an environmental gradient. This outcome is more likely if the gradient in fitness is sharp, so that dispersal mixes populations with substantially different optima.

Kirkpatrick and Barton's (1999) model assumed that genetic variance was fixed. If instead, genetic variance tends to increase in marginal populations (which itself might result from gene flow, as we saw above), then it becomes considerably harder for gene flow to prevent continued adaptation, and indeed, gene flow, instead of permitting a stable range margin, may lead to an evolutionary advance into novel terrain (Barton 2001; I. Filin, personal communication). Holt et al. (2003) explored an individual-based model of adaptive evolution in a sink habitat, with unidirectional migration from a source, comparable to the model described in Box 10.1. We demonstrated that an increase in the number of immigrants can increase the rate of adaptation to the sink habitat, and argued that this increase in part reflects the greater probability of drawing on genetic variation generated and maintained in the source habitat.

After the initial stage of adaptation to the new habitat, however, the perfection of local adaptation is hampered by continued migration from the source. If the new habitat is widespread, then following adaptation to any one patch of this habitat, the species could spread throughout an array of similar patches.

Over time, immigration from the initial source would become quantitatively trivial relative to the *in situ* production of these new populations, and gene flow from the source would have little or no influence on the maintenance and continued improvement of adaptation in the new habitat. With distinct habitats, stable maladaptation is also more likely if the sink habitat is relatively small relative to the source. We might predict that gene flow is less likely to hamper evolution in a widespread sink habitat to which the species is mildly maladapted than in a harsh sink because the fitness differences experienced by immigrants from the source are reduced in the former case, and more individuals are likely to be maintained there.

Immigration can alter local fitnesses

Holt and Gomulkiewicz (1995) and Gomulkiewicz et al. (1999) explored models for a "black-hole" sink, to which there was recurrent immigration from a source, but no backflow to the source from the sink. If we consider a single mutant that arises in such a sink habitat, it should increase in relative frequency if and only if it has an absolute fitness exceeding 1 (Gomulkiewicz et al. 1999).

If fitnesses are density-dependent, then changes in population size can affect the fate of favorable mutations. Immigration typically boosts population size, at least in simple models (e.g., Holt 1983); if there is negative density dependence (e.g., due to exploitation of a resource present in limited supply), then this increased abundance will lower average fitnesses. If there is negative density dependence in the sink habitat, adaptive evolution occurs most rapidly at an intermediate rate of immigration (Gomulkiewicz et al. 1999). The reason is that if immigration is very low, little variation is drawn in each generation from the source habitat, and so little variation is available for natural selection in the sink. Conversely, if immigration is high, numbers are boosted and, because of negative density dependence, fitnesses are lowered, reducing the likelihood of spread of favorable alleles. An intermediate rate of immigration appears to be optimal for adaptive evolution to harsh, novel environments, provided that density dependence is important at low initial densities.

This becomes even more likely if there are Allee effects at low densities. For instance, in very low-density sink populations, fitnesses may be further reduced because it is difficult for individuals of different sexes to find each other to set up mating pairs. An increase in immigration rate can boost local population size, alleviate Allee effects, and thereby indirectly facilitate adaptation to the sink environment (for details, see Holt et al. 2004b).

There is a temporal signature of niche evolution in a heterogeneous landscape. As discussed in more detail in Holt et al. (2003), in models of adaptation to sink habitats, given recurrent immigration from source habitats, one often observes a punctuational pattern, in which a population stays low in numbers and maladapted to the sink, often for long periods, and then undergoes a rapid increase in both adaptation and population size. This pattern could be expressed as a substantial lag in the spread of the invasion across space. A retrospective study of invasion lags could identify potential cases of niche evolution. If such evolution has occurred, then (1) one should be able to find environmental differences between the sites of original introduction and the sites in which spread later occurred, (2) there should be genetic differences between the original sites and the sites of later invasion, and (3) reciprocal transplants should show evidence of local adaptation. (Predictions 2 and 3 require that the evolution of adaptation to the novel environment not lead to significant gene flow back into the original site of introduction; Ronce and Kirkpatrick 2001.)

In invasion biology, models of evolution in sink habitats such as that sketched above could pertain to two distinct scenarios: evolution in a heterogeneous landscape, with initial establishment in a single habitat and subsequent spread to other habitats (our focus above), or repeated inputs of propagules drawn from the ancestral species range (we thank Jeb Byers for this observation). There is a potentially important difference between these two scenarios. Habitats within a heterogeneous landscape are likely to be correlated in significant ways—ways that are absent, on average, when one instead contrasts these initially unfavorable habitats with the sites of origination. For instance, an invader might be able to persist in a local site with disturbance, where certain native competitors and predators are absent or their effects are reduced. However, this site is likely to share climatic variables with a broader landscape, and also to be exposed to various natural enemies (e.g., mobile consumers that are habitat generalists). Once established in a disturbed site, the invader can then, in the fullness of evolutionary time, adapt to these other ecological factors. This in turn may make it more likely to invade (with niche evolution) sites in the landscape where colonization attempts by propagules from the ancestral range will almost surely fail. This scenario in effect permits a species to "bootstrap" its way through niche space (Holt and Gaines 1992) by gaining an original toehold in one habitat, from which it can spread as it evolves.

All these analyses become more complicated (and in interesting ways) if there is "backflow" from sinks to source habitats (see, e.g., Holt 1997; Kawecki and Holt 2002; Kawecki 2004). If adaptive trade-offs exist between habitats, then improvement in one comes at a cost of adaptation to the other. In this case, evolution in the habitat of initial colonization may make subsequent adaptation to other habitats more difficult and even lead to a kind of evolutionary "trapping" of a species in a limited habitat range (Ronce and Kirkpatrick 2001; Kisdi 2002; Holt 2003).

Conclusions

Boxes 10.2 and 10.3 summarize some key conclusions that emerge from considering invasions in the context of evolutionary theories of niche conservatism and evolution. We conclude this chapter with some speculations about which species are most likely to exhibit rapid niche evolution in the course of invasions.

BOX 10.2 *Key Insights from Evolutionary Theory*

1. The contingent details of genetic variation, evolution, and demographic stochasticity add considerable unpredictability to invasion success.
2. Propagule number influences the likelihood of invasion per colonizing episode via an interplay of adaptive evolution and demographic stochasticity. Propagules with more individuals provide more genetic variation drawn from the source, and also provide a longer window of opportunity for adaptive evolution to rescue a declining population from extinction. Consequently, predictive invasion models based purely on ecology (assessing niche requirements in the area of origin and ignoring the potential for evolution in the novel environment) should be more accurate for invading propagules containing few individuals.
3. In spatially heterogeneous environments, after the successful establishment of an invader in one habitat, evolution can then influence its spread into other habitats, either promoting or impeding such spread.
4. Migration has multiple effects on niche evolution:
    - It provides opportunities for evolution by sustaining local populations in sites outside the initial niche of the species (sink habitats).
    - It increases local abundances, potentially altering local fitnesses via density dependence and enhancing opportunities for local mutational input.
    - It introduces genetic variation from the source population.
    - It dilutes locally adapted gene pools, hampering adaptation.

    The relative importance of these effects can change in a time-dependent manner through the historical process of adaptation to a novel environment.
5. Recurrent migration provides repeated evolutionary trials for adaptation to a novel environment.
6. If colonization is rare and involves only propagules small in number, invasion usually occurs only within the preexisting niche. By contrast, if colonization is frequent and propagule numbers are large, niche evolution can occur.
7. Niche evolution is more likely if the novel environment is not too different from the species' fundamental niche. By contrast, adaptation to strongly maladaptive environments should be extremely slow.
8. Evolution along gentle environmental gradients is more rapid than across abrupt environmental transitions.
9. Long periods of stasis are possible before niche evolution occurs, and often the evolutionary shift is abrupt when it occurs.
10. Temporal environmental variation can increase the probability that niche evolution will occur, particularly when the variation is strongly autocorrelated.
11. Most traditional models of community assembly assume that species have fixed properties. Because community assembly consists of repeated invasion attempts by multiple species, theories of niche conservatism help characterize when purely ecological approaches should suffice. In particular, standard ecological approaches should work best when colonization episodes are infrequent and propagules are small in number, and when fitness dif-

BOX 10.2 *(continued)*

ferences between source and target communities are either minor or large, and temporally stable.

12. Adaptation to one habitat may lead to the evolutionary "pinning" of invasions in space if there are strong adaptive tradeoffs between the site of introduction (which will be the principal focus of initial adaptive evolution for an invader) and other habitats elsewhere in a landscape or geographic region.

As noted above, Holt et al. (2004b) recently argued that in populations that show Allee effects at low densities (e.g., due to the existence of distinct sexes), immigration can facilitate adaptive evolution in sink habitats because an increase in immigration typically increases population size. Given an Allee effect, at low densities, an increase in abundance *increases* individual fitness. This makes it more likely that alleles with small to moderate positive effects on fitness will yield an absolute fitness greater than unity, and so can be retained by selection. Other life history factors can also influence the probability of adaptation to novel environments. For instance, Kawecki (2003) recently suggested that in species without male parental care, female dispersal is more likely than male dispersal to lead to niche evolution. In this case, male dispersal mainly increases gene flow from source populations without enhancing local recruitment, whereas female dispersal can bolster local recruitment (with no more gene flow than for an equivalent amount of male dispersal), which can substantially affect the likelihood of adaptation to the sink. Thus, if niche evolution is required for an invading species to adapt and spread in a heterogeneous landscape, this process may be more likely to be observed for species with female-biased dispersal (or at least not strongly male-biased dispersal).

BOX 10.3 *Using Invasions as Critical Tests of Niche Evolution Theory: A Summary*

1. Few data exist to test many of the theoretical predictions for niche evolution, since what is required is a contrast between successful and failed invasions, and the latter are rarely recorded.
2. If retrospective analysis shows that many invasions stem from infrequent introductions of low-abundance propagules into harsh environments (as assessed by the niche properties in the ancestral range), then that finding would cast considerable doubt on the applicability of these theories.
3. If invasion lags involve adaptation to novel habitats, then the length of lag time should be positively correlated with the degree of difference between the novel and ancestral environments.

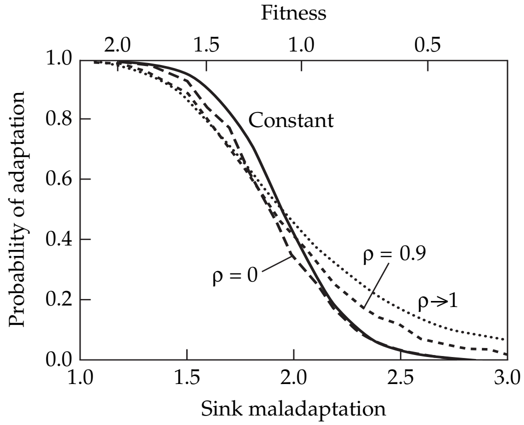

Figure 10.7 Probability of adaptation under constant conditions and with random variation in the degree of maladaptation to sink habitats (compared with the source optimum), with coefficient of variation (cov) = 0.2 and autocorrelation coefficients (ρ) of 0, 0.9, and approaching 1. The solid line denotes a constant environment. Other parameters and mating system are as in Figure 10.6. As noted in the text, this figure describes the probability of adaptation for a single bout of colonization. Autocorrelated variation in the degree of maladaptation facilitates adaptation to harsh sinks and makes adaptation less likely in sinks that are only slightly maladaptive (see also Holt et al. 2004a).

Recently we (Holt et al. 2004a) have argued that in some circumstances, autocorrelated temporal variation in a sink (e.g., in the degree of maladaptation experienced by immigrants) can facilitate adaptive evolution. If there are transient favorable periods during which the local population can grow, it can better escape the inhibitory effects of gene flow, permitting its numbers to grow even further. Temporal variation may also facilitate adaptive evolution in a sink even if there is no recurrent gene flow. In Figure 10.7 we revisit the situation explored in Figure 10.6 ($n = 1$ curve), in which we examined the probability of adaptation for one-time colonizations of empty sinks. Here, we assume that the local degree of maladaptation is described by a first-order autoregressive Gaussian process with a mean equal to the abscissa (which means that the degree of maladaptation experienced will sometimes be greater and sometimes less than the average degree of maladaptation, but the net effect will be no net change in the average degree of maladaptation experienced over time), and an autocorrelation coefficient of ρ. In sink environments that are on average quite maladapted, strongly autocorrelated variation can substantially enhance the probability of adaptation, and thus of invasion out of the initial source habitat.

An explanation for this comes from Jensen's inequality. Note that the functional form describing the probability of adaptation as a function of the degree of maladaptation in a constant environment is sigmoidal and is concave upward for harsh sinks (viz., where the initial degree of maladaptation faced by an immigrant propagule is large). If the autocorrelation coefficient approaches 1, this is in effect the same as imagining that an array of patches is available, with a fixed (Gaussian or normal) distribution among them in degrees of maladaptation. At high degrees of maladaptation, averaging over the functional form that describes the probability of adaptation over a given time horizon, as a function of the degree of initial maladaptation, leads to an expected value greater than the function evaluated at the average value. Note that the opposite is true at low degrees of maladaptation.

Thus, temporal variation in highly suboptimal sink habitats can make invasions more probable if there are at least some periods in which populations can adapt, persist, and then spread. Hoffman and Hercus (2000) argue that evolutionary patterns of diversification that show the greatest magnitude of adaptive evolution are observed in environments that are intermittently stressful. The causal mechanisms they suggest are somewhat different from those we suggest (e.g., they posit that stress could reduce gene flow), but the pattern they outline matches expectations from the theory presented here. The bottom line is that invasions into disturbed, temporally unstable environments may be facilitated for evolutionary as well as ecological reasons.

Invading species, we suggest, provide potential systems for testing many of these recent theoretical ideas about how demography can constrain (or, alternatively, at times facilitate) niche evolution. Levin (2003) has similarly suggested that invading species provide potential tests for understanding ecological speciation. Ecological speciation, he suggests, involves two stages: the colonization or invasion of a new habitat, and a subsequent process of selection on adaptation that refines the genotypic and phenotypic composition of the population to fit it better into its novel environment. Speciation can arise as a by-product of such selection.

Another issue to which we cannot do justice here is that dispersal itself is likely to evolve in a novel environment. In a landscape comprising a mix of good and bad habitats, if the latter are sufficiently bad, then selection should act on dispersal so that such habitats are avoided. Temporal variation can permit the evolutionary maintenance of dispersal, even into sink habitats. Evolutionary branching can occur so that a polymorphism in dispersal arises, with low-dispersal individuals concentrated in the habitat that initially has the higher carrying capacity and high-dispersal individuals concentrated in the lower-quality habitat (McPeek and Holt 1992; Mathias et al. 2001). This sets up an interesting situation in which, if a mutant arises that improves fitness in the lower-quality habitat, the population is preadapted to spread quickly over a much larger landscape.

Finally, our discussion has focused closely on evolutionary dynamics within invading species. More broadly, it is important for these microevolutionary processes to be embedded in a community context. Stable range limits often involve interactions with other species, including coevolutionary dynamics (Case et al. 2005). Success and failure in invasions may frequently reflect differences in the biotic environment experienced by invaders from that in their ancestral communities. A species that enjoys an escape from specialist natural enemies in a novel environment may be able to tolerate abiotic conditions from which it is excluded in their presence. If the species can persist, it can then adapt to suites of environmental factors that were originally outside its evolutionary repertoire.

In conclusion, almost all the processes studied by evolutionary biologists—the evolution of local adaptation versus generalized phenotypes, the evolution of dispersal, even mutational pressures—are potentially relevant to understanding the capacity of exotic species to persist in and invade novel environments. We have argued that a particularly pertinent area of evolutionary theory is that concerned with the evolution of the niche itself, because this abstract character describes the range of environments in which a species can persist, and thus defines the potential domain into which an exotic species can expand. An important and largely unaddressed challenge is utilizing the myriad opportunities provided by exotic species for empirically testing the emerging theory of niche conservatism and evolution. The theoretical models we have surveyed provide some expectations regarding invasion dynamics. For instance, climate-matching and other descriptive niche models (e.g., Peterson 2003) should be most successful at predicting invasion success when overall propagule pressure is low. Invasion associated with evolutionary transitions may be particularly likely in heterogeneous landscapes, where a species may in effect encounter gentle gradients in conditions relative to the ancestral environment to which it is already adapted. Finally, if it turns out that ancestral niche requirements describe not only the circumstances in which an invading species is initially established, but also the eventual range it occupies, then it is likely that there are strong constraints (e.g., due to absence of suitable genetic variation) on the evolution of that species' niche. To address these hypotheses, we suggest that broad qualitative surveys of factors correlated with successes and failures of attempted invasions may reveal patterns consistent with niche evolution being involved in invasions. Beyond this, more refined tests of the theory would require quantitatively rigorous population models that describe in detail spatial variation in demography, genetic variation in niche traits, and how the selective environment differs between ancestral locales and the sites of invasion.

An increasing number of empirical examples demonstrate that evolution frequently is associated with invasions (e.g., Thomas et al. 2001; Sexton et al. 2003; Blair and Wolfe 2004; Cox 2004; Maron et al. 2004; Muller-Scharer et al. 2004). It is an open question how often the evolution of species' niches is directly responsible for invasion success in any of these examples. It is our hope that the perspective we have presented in this chapter will foster further empirical studies of this important question.

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Literature Cited

Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. International Journal of Plant Science 164 (Supp.): S165–S184.

Antonovics, J. 1976. The nature of limits to natural selection. Annals of the Missouri Botanical Gardens 63:224–247.

Antonovics, J., T. J. Newman, and B J. Best. 2001. Spatially explicit studies on the ecology and genetics of population margins. In J. Silvertown and J. Antonovics, eds. *Integrated ecology and evolution in a spatial context*, pp. 97–116. Blackwell, London.

Ashley, M. V., M. F. Willson, O. R. W. Pergrams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionary enlightened management. Biological Conservation 111:115–123.

Barrett, S. C. H., and B. C. Husband. 1990. The genetics of plant migration and colonization. In A. H. D. Brown, M. T. Clegg, and A. L. Kahler, eds. *Plant population genetics, breeding and resources*, pp. 254–277. Sinauer Associates, Sunderland, MA.

Barton, N. H. 2001. Adaptations at the edge of a species' range. In J. Silvertown and J. Antonovics, eds. *Integrating ecology and evolution in a spatial context*, pp. 365–392. Blackwell, London.

Blair, A. C., and L. W. Wolfe. 2004. The evolution of an invasive plant: an experimental study with *Silene latifolia*. Ecology 85:3035–3042.

Boulding, E. G., and T. Hay. 2001. Genetic and demographic parameters determining population persistence. Heredity 86:313–324.

Bradshaw, A. D. 1991. Genostasis and the limits to evolution. Philosophical Transactions of the Royal Society of London B 333:289–305.

Brown, R. L., and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. Ecology 84:32–39.

Burger, R., and M. Lynch. 1995. Evolution and extinction in a changing environment: a quantitative-genetic analysis. Evolution 49:151–163.

Burt, A. 1995. Perspective—the evolution of fitness. Evolution 49:1–8.

Byers, J. E., and L. Goldwasser. 2001. Exposing the mechanisms and timing of impact of nonindigenous species on native species. Ecology 82:1330–1343.

Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. American Naturalist 155:583–605.

Case, T. J., R. D. Holt, and M. McPeek. 2005. The community context of species borders. Oikos 108:18–27.

Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: Linking classical and contemporary approaches*. University of Chicago Press, Chicago.

Coope, G. R. 1979. Late-Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. Annual Review of Ecology and Systematics. 10:247–267.

Cox, G. W. 2004. *Alien species and evolution*. Island Press, Washington, DC.

Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of invasive species: causes and implications. In O. T. Sandlund, P. J. Schei, and A. Viken, eds. *Invasive species and biodiversity management*, pp. 103–125. Kluwer, New York.

Crow, J. F., and M. Kimura. 1970. *An introduction to population genetics theory*. Harper and Row, New York.

D'Antonio, C., L. A. Meyerson, and J. Denslow. 2001. Exotic species and conservation. In M. E. Soulé and G. H. Orians, eds. *Conservation biology: Priorities for the next decade*, pp. 59–80. Island Press, Washington, DC.

Duncan, R. P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced into New Zealand. The American Naturalist 149:903–915.

Fisher, R. A. 1958. *The genetical theory of natural selection*. Dover Publications, New York.

Gaggiotti, O. E. 2003. Genetic threats to population persistence. Annales Zoologici Fennici 40:155–168.

Garcia-Ramos, G., and D. Rodriguez. 2002. Evolutionary speed of species invasions. Evolution 56:661–668.

Gomulkiewicz, R., and R. D. Holt. 1995. When does evolution by natural-selection prevent extinction? Evolution 49:201–207.

Gomulkiewicz, R., R. D. Holt, M. Barfield. 1999. The effects of density dependence and immigration on local adaptation and niche evolution in a black-hole sink environment. Theoretical Population Biology 55:283–296.

Grant, P. R., B. R. Grant, and K. Petren. 2001. A population founded by a single pair of individuals: establishment, expansion, and evolution. Genetica 112–113:359–382.

Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology 66:25–35.

Grinnell, J. 1917. The niche-relationships of the California thrasher. Auk 34:427–433.

Hansen, T. F., and D. Houle. 2004. Evolvability, stabilizing selection, and the problem of stasis. Evolvability, stabilizing selection, and the problem of stasis. In M. Pigliucci and K. Preston, eds. *The evolutionary biology of complex phenotypes*, pp. 130–150. Oxford University Press, Oxford.

Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. Biological Conservation 100:45–53.

Hedrick, P. W. 1985. *Genetics of populations*. Jones and Bartlett, Boston.

Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: measuring rates of contemporary microevolution. Evolution 53:1637–1653.

Hoffman, A. A., and M. J. Hercus. 2000. Environmental stress as an evolutionary force. Bioscience 50:217–226.

Hoffmann, A. A., and J. Merila. 1999. Heritable variation and evolution under favourable and unfavourable conditions. Trends in Ecology and Evolution 14:96–101.

Holt, R. D. 1983. Models for peripheral populations: The role of immigration. In H. I. Freedman and C. Strobeck, eds. *Lecture notes in biomathematics*, pp. 25–32. Springer-Verlag, Berlin.

Holt, R. D. 1996. Demographic constraints in evolution: Towards unifying the evolutionary theories of senescence and niche conservatism. Evolutionary Ecology 10:1–11.

Holt, R. D. 2003. On the evolutionary ecology of species ranges. Evolutionary Ecology Research 5:159–178.

Holt, R., and M. Gaines. 1992. The analysis of adaptation in heterogeneous landscapes: Implications for the evolution of fundamental niches. Evolutionary Ecology 6:433–447.

Holt, R. D., and R. Gomulkiewicz. 1997a. How does immigration influence local adaptation? A reexamination of a familiar paradigm. American Naturalist 149:563–572.

Holt, R. D. and R. Gomulkiewicz. 1997b. The evolution of species' niches: a population dynamic perspective. In H. Othmer, F. Adler, M. Lewis, and J. Dallon, eds. *Case studies in mathematical modeling: Ecology, physiology, and cell biology*, pp. 25–50. Prentice-Hall, New Jersey.

Holt, R. D. and R. Gomulkiewicz. 2004. Conservation implications of niche conservatism and evolution in heterogeneous environments. In R. Ferrière, U. Dieckmann, and D. Couvet, eds. *Evolutionary conservation biology*, pp. 244–264. Cambridge University Press, Cambridge.

Holt, R. D., R. Gomulkiewicz, and M. Barfield. 2003. The phenomenology of niche evolution via quantitative traits in a 'black-hole' sink. Proceedings of the Royal Society of London B 270:215–224.

Holt, R. D., M. Barfield, and R. Gomulkiewicz. 2004a. Temporal variation can facilitate niche evolution in harsh sink environments. American Naturalist 164:187–200.

Holt, R. D., T. M. Knight, and M. Barfield. 2004b. Allee effects, immigration, and the evolution of species' niches. American Naturalist 163:253–262.

Huntley, B. 1991. How plants respond to climate change: migration rates, individualism, and the consequences for plant communities. Annals of Botany 67 (Supp. 1): 15S–22s.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposiums on Quantitative Biology 22:415–427.

Hutchinson, G. E. 1978. *An introduction to population ecology*. Yale University Press, New Haven.

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

Kawecki, T. J. 2000. Adaptation to marginal habitats: contrasting influence of the dispersal rate on the fate of alleles with small and large effects. Proceedings of the Royal Society of London, B 267:1315–1320.

Kawecki, T. J. 2003. Sex-biased dispersal and adaptation to marginal habitats. American Naturalist 162:415–426.

Kawecki, T. J. 2004. Ecological and evolutionary consequences of source-sink population dynamics. In I. Hanski and O. E. Gaggiotti, eds. *Ecology, genetics and evolution of metapopulations*, pp. 386–414. Elsevier, Burlington, MA.

Kawecki, T. J., N. H. Barton, J. D. Fry. 1997. Mutational collapse of fitness in marginal habitats and the evolution of ecological specialization. Journal of Evolutionary Biology 10:407–429.

Kawecki, T. J., and R. D. Holt. 2002. Evolutionary consequences of asymmetric dispersal rates. American Naturalist 160:333–347.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164–170.

Keller, L. F., K. J. Jeffery, P. Arcese, M. A. Beaumont, W. M. Hachachka, M. N. M. Smith, and M. W. Bruford. 2001. Immigration and the ephemerality of a natural population bottleneck: evidence from molecular markers. Proceedings of the Royal Society of London B 268:1387–1394.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. American Naturalist 150:1–23.

Kisdi, E. 2002. Dispersal: risk spreading versus local adaptation. American Naturalist 159:579–596.

Lambrinos, J. G. 2004. How interactions between ecology and evolution influence contemporary invasion dynamics. Ecology 85:2061–2070.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. Res. Popul. Ecol. 40:259–269.

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

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology and Evolution 17:386–391.

Lenormand, T. 2002. Gene flow and the limits to natural selection. Trends in Ecology and Evolution 17:183–189.

Levin, D. 2003. Ecological speciation: lessons from invasive species. Systematic Botany 28:643–650.

Levin, D., and K. Clay. 1984. Dynamics of synthetic *Phlox drummondii* populations at the species margin. American Journal of Botany 71:1040–1050.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

Lewontin, R. C. 1965. Selection for colonizing ability. In H. G. Baker and G. L. Stebbins, eds. *The genetics of colonizing species*, pp. 77–91. Academic Press, New York.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

Lyford, M. E., S. T. Jackson, J. L. Betancourt, and S. T. Gray. 2003. Influence of landscape structure and climate variability on a late Holocene plant migration. Ecological Monographs 73:567–584.

Lynch M, J. Conery, and R. Burger. 1995. Mutational meltdowns in sexual populations. Evolution 49:1067–1080.

Lynch, M. J., and R. Lande. 1993. Evolution and extinction in response to environmental change.In P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, eds. *Biotic interactions and global change*, pp. 234–250. Sinauer Associates, Sunderland, MA.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, and M. Clout. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:698–710.

Maguire, B. J. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. American Naturalist 107:213–246.

Maron, J. L., M. Vila, R. Bommarco, S. Elmendorf, and P. Beardsley. 2004. Rapid evolution of an invasive plant. Ecological Monographs 74:261–280.

Mathias, A., E. Kisdi, and I. Olivieri. 2001. Divergent evolution of dispersal in a heterogeneous landscape. Evolution 55:246–259.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 6:1010–1027.

Merila, J., B. C. Sheldon, and L. E. B. Kruuk. 2001. Explaining stasis: microevolutionary studies in natural populations. Genetica 112–113:199–222.

Muller-Scharer, H., U. Schaffner, and T. Steinger. 2004. Evolution in invasive plants: implications for biological control. Trends in Ecology and Evolution 19:417–422.

Nei, M., T. Maruyam, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution 29:1–10.

Okubo, A., and S. A. Levin. 2001. *Diffusion and ecological problems*. Springer-Verlag, New York.

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19:18–24.

Pease, C. M., R. Lande, and J. Bull. 1989. A model of population-growth, dispersal and Evolution in a changing environment. Ecology 70:1657–1664.

Peterson, A. T. 2003. Predicting the geography of species' invasions via ecological niche modeling. Quarterly Review of Biology 78:419–433.

Peterson, A. T., and R. D. Holt. 2003. Niche differentiation in Mexican birds: using point occurrence data to detect ecological innovation. Ecology Letters 6:654–664.

Peterson, A. T., J. Soberon, and V. Sanchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. Science 285:1265–1267.

Quinn, T. P., M. J. Unwin, and M. T. Kinnison. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced chinook salmon populations. Evolution 54:1372–1385.

Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112–113:183–198.

Rice, K. J., and N. C. Emery. 2003. Managing microevolution: restoration in the face of global change. Frontiers in Ecology and the Environment 1:469–478.

Ronce, O., and M. Kirkpatrick. 2001. When sources become sinks: Migrational meltdown in heterogeneous habitats. Evolution 55:1520–1531.

Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. Nature 392:491–494.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.

Sax, D. F., and J. H. Brown. 2000. The paradox of invasion. Global Ecology and Biogeography 9:363–371.

Schopf, K. M. 1996. Coordinated stasis: biofacies revisited and the conceptual modeling of whole-fauna dynamics. Paleogeography, Paleoclimatology, Paleoecology 127:157–175.

Sexton, J. P. J. K. McKay, and A. Sala. 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climate in North America. Ecological Applications 12:1652–1660.

Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176.

Shigesada, N., and K. Kawasaki. 1997. *Biological invasions: Theory and practice*. Oxford University Press, Oxford.

Stockwell, C. A., and M. V. Ashley. 2004. Rapid evolution and conservation. Conservation Biology 18:272–273.

Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology and Evolution 18:94–101.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature 411:577–581.

Tufto, J. 2001. Effects of releasing maladapted individuals: a demographic-evolutionary model. American Naturalist 158:331–340.

Veltman, C. J., and S. Nee. 1996. Correlates of introduction success in exotic New Zealand Birds. American Naturalist 147:542–557.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.

Whitlock, M. C., C. K. Griswold, and A. D. Peters. 2003. Compensating for the meltdown: the critical effective size of a population with deleterious and compensatory mutations. Annales Zoologici Fennici 40:169–183.

With, K. A. 2002. The landscape ecology of invasive spread. Conservation Biology 16:1192–1203.