CHAPTER 10

Metapopulation Perspectives on the Evolution of Species' Niches

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Abstract. The tapestry of the history of life reveals striking examples of both niche conservatism, and rapid niche evolution, where "niche" is used in the Grinnellian sense as that set of conditions, resources, etc. which permit populations of a species to persist in a locality without recurrent immigration. Recent years have seen the development of a rich body of theoretical studies aimed at understanding when one might expect niche conservatism vs. evolution in spatially and temporally heterogeneous environments. This literature has illuminated the role of many factors, such as genetic architecture, density dependence, and asymmetries in dispersal, in determining the likelihood of niche conservatism. However, most studies have assumed very simple spatial scenarios, such as a single source population (with conditions within a species' niche) supplying immigrants into a sink population (where conditions are outside the niche). In this contribution, after summarizing key insights from this prior literature, we will present the results of theoretical studies which examine how the spatial structure of the landscape can modulate the direction and pattern of niche evolution.

10.1 Introduction

The term "niche" refers to the range of conditions, resources – and indeed all biotic and abiotic factors – that permit populations of a species to persist (deterministically) in a given habitat without immigration. In effect, the niche is a mapping of population dynamics onto an abstract environment space (e.g., with axes of temperature, pH, food availability, predator density, etc.; Hutchinson 1958, Maguire 1973, Holt and Gaines 1992), emphasizing in particular the limits outside of which a species faces extinction. Formally, if environmental conditions in a given habitat are such that

the low-density intrinsic rate of growth r (instantaneous per capita birth rate – per capita death rate) is negative, then conditions by definition are outside the niche, and introductions of the species should fail. By contrast, introductions into a habitat with $r > 0$ should tend to increase. So the niche of a species in effect partitions the world into areas where it can persist, and areas where it faces extinction. (For a species with discrete generations, sources and sinks can be defined in terms of the average fitness at low density, with unity being the threshold.)

To a first approximation, the geographical distribution of a species should be determined by its niche (Pulliam 2000), as should its habitat distribution at a more local, landscape scale. Understanding niches is of great practical importance, for instance in predicting how changes in climate might lead to shifts in distribution, and changes in land use can lead to altered patterns of abundance on a landscape. But all such predictions – and the scientific literature is replete with them – rest on the assumption that species' niches remain unchanged, even as the world changes. Such evolutionary conservatism, or the lack of change in the niche in a heterogeneous world, is called "*niche conservatism.*"

The literature of evolutionary biology contains many examples that suggest niche conservatism, from short to long time scales (Bradshaw 1991, Wiens and Graham 2005). There are also many instances of rapid niche evolution, such as the evolution of antibiotic resistance in microbes, and the evolution of tolerance to heavy metal toxins. Understanding the factors that lead to niche conservatism, on the one hand, and rapid niche evolution, on the other, has been the focus of considerable theoretical attention and an increasing amount of empirical study (Holt 1996, Kawecki 2008). There are two circumstances in which one might look for niche evolution, or try to understand what leads to niche conservatism. First, in a spatially closed population (e.g., on an oceanic island), a temporal change in the environment can force a species to experience conditions outside its niche. Alternatively, in a spatially open population existing in a heterogeneous landscape, dispersal can take individuals out of habitats within the niche – source habitats – and place them into habitats outside the niche. This is a likely scenario at the edge of a species' range, for instance. Given genetic variation, evolution can potentially occur in both circumstances, so that sink populations can be transformed into source populations. Alternatively, even though genetic variation is present, sinks may remain sinks, and niche conservatism will be observed. The goal of theory is to provide insights into conditions under which each of these outcomes will occur.

Prior theory has largely focused on very simple landscapes, comprised either of species with random dispersal distributed over smooth gradients or a single source patch coupled by dispersal to a single sink patch. In this paper, we take steps towards examining niche evolution in more complex landscapes. We first review highlights (including previously unpublished results) from studies of models of niche evolution for sources and sinks coupled by dispersal, and then use these to motivate models for evolution in metapopulations comprised of two kinds of patches linked by dispersal.

We consider two limiting cases of a metapopulation. In both, the models track pres-

ence and absence of a species. The first is a "mainland-island" scenario of asymmetrical colonization. A species is established on a mainland, where it is adapted to one habitat type. The mainland population provides colonists onto islands made of the second habitat type, where the colonists are initially maladapted, and sufficiently so that the islands are sink habitats. In the absence of evolution, successful colonization is impossible. The question is how island area and distance influence colonization and extinction rates, taking into account the effects of selection and gene flow on adaptive colonization outside the niche. The second limiting case is that of classic metapopulation theory, which assumes we can ignore the details of spatial arrangements of the patches, and focus instead on the aggregate rates of colonization determined by average occupancy across the entire landscape.

10.2 Models for adaptive colonization into sink habitats

Theoreticians often assume that rates of dispersal are fixed parameters (e.g., a constant diffusion parameter). In reality, dispersal rates can often be highly variable. For instance, physical transport processes (e.g., the wind) can fluctuate greatly in strength, and source populations for dispersal propagules (or dispersal vectors) may vary greatly in density. Boreal forest bird species such as pine siskins and crossbills may be absent from the southern United States for many years, and then experience a large pulse of movement southward after failure of their food supply. The bottom line is that dispersal onto distant islands or habitat patches can be episodic, so that there is a substantial time lag between successive colonizing attempts. This assumption is implicit in classic island biogeography theory and much of metapopulation theory. We start with an island biogeographic perspective, which assumes that species persist and are at evolutionary equilibrium on a mainland, but colonize onto islands where persistence is enhanced by adaptive evolution to conditions on the islands. We then will move to a heterogeneous metapopulation, where colonization in effect is among islands in an archipelago or patches in a landscape.

We consider first a single episode of attempted colonization onto an island, where the colonists find themselves "outside the niche," hence declining in numbers. The fate of this population depends on the outcome of a race between demography and evolution. Without genetic variation, extinction is inevitable. If genetic variation is present in the dispersal propagule, or generated *in situ* via mutation, natural selection may increase the growth rate sufficiently to make it positive in the novel environment. However, before this can occur, the population might reach low levels at which it risks extinction. Fig. 10.1 schematically shows the expected pattern of population growth.

A quantitative genetics model for adaptation to a sink habitat

Gomulkiewicz and Holt (1995) (see also Holt and Gomulkiewicz 1997) provided a first step towards examining this process. They assumed that a single quantitative trait is undergoing selection. At each time step, the population declines (or grows)
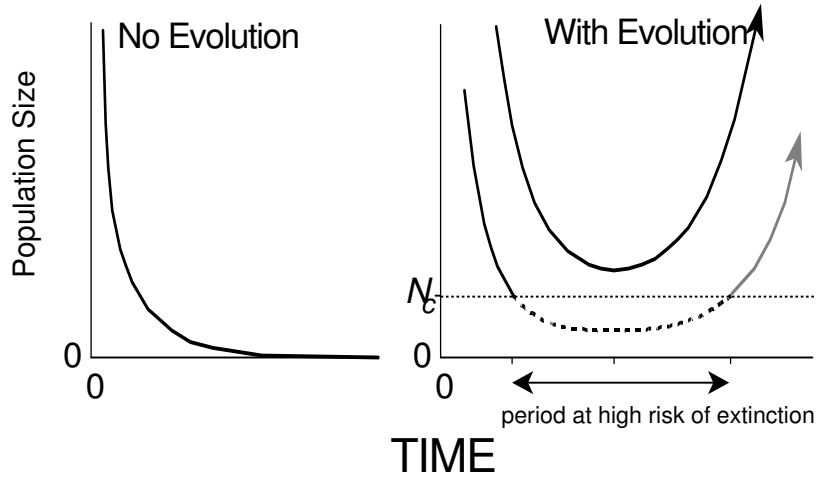
Figure 10.1 Population dynamics for introduction into a sink habitat. Left panel: Without evolution, extinction is ensured. Right panel: With evolution, the population may persist. However, if a population starts at low densities, and/or adapts slowly, it might spend time at very low densities, where it risks extinction. Adapted from Gomulkiewicz and Holt (1995).

multiplicatively. The rate of growth itself changes over time, due to a single quantitative trait that is under selection in the novel environment. They assumed that evolution fits the standard assumptions of quantitative genetics (Falconer 1989). The model is deterministic in both its demography and genetics; to heuristically address extinction, they assumed that there is a critical population size, N_c, below which a population is quickly vulnerable to extinction (e.g., due to Allee effects, or because of demographic stochasticity). Here we describe the assumptions of the model and some conclusions, and refer the reader to the original papers for derivations.

The basic scenario is depicted in Fig. 10.2. There is a single phenotypic trait z. On the mainland, stabilizing selection occurs, and genetic variation is maintained at a constant level (presumably by mutation, though this is implicit, not explicit). The colonizing propagule thus should have a distribution (assumed to be normal, which is typical for a quantitative trait) around the optimum on the mainland, d_0. P is the phenotypic variance of this distribution, which includes non-genetic sources of variation among individuals, such as developmental noise, as well as heritable variation. On the island, there is also potentially stabilizing selection on the trait, but around a new optimum (scaled to 0 in the figure; fitness is given by the dashed line). The
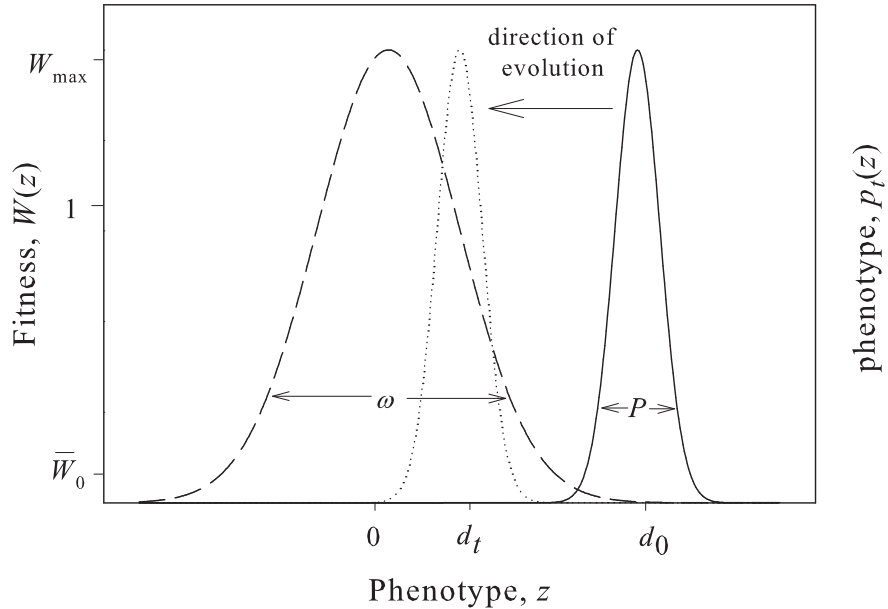
Figure 10.2 Evolution of Gaussian character z in a population with discrete generations. The solid line is the initial phenotypic distribution, the dashed line is the fitness function, and the dotted line is the phenotypic distribution after a period of evolution. The initial fitness is low, so the population size will decline initially, but could rebound once evolution has occurred, if the population avoids extinction after the initial decline. Adapted from Gomulkiewicz and Holt (1995).

fitness of an individual with phenotype z in the sink is given by a Gaussian function

$$W(z) = W_{\max} \exp[-z^2/2\omega], \tag{10.1}$$

where $W_{\max}$ is the fitness an individual enjoys when it has the optimal phenotype on the island, and ω is an inverse measure of the strength of selection. When ω is high, a small deviation of an individual's phenotype from the local optimum is not very costly; when small, selection severely acts against such individuals. The initial mean trait value of a group of colonists introduced onto the island is d_0, which means they are initially maladapted; the larger is d_0, the lower is their initial fitness. Directional selection acts on the colonists, pushing their mean phenotypic value in the direction of the local optimum, and so reducing their degree of maladaptation (measured by z). The rate at which this happens is determined by the character's heritability, h^2 (which we assume fixed; this is one of many assumptions relaxed in the individual-based models discussed below).

Because the average trait value of individuals in the colonizing propagule is well displaced from the island optimum, the initial fitness of the colonizers is assumed to be well below one (the criterion for a sink with discrete generations), and so the population initially declines towards extinction. Propagules that potentially could persist after a period of adaptation may nonetheless initially decline so much that they risk extinction. Gomulkiewicz and Holt (1995) developed a discrete-time, deterministic quantitative genetic model for a population initially declining, but adapting to a sink environment, which based on the above assumptions led to the following equations for coupled demographic and evolutionary change:

$$N_{t+1} = \bar{W}_t N_t,$$

$$d_{t+1} = kd_t,$$

$$\bar{W}_t = \hat{W} \exp\left[\frac{-d_t^2}{2(P+\omega)}\right].$$

(10.2)

Here,

$$\hat{W} = W_{\max}\sqrt{\omega/(P+\omega)}$$

(10.3)

is the population growth rate when the mean phenotype has reached the local optimum; this is less than the maximal possible growth rate because it reflects an average over the distribution of trait values, and this distribution at evolutionary equilibrium includes individuals with suboptimal phenotypes. The rate of evolution is determined by the quantity

$$k = \frac{\omega + (1-h^2)P}{P+\omega},$$

(10.4)

which can be viewed as a measure of evolutionary inertia. If heritability is very low, k is near unity, so the character changes very slowly; if ω is large, selection is weak, and again evolution is slow.

This pair of coupled difference equations can be solved in closed form, leading to

$$N_t = N_0 \hat{W}^t \exp\left[\frac{-d_0^2(1-k^{2t})}{2(P+\omega)(1-k^2)}\right].$$

(10.5)

One can then calculate a number of quantities, such as the combination of initial conditions and parameter values that lead an introduced population to experience times when its abundance is below N_c, and for those populations that do dip below this value, how long they will stay there. If a population is strongly maladapted to start with, its numbers will plummet, and even though it has the genetic potential to persist in the new environment, the model suggests it is highly likely to go extinct first. Populations that evolve slowly (high k) are also likely to go extinct, as are populations which are initially low in numbers (even if they are evolving rapidly). In effect, this exercise provides qualitative insight into the likelihood of adaptive colonization, as a function of the degree of maladaptation in the novel environment, and the number of immigrants, among other ecological and genetic factors.

Stochastic models

The above paragraph used the word "likely," which is strictly speaking inaccurate. The model is deterministic and treats N as a continuous variable, and so numbers will not actually reach zero. Ergo, no extinction. A rigorous analysis of extinction (i.e., $N = 0$) requires one to grapple with the fact that organisms are discrete, and births and deaths are probabilistic. This is a large and challenging problem. Holt and Gomulkiewicz (1997) used a branching process approach to examine this problem, assuming genetic variation at a single haploid genetic locus. They developed a probability generating function, and found that the qualitative conclusions drawn from the deterministic model are upheld. Recently, Orr and Unckless (2007) have developed stochastic models that also include novel mutations, and reached similar conclusions. But for stochastic models to be analytically tractable, they have to simplify many of the complex phenomena that occur in declining populations. When a population is declining towards extinction, while simultaneously evolving, many stochastic processes are at play at the same time. Genetic variation itself can be changing due to selection, and as numbers get small the vicissitudes of demographic stochasticity loom large. Gene frequencies and genetic variation change due to drift, and when multiple genetic loci are considered (as is appropriate for quantitative traits such as body size and thermal tolerance), linkage disequilibrium can shift stochastically. If populations decline slowly, mutational input can provide a significant source of genetic variation.

To develop an understanding of coupled evolutionary and demographic dynamics when all these processes are occurring at once, in previous papers we have reported the results of simulation studies based on individual-based models in which we track each individual and its genotype in source and sink environments (e.g., Holt et al. 2005). These models include all the above sources of stochastic variability. Here we just briefly sketch the assumptions of the models, and present a few results, that help motivate the metapopulation model presented below.

The basic life-history framework of these models is shown in Fig. 10.3. Individuals move synchronously through a series of life history stages. Selection occurs on a trait that influences juvenile survival, and density dependence is imposed as a ceiling number of breeding adults (K). In our genetic assumptions, we follow those used by Burger and Lynch (1995) in exploring evolution in a constantly changing environment. There are n loci that contribute additively to a single quantitative trait z, with free recombination. In the source, mutational input maintains variation (according to a continuum-of-alleles model), with a Gaussian distribution of mutational effects, and an environmental noise term (a zero-mean, unit-variance Gaussian random variable). Therefore, heritability emerges as an output of the model, rather than being a fixed quantity [as in the above model (10.1)-(10.4)]. Mutation can also occur (and at the same rate) in the sink. Juvenile survival is a Gaussian function of an individual's phenotype (z), with different habitats having different phenotypes at which survival reaches its maximum (so an individual adapted to the source generally has low survival in the sink). We allow the source population to reach an evolutionary

equilibrium, with an emergent heritability of the trait reflecting the balance between mutation, selection, and drift, and then we pluck a propagule of adults at random and place them as immigrants in the sink habitat. After doing this a large number of times, and across a wide range of parameter values, patterns emerge that characterize when one might observe colonization outside the niche.

Persistence in the sink requires adaptation, and because colonization is occurring outside the niche, and adaptation is not instantaneous, colonization attempts can readily fail. Fig. 10.4 shows examples of time-series of population size against time. In these examples, 64 individuals are introduced into the sink. Some attempted colonizations (the solid lines) fail, but others succeed (dashed lines), after an initial period of decline. Even though all colonizing propagules are drawn from the same type of source population, there is considerable heterogeneity among successful replicate colonizing episodes (see Discussion).

With such simulations in hand, we can quantify adaptive colonization as a function of the degree of initial maladaptation and the number of colonists in the initial propagule. The maladaptation is the difference between the phenotypic optima of source and sink, a larger value indicating a lower expected fitness of source individuals introduced into the sink. Fig. 10.5 shows two patterns, emphasizing the relationship between adaptive colonization and on one hand the harshness of the sink environment, and on the other the number of individuals in the colonizing propagule. In Fig. 10.5a (adapted from Holt et al. 2005), we depict the probability of adaptive colonization as a function of the degree of maladaptation experienced in the sink by immigrants drawn from the source, for three different propagule sizes (numbers of introduced individuals). In the figure the top axis translates maladaptation (the bottom horizontal axis) into fitness. Even in favorable environments inside the niche, where fitness exceeds unity at low densities, demographic stochasticity can doom small propagules, but large propagules should be able to establish with a probability near one. However, in unfavorable environments, where fitness is initially less than unity, in the absence of genetic variation extinction is ensured regardless of initial population size. Given that genetic variation is present (as in the examples of Fig. 10.4), adaptive colonization becomes possible. The harsher the sink environment, however, the less likely this will occur. Basically, there is a footrace between demography (pushing a population towards extinction), and evolution by natural selection (increasing fitness). When initial fitness is low, and propagule size is small to modest, demography will overwhelm evolution, and colonization will fail.

The larger the number of individuals, the greater the chance of adaptive colonization. Fig. 10.5b shows that the likelihood of persistence over a thousand generations (which essentially always requires adaptation to the sink environment) has a sigmoidal dependence upon the logarithm of the number of individuals introduced into the sink. Recent experiments using yeast introduced into experimental sink habitats (created by increasing the salt concentration of the medium to be outside the initial niche of the species) by Andy Gonzalez and Graham Bell at McGill University (pers. comm.) have demonstrated a sigmoidal dependence of population survival on the logarithm of initial numbers in a sink, consistent with the prediction of this

Individual-based Model

N_t parents   Schematic Life Cycle

Reproduction, f

$\Longleftarrow$ Random mating Stochasticity
$\Longleftarrow$ Mutation   (Genetic drift)
        (on gametes)

$N_t f$ offspring

Survival

$\Longleftarrow$ Viability selection Stochasticity
        (probabilistic)   (Genetic drift
                              +
                              demographic
                              stochasticity)

$N_t' = N_t f\overline{w}$
(expected)

$\Longleftarrow$ Immigration Stochasticity
                            (Genetic drift)

$N_t'' = N_t' + I$

$N_{t+1}=N_t''$ if $N_t'' < K$; otherwise
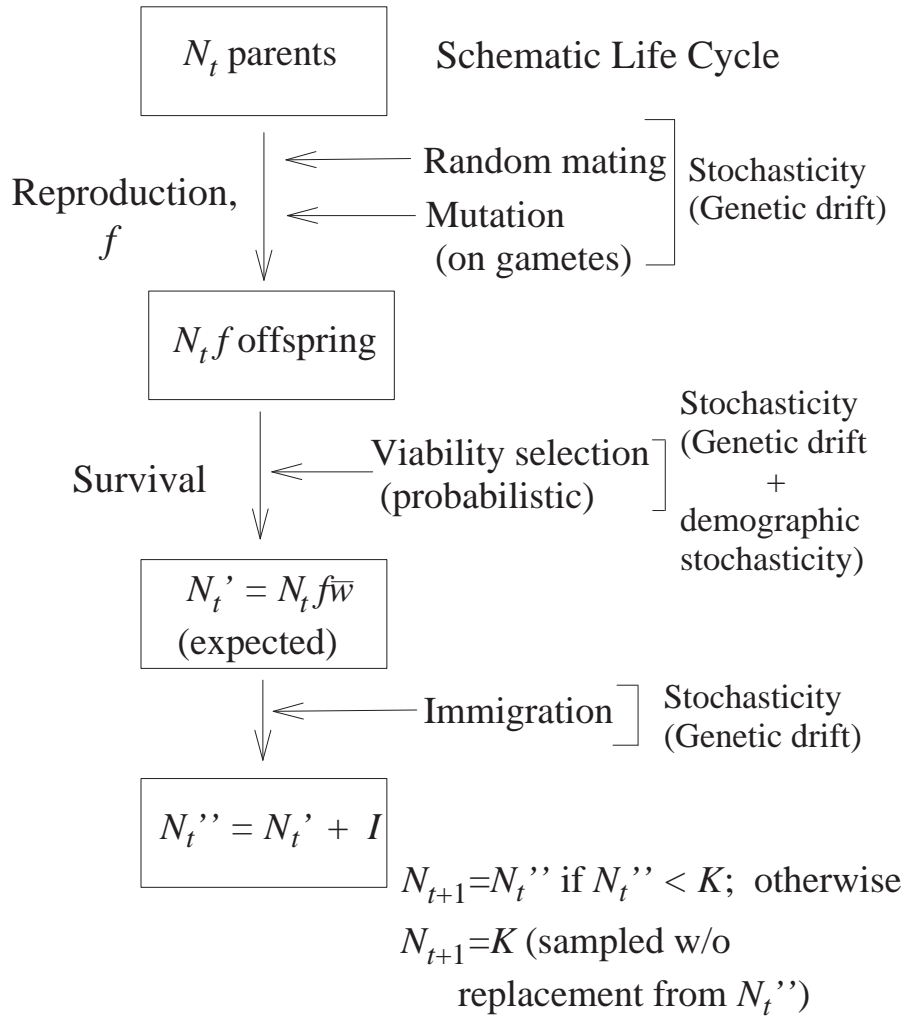$N_{t+1}=K$ (sampled w/o
        replacement from N_t'')

Figure 10.3 Schematic diagram of the life cycle in each habitat of the individual-based model, indicating the sources of stochasticity included. Note that migration from the source to the sink occurs before density regulation, and immigrants and residents have equal chances entering the mating pool.
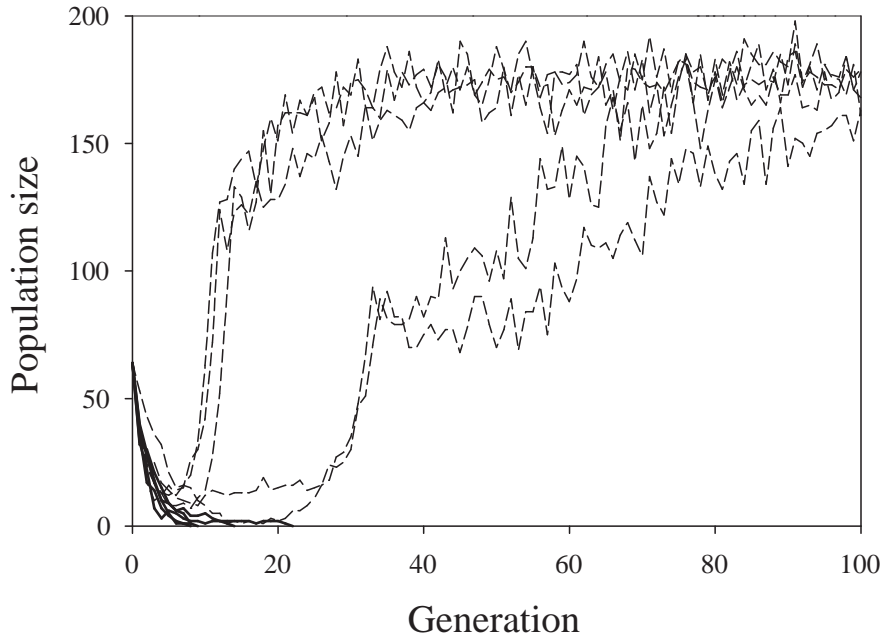
Figure 10.4 Sample trajectories for adult population size for populations introduced into a sink habitat. Initially, all populations decline in abundance, some going extinct (solid), but some rebounding (dashed). $K = 64$, mutational rate per haplotype = 0.01, mutational variance $\alpha^2 = 0.05$, strength of selection $\omega^2 = 1$, propagule size = 64; 4 births per pair. The difference between source and sink phenotypic optima is 2.5.

individual-based model. A variety of different assumptions about the genetic architecture underlying trait variation can also generate this relationship between initial population size and persistence (R. Gomulkiewicz, pers. comm.). A function that gives a good phenomenological fit to the output of these individual-based simulations is a logistic function of $\ln N_0$ and d_0:

$$\text{Prob}(\text{adaptive colonization}|N_0, d_0) = \frac{N_0^a}{N_0^a + a' \exp\{a''d_0\}} \qquad (10.6)$$

where a, a', and a'' are all positive constants.

Of course, if there are repeated attempts at colonization, as long as there is a non-zero probability of adaptive colonization, eventually adaptation to the sink will occur. If the probability of adaptive colonization per colonizing bout is p, the probability of successful colonization after n colonization attempts is $1 - (1 - p)^n$. In a mild sink, where initial fitness is not much below unity, p is not far below one, and adaptive colonization is likely over reasonably short time-horizons. But in a severe sink, where
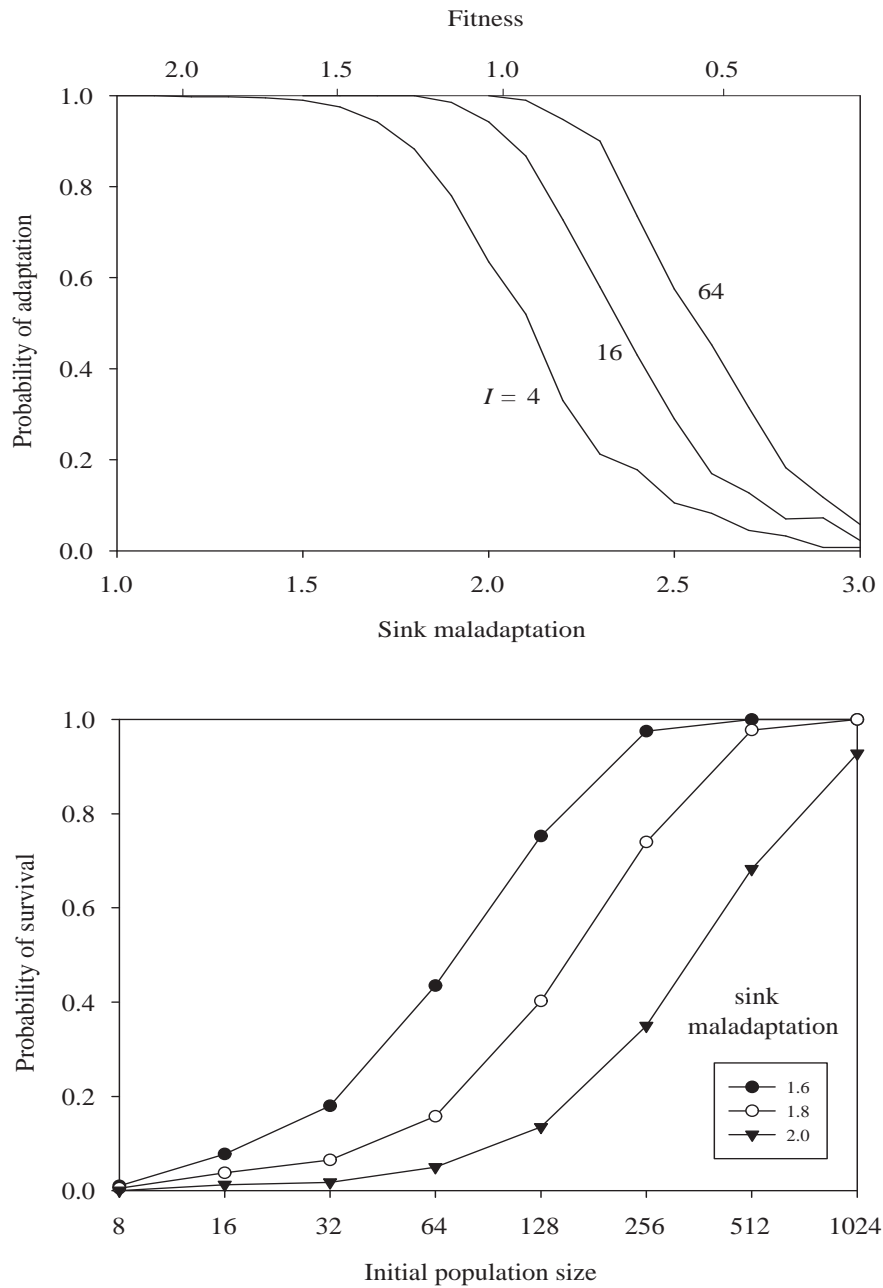
Figure 10.5 The probability of persistence and adaptation, as a function of (a)(top panel) degree of initial maladaptation in the sink habitat, for three different sizes of initial colonizing propagule, and (b)(bottom panel), initial population size. Other parameters as in Figure 10.4, except panel (b) has a fecundity of 2 rather than 4.

p is very low, there can be a very long lag before successful colonization occurs. Niche conservatism thus may not be absolute, but reflect quasi-equilibrial, long-term transients.

10.3 An island-mainland model with infrequent adaptive colonization

The bottom line is that in a metapopulation, in colonizing empty habitats outside the niche, higher propagule numbers, or an increase in the frequency of colonizing attempts, should facilitate adaptive colonization. This could lead to both distance and area effects on the rates of adaptive colonization. The number of colonization attempts into an island per unit time should decline with increasing distance from a source. The number of viable individuals in a colonizing propagule could also decline with distance (e.g., due to mortality in transit). The number of propagules landing on an island might increase with island size. Productive sources, or sources large in area, are more likely to be the progenitors of adaptive colonization into sink habitats, simply because more colonization attempts should emerge from such sources.

We can modify the familiar equilibrial model of island biogeography (MacArthur and Wilson 1967) to include adaptive colonization as follows (Holt and Gomulkiewicz 1997). Each island can be in one of three states: empty, recently colonized and maladapted, and adapted. The fraction of islands in each state are respectively P_0, P_m, and P_a. A simple dynamical model describing transitions among these states is:

$$\frac{dP_m}{dt} = c_m(1 - P_a - P_m) - EP_m - e_m P_m,$$

$$\frac{dP_a}{dt} = EP_m - e_a P_a. \tag{10.7}$$

where c_m is the rate of colonization, e_m is the rate of extinction of maladapted populations, e_a is the rate of extinction of adapted populations, and E is the rate at which maladapted populations become adapted. (The sum of the three fractions is 1, so $P_0 = 1 - P_m - P_a$.)

At equilibrium,

$$P_a^* = \frac{E}{e_a} P_m^*,$$

$$P_m^* = \frac{c_m e_a}{c_m(E + e_a) + (E + e_m)e_a}. \tag{10.8}$$

The total occupancy is $P^* = P_a^* + P_m^*$. The fraction of occupied islands that are adapted is $E/(E + e_a)$. Adaptation means that there will be genetic differentiation between the island and mainland populations, and so this quantity is the fraction of occupied islands that have endemic species. A little manipulation of (10.8) shows that adaptation increases occupancy if $e_a < e_m$, which makes intuitive sense. It is interesting that the degree of endemism on occupied islands is not affected by either the colonization rate, or the rate of extinction of maladapted populations, but only the

rate of evolution and the rate of extinction of adapted populations. This conclusion is altered if there is heterogeneity among islands or species in extinction rates (R.D. Holt, unpublished results).

At this point we could use expression (10.6) to craft some more quantitative predictions about how island area and distance might affect the likelihood of niche evolution. Rather than pursue that route, we instead note that there is an important evolutionary process that we have not yet considered which complicates predictions about the relationship between distance (between the island and mainland) and the likelihood of observing niche evolution – gene flow.

10.4 Gene flow and population extinction

The expected relationship between island distance and the likelihood of adaptive colonization could break down if dispersal is sufficiently frequent that there are immigrants entering the population each generation, because recurrent gene flow can hamper local adaptation. The classic view of the evolutionary impact of dispersal is that it leads to gene flow that can force local populations away from their local adaptive optima. The genetic reason is that in a sexual species with random mating, if selection in the local environment leads towards local adaptation, on average immigrants should carry genes that lower fitness, compared to the genes carried by residents. The offspring of crosses between a resident and an immigrant should thus have lower expected fitness than do the offspring of crosses between two residents. This reproductive cost is what drives the classic scenario of gene flow "swamping" selection, potentially permanently preventing local adaptation. On top of this, a high rate of immigration can lead to ecological effects such as competition which depress the fitness of residents, and thus hamper selection improving local adaptation.

Fig. 10.6 shows an example of this effect for the individual-based model described above, for two habitats coupled by equal per capita rates of movement. Initially, we allow a population in each habitat to reach evolutionary equilibrium. There is ceiling density dependence, with 64 breeding adults in each habitat. The two habitats differ from each other very sharply in phenotypic optima, however (a difference of 6 on the scale shown in Fig. 10.5a). Each generation, there is a probability of 0.1 that an individual will move from its natal habitat (here we are allowing two-way dispersal, and not just a flow of individuals from the source to the sink). The figure shows the trajectory of population size in each habitat (censused after selection, but before density dependence is imposed). Because of demographic stochasticity, there is fluctuation in population size around its equilibrium. Initially, in some generations, one habitat has more individuals; in others, the other habitat does (the thin line; the dashed line indicates equal population sizes), so the two habitats remain roughly demographic equals. But eventually the system drifts to a state in which there are consistently more individuals in one habitat than the other (heavy line), and the system then collapses to a state in which the species is completely adapted to one habitat, and no individuals survive selection in the other habitat. The reason is that asymmetries in abundance
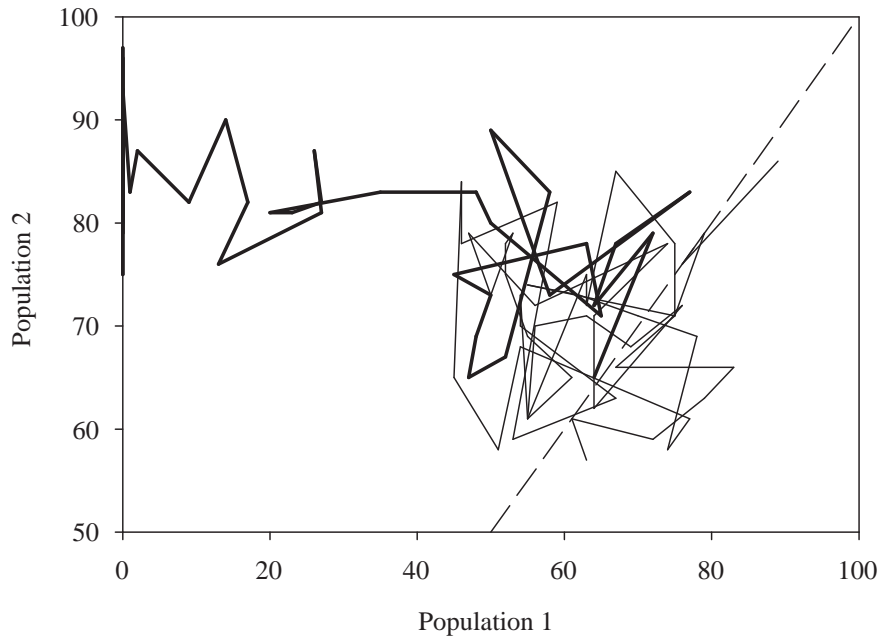
Figure 10.6 Population size phase plot for the individual-based model for two populations differing in phenotypic optima by 6 (a large amount) and with migration of 10% of each population each generation to the other habitat. Each habitat is limited to 64 mating individuals; other parameters as in Figure 10.4. Initially (thin line), the habitat with the larger population size varied with time. Eventually, however, the population in habitat 1 starts to decline, and due to positive feedback this leads to its maladaptation and extinction (heavy line), i.e., no individuals survive the phase of the life cycle where selection occurs.

between habitats lead to more individuals leaving the high-abundance habitat, than returning to it. This implies that relatively more matings in the low-abundance habitat are between residents and immigrants, which on average degrades local adaptation in this habitat, which in turn further decreases population size. Thus, relatively modest asymmetries in abundance are quickly magnified by a positive feedback process, enhancing the role of gene flow suppressing local selection. Therefore, once the local population is moderately maladapted, it quickly loses its ability to replace itself, and so relies entirely upon immigration. If we now were to cut off migration, the individuals found in the "wrong" habitat would be so strongly maladapted there, that extinction would be inevitable.

Ronce and Kirkpatrick (2001) called this phenomenon "migrational meltdown." Harding and McNamara (2002) suggest that this perverse effect of recurrent dispersal on persistence might be called an "anti-rescue" effect. The basic idea is that asymmet-

rical dispersal can lead to a kind of suppression of natural selection. The example shown in the figure is for a single pair of patches. But much the same phenomenon should emerge in metapopulations comprised of a mixture of distinct kinds of habitats, where selection operates in different directions in different habitats (e.g., optimal body size might vary with temperature or food availability). Too much dispersal from one habitat type to another could lead to enhanced extinction rates.

Broadly, we can imagine three avenues through which gene flow between habitats could elevate extinction rates in a metapopulation. First, there could be direct extinction, as in the example of migrational meltdown shown in Fig. 10.6. Second, gene flow could lead to depressed average population size (an example is in Holt 1983), and thus increase the risk of local extinction due to demographic stochasticity. Finally, a population which is displaced from its local adaptive optimum is likely to suffer a reduced growth rate when rare, which means that it is harder for it to rebound following a disturbance.

10.5 A metapopulation model with maladaptive gene flow

We now develop a metapopulation model that captures the flavor of these microevolutionary processes, and show that the enhancement of local extinction rates by gene flow can lead to alternative evolutionary states in a heterogeneous landscape. In this model, space is implicit, rather than explicit. A species occupies two distinct habitat types ($i = 1, 2$), each of which occupy a fraction h_i of the patches on a landscape. The fraction of the total patches that are of type i and occupied is p_i. The colonization rate from patch type i to patch type j is c_{ji}. Because adaptive colonization should be more difficult than colonization that does not require adaptation, we assume that cross-habitat colonization, though it may occur, happens at a lower rate than does colonization within a given habitat type.

If dispersal is at random, there should be an increasing rain of propagules across the two habitats, as the occupancy in either habitat increases. This means that the opportunity for migrational meltdown (or the other mechanisms by which gene flow can increase extinction listed above) in a patch of type i should increase with the occupancy of patch type j. This is modeled by making the extinction rate for each patch type an increasing function of the occupancy of the other patch type, with baseline extinction rates e_i; the extinction rates then increase with p_j at proportional rates γ_{ij}. A metapopulation model that permits both adaptive colonization, and anti-rescue due to migrational meltdown, is as follows:

$$\frac{dp_1}{dt} = (h_1 - p_1)(c_{11}p_1 + c_{12}p_2) - e_1(1 + \gamma_{12}p_2)p_1,$$

$$\frac{dp_2}{dt} = (h_2 - p_2)(c_{22}p_2 + c_{21}p_1) - e_2(1 + \gamma_{21}p_1)p_2.$$

(10.9)

The first terms on the right-hand side describe colonization of empty habitats of each habitat type, due to dispersers moving both within- and among-habitat types, in a metapopulation that is a mixture of two habitats (Holt 1997).

As a limiting case of the above model, we assume that there is no cross-colonization into empty habitats, $c_{12} = c_{21} = 0$, so the equations reduce to:

$$\frac{dp_1}{dt} = (h_1 - p_1)c_{11}p_1 - e_1(1 + \gamma_{12}p_2)p_1,$$

$$\frac{dp_2}{dt} = (h_2 - p_2)c_{22}p_2 - e_2(1 + \gamma_{21}p_1)p_2. \tag{10.10}$$

For Eq. (10.10), an equilibrium with neither species present is stable if and only if

$$e_i > c_{ii}h_i \tag{10.11}$$

for each habitat type. If this is true for habitat type i but not for habitat j, then the species can increase when rare in the latter habitat, and will go to the stable equilibrium density $p_j = (c_{jj}h_j - e_j)/c_{jj}$ (while fixing $p_i = 0$). This equilibrium can also be stable if inequality (10.11) is violated for both habitat types, because the presence of the species in one habitat type increases the extinction rate in the other, and therefore makes it harder for the species to persist there (or increase when rare).

The condition for p_i to increase when rare at the above (p_j only) equilibrium is

$$e_i[1 + \gamma_{ij}(c_{jj}h_j - e_j)/c_{jj}] < c_{ii}h_i. \tag{10.12}$$

Assuming $\gamma_{ij} > 0$, this condition requires a lower basic extinction rate e_i (or higher $c_{ii}h_i$) than would be required if $\gamma_{ij} = 0$ [or $p_j = 0$, either of which give the condition $e_i < c_{ii}h_i$, which is the reverse of condition (10.11)]. Similarly, if the species is established in habitat i, it can prevent invasion of habitat j in some cases for which habitat j could otherwise be invaded. Therefore, there is the possibility of two stable alternative equilibrial landscapes, in each of which adaptation to one habitat suppresses presence and adaptation to the other. These alternative landscape states arise when inequality (10.11) is violated for each habitat type in turn (i.e., each habitat type could be invaded if the other one was not already occupied), and inequality (10.12) is also violated for each habitat type (i.e., neither can be invaded if the other is at its equilibrium). In the symmetrical case, this reduces to $c < \gamma e$ (where $c_{11} = c_{22} = c$, $\gamma_{12} = \gamma_{21} = \gamma$ and $e_1 = e_2 = e$). In this symmetrical case, there is an equilibrium with both habitats occupied, but it can be shown that this equilibrium is unstable, if the two single-habitat equilibria are both stable.

In the case above, the presence of the species in one habitat type has only a negative effect on the species in the other habitat type, through increased extinction rate, because we assumed there was no cross-colonization. If there is cross-colonization, then the presence of the species in one habitat type can increase its occupancy in the other through colonization. However, it is still possible for there to be alternative stable equilibria, if the negative effect on extinction is greater than the positive effect of cross-colonization. But it is reasonable to expect that alternative stable equilibria will be less likely with cross-colonization.

Without cross-colonization, we showed above that the species in one habitat type can completely exclude it in the other (the alternative stable equilibria have 0 occupancy for one habitat type). If there is cross-colonization, then the presence of the species

in one habitat type guarantees its persistence in the other through colonization from one habitat type to the other. Therefore, if there are alternative stable equilibria, both habitat types will have a positive occupancy in both equilibria (assuming both cross-colonization terms are positive). The system [Eq. (10.9)] is now more difficult to analyze, because all equilibria (other than $p_1 = p_2 = 0$) have both habitats occupied, and must be solved by setting the derivatives in (10.9) to 0 and solving for p_1 and p_2. Unfortunately, there are no simple closed-form expressions for these equilibria in general.

One case that can be solved with cross-colonization is to assume symmetry. So again let $c_{11} = c_{22} = c$, $\gamma_{12} = \gamma_{21} = \gamma$ and $e_1 = e_2 = e$, and in addition let $c_{12} = c_{21} = c_x$ ("x" for cross). In this case, there is a symmetric equilibrium, which can be solved by setting the derivative in (10.9) to 0, setting $p_1 = p_2 = p$, and solving for p. This gives the symmetric equilibrium

$$p = [h(c + c_x) - e]/(c + c_x + e\gamma). \tag{10.13}$$

It is instructive to examine the isoclines for the model (Fig. 10.7). For example, the isocline for p_1 is found by setting the derivative in the first equation of (10.9) to 0, giving an equation relating p_1 and p_2. This isocline is hyperbolic. It has a vertical asymptote at $p_1 = h_1 c_{12}/(e_1 \gamma_{12} + c_{12})$ and intersects the positive p_1 axis at $(h_1 c_{11} - e_1)/c_{11}$. The isoclines always cross in the first quadrant (assuming both cross-colonization terms are positive). For some parameters, the isoclines cross only once, but for others they can cross three times (Fig. 10.7). In the symmetric case, if the magnitude of the slope of the p_2-isocline is higher at the symmetric equilibrium (as in Fig. 10.7), then this isocline is higher than the p_1-isocline for p_1 values just below the equilibrium. However, the p_1-isocline has a vertical asymptote at a positive p_1, while the p_2-isocline is approaching an oblique asymptote. Therefore, the isoclines must cross again at a lower p_1, and by a similar logic they must also cross at a higher p_1. In this case, the symmetric equilibrium is unstable, and there are alternative stable equilibria. The condition for this is

$$(e\gamma - c)(hc - e) > hc_x(2c + c_x + e\gamma) + ec_x. \tag{10.14}$$

If $c_x = 0$, this reduces to the symmetric result above (the species cannot persist unless $hc > e$, so the second term on the left must be positive). The presence of cross colonization makes alternative stable states more difficult, since not only must $\gamma e > c$, but it must be higher by a greater amount, for greater c_x. The parameters used in Fig. 10.7 satisfy inequality (10.14), and therefore alternative equilibria exist, as shown.

Thus, migrational meltdown can lead to alternative stable states in a metapopulation, assuming cross-colonization between habitat types is not too common. It can also lead to other effects, which we note below.
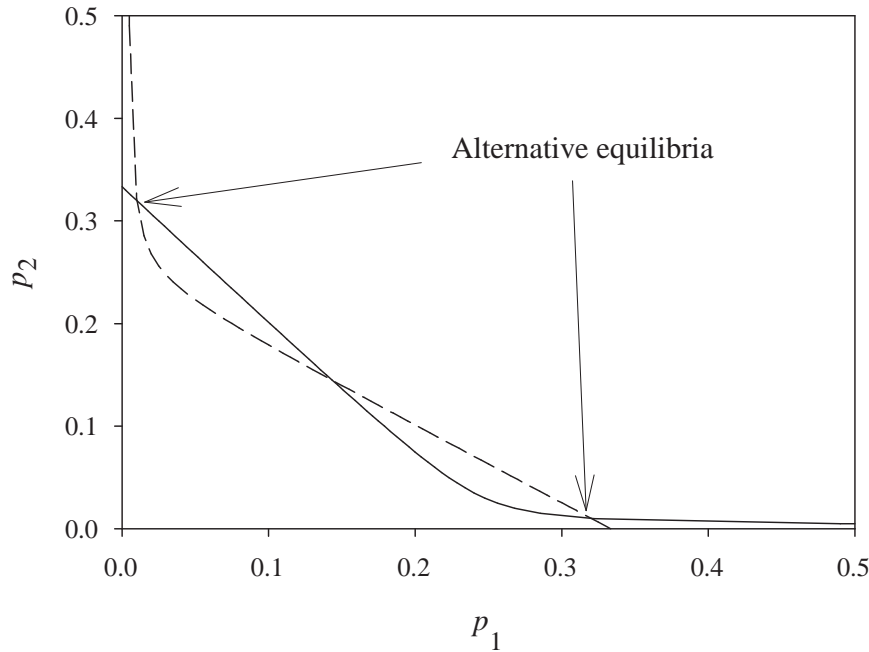
Figure 10.7 Isoclines for a symmetric metapopulation model with two alternative equilibrial states. Dashed line is isocline for habitat type 1. Parameters are $h = 0.5$, $c = 0.3$, $c_x = 0.001$, $e = 0.1$ and $\gamma = 4$. The species, if adapted to one habitat type, by gene flow sufficiently elevates extinction in the other habitat type that it remains maladapted there and hence sparsely occupies the available habitat patches.

10.6 Discussion

We have presented several complementary models that provide building blocks for examining niche evolution in heterogeneous landscapes. We started with models that look closely at evolutionary processes in particular habitats that have conditions outside a species' niche requirements, where with rare dispersal, extinction is inevitable unless there is adaptive evolution, and with frequent dispersal, recurrent gene flow can hamper adaptation.

The first deterministic model [Eqs. (10.2)-(10.4)] leads to heuristic insights about how initial population size and the degree of maladaptation influence the likelihood of extinction rather than adaptive changes sufficient to permit persistence in a sink habitat. These results motivate studies of individual-based models (IBMs) that incorporate stochasticity in both demography and genetics. These IBMs confirm the suggestions drawn from the deterministic models and help highlight issues that warrant closer theoretical scrutiny.

One of these issues is distinguishing among distinct sources of variation in adaptation to sink environments. Consider again the populations of Fig. 10.4. Although all colonizing propagules are drawn from the same type of source population, the surviving populations show considerable heterogeneity in their patterns of evolutionary rescue. Some populations start to evolve higher fitness permitting persistence quite quickly, and then rapidly reach their maximum population, at which they are fully adapted. Others barely hang on, and then even after they evolve sufficiently to persist, take longer to increase fitness and eventually reach full adaptation (and maximum population size). To understand this heterogeneity in responses, it is useful to reflect on the sources of genetic variation in these novel populations and how this variation is altered by drift, recombination, and mutation.

There are only two possible sources of genetic variation in the sink. First, colonizing propagules can sample preexisting variation in the source. Second, there can be mutational input. Without novel mutations arising in the sink, evolutionary rescue entirely depends upon genotypes with expected fitness greater than unity being potentially present in this initial sample from the source (the genotypes may only be "potentially" present because they are generated by mating and recombination among the immigrants and their descendents, rather than literally present in the initial generation). At low population sizes, genetic variation is lost by drift. The longer a population spends at low numbers, the greater the amount of variation brought in by sampling from the source that will be lost by drift. If a population persists in a genetically depleted state after going through such a long bottleneck, further evolution may largely depend upon the input of novel mutations, which will typically play out over a longer time scale than the reassortment of variation present in the initial propagule. In Fig. 10.4, the populations that spend the greatest time at low densities also seem to have the most sluggish rate of evolution, once they have adapted sufficiently to survive.

Models of demographic stochasticity show that initial population size has a large effect on population persistence, even in favorable environments. If mean fitness is less than one, and there is no evolution, the probability of extinction is unity. With genetic variation permitting adaptive colonization, we have shown that initial population size again has a strong influence on population persistence. There are several distinct reasons that initial population size matters in adaptive colonization into a sink. First, a larger colonizing propagule means more variation from the source is sampled. Second, for a given rate of decline in the sink, a larger initial population provides a larger demographic window for novel mutations to arise and potentially rescue the declining population. In a homogeneous population declining at a constant rate, a classic result in branching process theory is that the number of replication events that occur before extinction for a population initially at size N_0 and declining at average rate R is $N_0/(1 - R)$ (Feller 1968, p. 299). Since mutation happens during replication, the potential input of novel mutations should be governed by the number of replication events. All else being equal, larger initial populations have greater scope to experience novel mutations permitting adaptation and persistence, before extinction, than do small populations. In like manner, the less harsh the sink environment (i.e.,

the closer initial fitness is to unity), the larger the number of replication events that will be observed before extinction, and so the greater the opportunity for the input of novel mutations. An interesting challenge for future theoretical work is to tease apart the relative roles of sampling from established populations and *in situ* mutation as sources of genetic variation for selection to act upon in sink populations. (A similar partitioning pertains to recurrent immigration; variation can be sampled from the source, or generated by mutation in the sink.)

Environmental heterogeneity provides an opportunity for local adaptation, but gene flow can prevent this from occurring. When adaptation is required for persistence, gene flow can enhance extinction risks for some local populations. Our model for a metapopulation in a landscape comprised of two distinct habitat types shows that alternative landscape states are possible, in which a species by being initially adapted to one habitat prevents itself from becoming adapted to the other. The model suggests that evolutionary "dominance" in a metapopulation is more likely if 1) cross-habitat, adaptive colonization is difficult (i.e., in our quantitative genetics model, there is a large difference in adaptive optima in the two habitats); 2) recurrent gene flow across habitats substantially increases extinction risks in the recipient habitat; and 3) one habitat is sparse in the landscape, or high in intrinsic extinction rate, or low in intrinsic colonization rate, relative to the other habitat. Given these conditions, "success breeds success," and the habitat that a species becomes adapted to can indirectly suppress adaptation in the other habitat, and thus constrain the fraction of the landscape occupied by the species.

The model helps point out the importance of historical contingencies for determining the ultimate habitat range of a species. A species that colonizes this landscape may evolve in a number of different directions, leading to different ultimate patterns of habitat specialization. If it is difficult to colonize across habitats, but the anti-rescue effect is unimportant, a species initially adapted to just one habitat type may invade and rapidly fill up those habitats to which it is initially well-adapted, and then begin to colonize the other habitat (Fig. 10.8a). If adaptive colonization is difficult, then this may be a slow process. If dispersal is sufficient in magnitude to lead to anti-rescue effects (migrational meltdown), then a variety of additional phenomena may occur. A species may initially be a generalist, adapted to both habitats. But if one habitat is sparse, and the other widespread, generalization may be lost, because adaptation is biased towards the more common habitat. Or a species may actually be adapted initially to the sparser habitat, but then switch in its habitat specialization over to the other, more widespread, habitat, and lose its ability to persist in its ancestral habitat (Fig. 10.8b). In this case, niche evolution is actually a niche switch between habitats. Note that there is only one stable equilibrium for the parameters of both panels of Fig. 10.8. The equilibrium is symmetric for the parameter choices leading to Fig. 10.8a, but very asymmetric for the parameter choices used in Fig. 10.8b, with habitat 1 having a very low occupancy.

One limitation in the above model is that when the species occupies a substantial fraction of both habitat types in a landscape, the immigrants showing up in any given occupied patch are likely to be a mixture of emigrants from each of the habitat types.
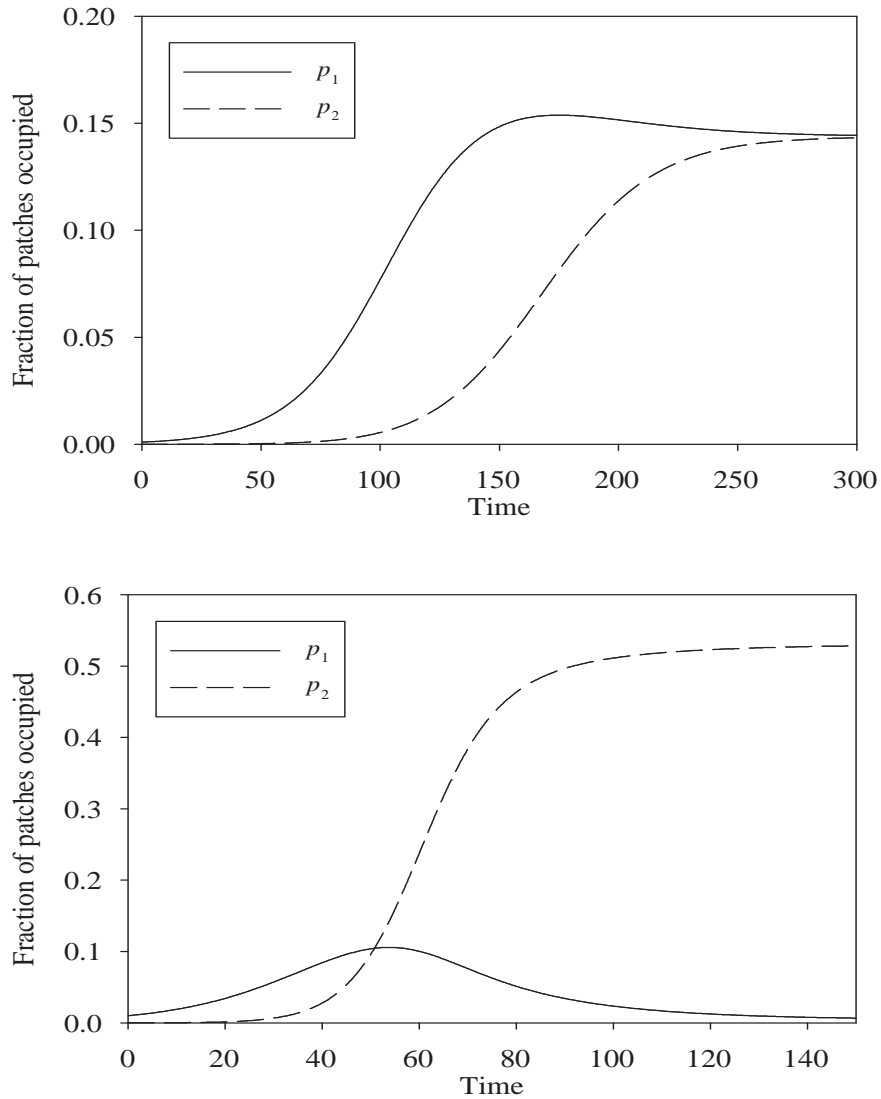
Figure 10.8 (a) Time plots for symmetric metapopulation model with $h = 0.5$, $c = 0.3$, $c_x = 0.001$, $e = 0.1$, and $\gamma = 0.5$. Initially, habitat type 2 is empty, while habitat type 1 has an occupancy of 0.001. Because within-habitat-type colonization is much higher than cross-colonization, habitat type 2 is occupied only after a lag. (b) Time plots for the metapopulation model that is symmetric except for abundance of the two habitat types and colonization rates. Parameters are $h_1 = 0.3$, $h_2 = 0.7$, $c_1 = 0.4$, $c_2 = 0.3$, $c_x = 0.001$, $e = 0.05$ and $\gamma = 4$. Initially, habitat type 2 is empty, while habitat type 1 has an occupancy of 0.01. Because habitat type 2 is more abundant on the landscape, the species there is able to suppress the species in habitat type 1.

This observation does not affect our conclusions about the existence of alternative stable equilibria, but could shift the range of parameter values where one observes this outcome.

Future extensions of this work will include examining evolution in spatially explicit landscapes, and a consideration of multiple habitat types, arranged in various spatial configurations. Studies with individual-based models in landscapes with three distinct habitats reveal some unexpected effects, reflecting how the interplay of dispersal and selection affects the entire distribution of allelic values, within and among habitats (Holt and Barfield, in prep.). Understanding niche conservatism and evolution requires a simultaneous consideration of how the structure of the environment influences the pattern and strength of natural selection, and how selection in conjunction with other evolutionary forces modifies the pool of variation available for evolution. Grappling with this issue is central to many basic questions in evolutionary biology, and is also of urgent practical importance, given the rapidly changing environments we humans are currently forcing the biota of the globe to experience.

10.7 Acknowledgements

10.8 References

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