CHAPTER 4

Metapopulations

Model Presentation and Predictions

In Chapters 1–3, we explored several models of population growth. These models differed in their major assumptions: unlimited resources (Chapter 1) versus a finite carrying capacity (Chapter 2), and a homogenous population (Chapter 1) versus an age-structured one (Chapter 3). All of these models described a **closed population**. In other words, the population changed size because of births and deaths that occurred locally. We explicitly assumed that individuals did not move between populations.

This assumption of a closed population was mathematically convenient, but not biologically realistic. For migratory animals, such as North American songbirds that overwinter in the tropics, or oceanic salmon that spawn in freshwater streams, the seasonal movement of individuals is the dominant cause of population change. Many nonmigratory species also move between populations. In particular, organisms with complex life histories often have seeds or larvae that are adapted for movement to new populations. The ascidians described in Chapter 2 are a good example. The adults are filter-feeding invertebrates that attach permanently to rock walls, but the "tadpole" larvae are free-swimming and drift in the current for several days before settlement and metamorphosis. Consequently, the "births" in a local ascidian population consist of juveniles that originated from many different sites.

The movement of individuals between populations may be density-dependent. In territorial species, such as black-throated blue warblers (*Dendroica caerulescens*), not all individuals are able to establish territories, and those that do not may migrate in search of less crowded populations. Mathematical models that ignore the biology of animal and plant movement may not give an accurate description of population dynamics.

In this chapter, we will develop a class of simple models that takes into account the fact that individuals do move among sites and that such movement is potentially important to the persistence and survival of populations. This chapter explores the concept of a **metapopulation**. The metapopulation can be thought of as a "population of populations" (Levins 1970)—a group of several local populations that are linked by immigration and emigration.

In order to study metapopulations, we need to make two important shifts in our frame of reference. The first shift concerns how we measure populations. In Chapters 1–3, our models predicted the *size* of a population—the number of individuals at equilibrium. Our metapopulation models will not predict the size of a population, but only its *persistence*. Thus, the range of numbers representing population size will be collapsed to only two possible values: 0 (local extinction) or 1 (local persistence). We will no longer distinguish between large and small populations, or between populations that

cycle, fluctuate, or remain constant. Instead, the only distinction is between populations that persist and those that go extinct.

The second shift concerns the spatial scale at which we study populations. In Chapters 1–3 we emphasized equilibrium solutions for population size, implicitly focusing on local populations that persisted through time. In contrast, the metapopulation perspective is that local populations frequently go extinct, and that the appropriate spatial scale for recognizing an equilibrium is the regional or landscape level, which encompasses many connected sites. At this scale, we will no longer focus on the persistence of any particular population. Instead, we will build a model that describes the fraction of all population sites that are occupied. Thus, we will ignore the fate of individual populations and model the extent to which populations fill the landscape. This large-scale view will allow us to use simple mathematics and avoid the complexities of trying to explicitly model local population size and individual migration. As an analogy, if we were modeling the dynamics of a busy parking lot, we would try to predict how many parking spaces were filled, not which particular spaces were occupied.

METAPOPULATIONS AND EXTINCTION RISK

The metapopulation perspective allows us to make a distinction between **local extinction**, in which a single population disappears, and **regional extinction**, in which all populations in the system die out. Even if populations are not connected by migration, the risk of regional extinction is usually much lower than the risk of local extinction.

To explore this concept quantitatively, we can define p_e as the **probability of local extinction**—that is, the probability that the population in an occupied patch goes extinct. This probability is a number that ranges between 0 and 1. If $p_e = 0$, persistence is certain, whereas if $p_e = 1$, extinction is certain. All populations go extinct in the long run, so probabilities of extinction must be measured relative to a particular time scale. For metapopulation dynamics, the appropriate time scale is often years or decades.

Suppose that $p_e = 0.7$, for probabilities measured on a yearly time scale. This means there is a 70% chance (100×0.7) that a population will go extinct during a single year, and a 30% chance that it will persist ($1 - p_e = 0.3$). What are the chances that the population will persist for two years? The **probability of persistence** for two years is the probability of no extinction in the first year ($1 - p_e$) multiplied by the probability of no extinction in the second year ($1 - p_e$). Thus:

$$P_2 = (1 - p_e)(1 - p_e) = (1 - p_e)^2 \qquad \text{Expression 4.1}$$

The probability that a population will persist for n years (P_n) is the probability of no extinction for n years in a row:

$$P_n = (1-p_e)^n \qquad \text{Equation 4.1}$$

For example, if $p_e = 0.7$, and $n = 5$, $P_n = (1 - 0.7)^5 = 0.00243$. So, if there is a 70% chance that a population goes extinct in one year, the chance of persistence for five years in a row is only 0.2%.

Now suppose that instead of a single population, we have two identical populations, each with a p_e of 0.7. For now, we assume that these populations are independent of one another—the chance of extinction in one patch is not affected by the presence or absence of populations in other patches. For this pair of populations, what is the probability of regional persistence, that is, what are the chances that *at least* one population persists for one year? The probability of regional persistence for one year (P_x) is 1 minus the probability that both patches go extinct during the year:

$$P_2 = 1-(p_e)(p_e) = 1-(p_e)^2 \qquad \text{Expression 4.2}$$

The **probability of regional persistence** in a set of x patches is the probability that all x patches do not go simultaneously extinct:

$$P_x = 1-(p_e)^x \qquad \text{Equation 4.2}$$

Thus, if we had 10 patches, each with $p_e = 0.7$, the probability of regional persistence is $P_{10} = 1 - (0.7)^{10} = 0.97$. In other words, with 10 patches, there is a 97% chance that at least one population will persist, even though it is likely that any particular population will go extinct ($p_e = 0.7$)! Figure 4.1 shows that P_x increases rapidly as more patches are added, although there is an overall decrease as p_e is increased.

Equation 4.2 illustrates an important principle: multiple patches "spread the risk" of extinction. Even if individual populations are doomed to extinction, a set of populations can persist for a surprisingly long time. In the next section, we will build metapopulation models in which these local populations are linked to one another, so that probabilities of local extinction and local colonization depend on patch occupancy.

A MODEL OF METAPOPULATION DYNAMICS

Imagine a set of homogenous patches, each of which can be occupied by a single population. Let f equal the **fraction of sites occupied**, that is the proportion of patches that contain populations. Thus, f is a number constrained between 0 and 1. If $f = 1$, all sites are occupied by populations, and the landscape is saturated. If $f = 0$, all sites are unoccupied, and the metapopulation is regionally extinct.

How does f change with time? f can increase if empty sites are successfully colonized. Let I = the **immigration rate**: the proportion of sites successfully

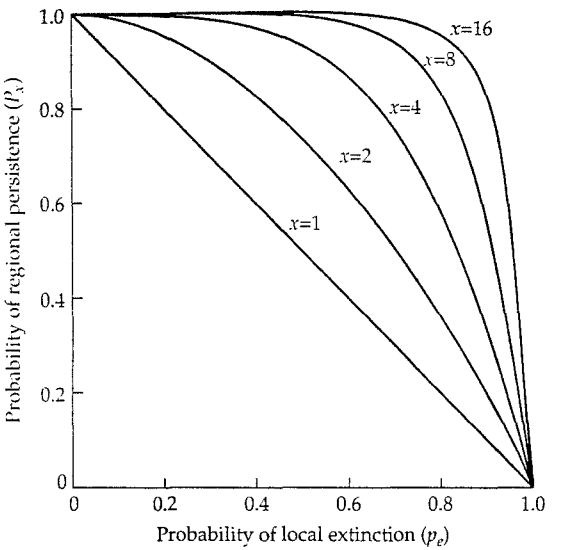

Figure 4.1 The relationship between the probability of regional persistence (P_x), the probability of local extinction (p_e), and the number of populations (x). Note that as the number of populations is increased, the probability of regional persistence is substantially higher, for a given probability of local extinction.

colonized per unit time.* f can also decrease if occupied sites undergo extinction. Let E = the **extinction rate**, that is, the proportion of sites that go extinct per unit time. The change in f is determined by the balance of gains from colonization and losses from extinction:

$$\frac{df}{dt} = I - E \qquad \text{Expression 4.3}$$

There is a close analogy between Expression 4.3 and our initial derivation of the exponential growth model in Chapter 1 (Expression 1.5). In the exponential growth model, there was continuous turnover of individuals from births and deaths. Population size (N) reached an equilibrium only if the birth rate precisely equaled the death rate. Similarly, at the metapopulation level, there is continuous turnover of individual *populations* through colonization and extinction. The fraction of population sites (f) reaches an equilibrium when the immigration rate precisely equals the extinction rate. We will see this same derivation once more in Chapter 7, when we model the number of species in a community.

*Technically, we should refer to this as the colonization, not the immigration, rate, but we use this terminology for consistency with the MacArthur–Wilson model, which is developed in Chapter 7.

We now wish to describe the immigration and extinction functions in more detail. The immigration rate depends on two factors. First is the **probability of local colonization**, p_i. If each site is colonized independently, this probability will depend only on the physical and biological conditions within a patch. Many factors can affect p_i, including patch area, the availability of critical habitats and food resources, and the absence or scarcity of predators, pathogens, and competitors.

The probability of local colonization can also be affected by factors that are external to the site. Specifically, if the sites are linked by migration, the probability of colonization may depend on the presence of populations in other sites. In other words, when many sites are occupied (large f), there are many individuals migrating, so the probability of colonization is higher than when few sites are occupied (small f). Therefore, p_i will depend on f. In the following sections, we will develop models in which p_i is either dependent or independent of f (Gotelli 1991).

The immigration rate depends not only on p_i, but also on the availability of unoccupied sites, which is measured by $(1-f)$. The more sites available for colonization, the faster the overall immigration rate. Thus, the immigration rate is the product of the probability of local colonization (p_i) and the fraction of unoccupied sites $(1-f)$:

$$I = p_i(1-f) \qquad \text{Expression 4.4}$$

The immigration rate will equal zero in two cases: first, if the probability of local colonization is zero ($p_i = 0$); and second, if all the sites in the metapopulation are occupied ($f = 1$).

If we follow a similar line of reasoning, the extinction rate, E, is the product of the probability of local extinction (p_e) and the fraction of sites occupied (f):

$$E = p_e f \qquad \text{Expression 4.5}$$

The extinction rate equals zero if the probability of extinction is zero ($p_e = 0$), or if none of the sites in the metapopulation is occupied ($f = 0$). Substituting Expressions 4.4 and 4.5 back into 4.3 gives us a general metapopulation model:

$$\frac{df}{dt} = p_i(1-f) - p_e f \qquad \text{Equation 4.3*}$$

*Because this is a continuous differential equation, p_i and p_e are technically not probabilities, but fractional rates. However, p_i and p_e behave as probabilities when they are multiplied by a finite time interval. Over such a time interval, we would need to add a correction term to Equation 4.3 to account for the chance that an occupied patch could undergo an extinction and a recolonization (Ray et al. 1991). However, the correction term is small, and it is simpler to use the continuous differential equation and to interpret p_i and p_e as immigration and extinction probabilities.

Equation 4.3 is a simple model of metapopulation dynamics that will serve as a template for developing alternative models. By changing some of our assumptions about colonization and extinction processes, we can generate new metapopulation models that make different predictions about the fraction of sites occupied at equilibrium ($\hat{f}$). Before exploring these variations, we will first examine the general assumptions of this model.

Model Assumptions

Equation 4.3 makes the following assumptions:

- ✓ ***Homogenous patches.*** The population sites must not differ in their size, isolation, habitat quality, resource levels, or other factors that would affect the probability of local colonization and local extinction.
- ✓ ***No spatial structure.*** The model assumes that probabilities of colonization and extinction may be affected by the overall fraction of occupied sites (f), but not their spatial arrangement. In a more realistic metapopulation model, the probability of colonization for a particular site would depend on the occupancy of close neighboring patches, rather than on the overall f. This sort of "neighborhood" model can be studied by computer simulation or by using equations of diffusion, in which the spread of populations through empty sites is analogous to the dispersion of an ink droplet through a beaker of water.
- ✓ ***No time lags.*** Because we are describing metapopulation dynamics with a continuous differential equation, we assume that the metapopulation "growth rate" (df/dt) responds instantly to changes in f, p_i, or p_e.
- ✓ ***Constant p_e and p_i.*** The probabilities p_e and p_i do not change from one time period to the next. Although we cannot say precisely which populations will go extinct and which will be colonized, the probabilities of these events do not change.
- ✓ ***Regional occurrence (f) affects local colonization (p_i) and extinction (p_e).*** Except for the basic island–mainland model (see below), metapopulation models assume that migration is substantial enough to affect local population dynamics and influence probabilities of colonization and/or extinction. Consequently, p_i and/or p_e are functions of f.
- ✓ ***Large number of patches.*** The fraction of occupied sites in our model can become infinitely small, and the metapopulation will still persist. Thus, we are not assuming any demographic stochasticity (see Chapter 1) of the metapopulation due to small patch numbers.

Model Variations

THE ISLAND–MAINLAND MODEL

The simplest model for our metapopulation is that both the p_i and p_e are constants. If p_e is a constant, the probability of extinction is the same for each population and does not depend on the fraction of patches occupied. This assumption is analogous to a density-independent death rate in a population growth model, because the death rate does not depend on population size (see Chapter 2). Similarly, the probability of colonization may be fixed. Constant p_i implies a **propagule rain**—a continuous source of migrants that could potentially colonize an empty site (Figure 4.2a). If there is a large, stable "mainland" population, it may generate a propagule rain for a set of "islands" in the metapopulation. A propagule rain may also characterize some plant populations that may be colonized by a seed bank of long-lived buried seeds. The equilibrium value of f for this **island–mainland model** can be found by setting Equation 4.3 equal to zero and solving for f:

$$0 = p_i - p_i f - p_e f \qquad \text{Expression 4.6}$$

$$p_i f + p_e f = p_i \qquad \text{Expression 4.7}$$

Dividing both sides of Expression 4.7 by $(p_i + p_e)$ gives $\hat{f}$, the equilibrium for f:

$$\hat{f} = \frac{p_i}{p_i + p_e} \qquad \text{Equation 4.4}$$

In the island–mainland model, the fraction of sites occupied at equilibrium is a balance between extinction and immigration probabilities. Notice that even if the probability of extinction (p_e) is very large and the probability of colonization (p_i) is very small, at least some of the sites in the metapopulation will be occupied ($\hat{f} > 0$), because the metapopulation is continually replenished by the external propagule rain.

INTERNAL COLONIZATION

Now we will relax the assumption of the propagule rain and instead imagine that the only source of propagules for the metapopulation is the set of occupied population sites (Figure 4.2b). In other words, there is **internal colonization** such that:

$$p_i = if \qquad \text{Expression 4.8}$$

The constant i is a measure of how much the probability of colonization of empty sites increases with each additional patch that is occupied. In this

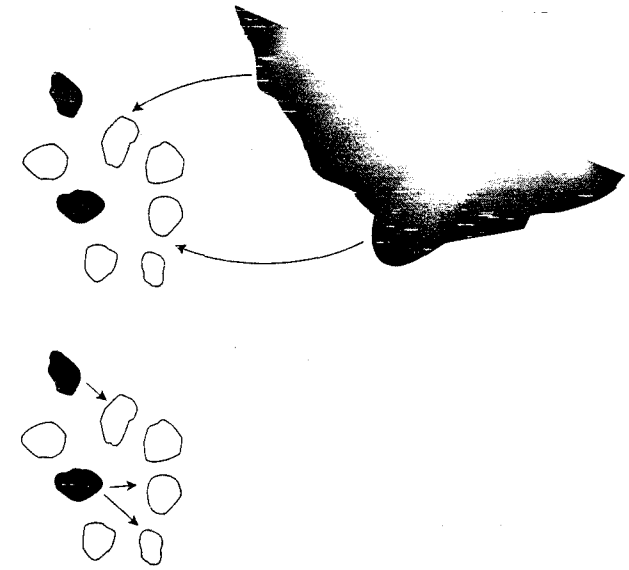

Figure 4.2 (a) Colonization in the island–mainland model. Colonists for a set of islands always come from a large mainland area. Open islands represent empty sites and filled islands represent sites that contain populations. (b) Colonization in the internal model. Colonists do not originate from a permanent external source, but instead originate only from currently occupied islands.

model, each population contributes individuals to a pool of propagules, which then have the potential to colonize unoccupied sites. Note that if all of the populations go extinct ($f = 0$), the probability of colonization goes to zero because there is no other source of colonists. This condition is in contrast to the island–mainland model, in which colonists were always present because of the external mainland population.

Assuming that the extinctions are still independent and substituting Expression 4.8 back into the general model (Equation 4.3) gives (Levins 1970):

$$\frac{df}{dt} = if(1-f) - p_e f \qquad \text{Equation 4.5}$$

Again, we set this equation equal to zero and solve for the equilibrium f:

$$p_e f = if(1-f) \qquad \text{Expression 4.9}$$

$$p_e = i - if \qquad \text{Expression 4.10}$$

$$if = i - p_e \qquad \text{Expression 4.11}$$

Dividing both sides by i yields:

$$\hat{f} = 1 - \frac{p_e}{i} \qquad \text{Equation 4.6}$$

In contrast to the predictions of the island–mainland model, persistence of the metapopulation ($\hat{f} > 0$) is no longer guaranteed. Instead, the metapopulation will persist only if the strength of the internal colonization effect (i) is greater than the probability of local extinction (p_e). If this condition is not met, the metapopulation will go extinct ($\hat{f} \leq 0$). Extinction can happen because the metapopulation is no longer receiving the benefit of external colonization.

THE RESCUE EFFECT

Our first two metapopulation models (island–mainland and internal colonization) both assumed that the probability of extinction was independent of the fraction of sites occupied. Now we should consider the possibility that extinction might be affected by f. How might this happen? As before, we assume that each occupied site produces an excess number of propagules that leave the site and arrive at other populations. If the propagules arrive at an empty site, they represent potential colonists. If conditions are good, these propagules may be able to establish a breeding population in the site. But migrants may also arrive at occupied sites and increase the size of established populations. This increase in N is a **rescue effect** that may prevent the local population from going extinct due to demographic and environmental stochasticity (see Chapter 1). The rescue effect is defined as the reduction in the probability of extinction that occurs when more population sites are occupied, and hence more individuals are available to boost local population sizes.

The tradeoff of propagules leaving a site and those entering from other sites cannot be strictly linear. Otherwise, it would not be possible to achieve a rescue effect—the reduction in p_e due to immigration would be canceled by the increase in p_e due to emigration. However, the loss of some individuals as migrants may have a negligible effect on p_e. In fact, if migration is density-dependent, individuals that do not migrate to other population sites might reproduce or survive poorly in their sites of origin. An explicit model of the rescue effect would need to include parameters for N, p_e, and migration. But we can capture the essence of the rescue effect in our simple metapopulation model by assuming that:

$$p_e = e(1-f) \qquad \text{Expression 4.12}$$

Expression 4.12 says that the probability of local extinction decreases as more population sites are occupied. e is a measure of the strength of the rescue effect, because it controls how much p_e decreases with the addition of another occupied site. Notice that if all population sites are occupied ($f = 1$), the probability of local extinction is zero. This is unrealistic, because even in a saturated landscape there should be some intrinsic background extinction risk. But we would have to introduce another parameter into the model to account for background extinction, so instead we will use Expression 4.12 to keep things simple. Assuming an external propagule rain and a rescue effect, we substitute Expression 4.12 into the general model (Equation 4.3):

$$\frac{df}{dt} = p_i(1-f) - ef(1-f) \qquad \text{Equation 4.7}$$

As before, we set Equation 4.7 equal to zero and then solve for the equilibrium value of f:

$$ef(1-f) = p_i(1-f) \qquad \text{Expression 4.13}$$

$$ef = p_i \qquad \text{Expression 4.14}$$

Dividing both sides by e gives:

$$\hat{f} = \frac{p_i}{e} \qquad \text{Equation 4.8}$$

As in our original island–mainland model, persistence of the metapopulation is assured when there is both a propagule rain and a rescue effect. In fact, if the extinction parameter (e) is less than the probability of colonization (p_i), the metapopulation will be saturated at equilibrium, and all population sites will be occupied ($\hat{f} = 1$).

OTHER VARIATIONS

One final variation based on our simple metapopulation model would be to combine internal colonization with the rescue effect. In this case, the metapopulation is entirely closed to outside influences; both colonization and extinction probabilities are a function of the fraction of sites occupied. The equation for this model comes from substituting Expression 4.8 (internal colonization) and Expression 4.12 (rescue effect) into Equation 4.3 (the general model):

$$\frac{df}{dt} = if(1-f) - ef(1-f) \qquad \text{Equation 4.9}$$

However, if you try to set Equation 4.9 equal to zero and then solve for f, you will find there is no simple solution. Instead, the "equilibrium" depends on the relative sizes of i and e. If $i > e$, the immigration rate $[if(1-f)]$ will always be greater than the extinction rate $[ef(1-f)]$, so the metapopulation will "grow" until $f = 1$ (landscape saturation). Conversely, if $e > i$, the extinction rate exceeds the immigration rate, and the metapopulation will contract until $f = 0$ (regional extinction). If i and e vary stochastically, the metapopulation may fluctuate between these two equilibrium points (Hanski 1982). Finally, if i equals e, f will not change because the immigration rate will always equal the extinction rate. If some external force changes f, it will then stay at this new equilibrium value. We refer to this as a **neutral equilibrium**.

The metapopulation models that we have considered here have treated colonization as either internal or external. Similarly, extinctions were either independent or mediated by a rescue effect (Table 4.1). These four alternatives actually represent endpoints of a continuum. Colonization in most metapopulations is probably both from propagules generated from within the system and from propagules derived from external "mainland" sources. Similarly, there are extrinsic and intrinsic forces leading to extinction. These factors can be incorporated into a more general metapopulation model, which includes the four models developed in this chapter as special cases (Gotelli and Kelley 1993).

The derivations presented here just scratch the surface of metapopulation models (Hanski and Gilpin 1991). Other metapopulation models predict N directly, rather than just the presence or absence of populations. Metapopulation models have also been extended to two-species models of competitors or predator and prey. In some cases, species may coexist regionally that cannot coexist locally in closed populations. In other instances, exposing local populations to competitors or predators can lead to extinctions that might not have occurred otherwise. In Chapter 7, we will again return to a discussion of "open" systems when we model the colonization of an island by an entire community of species. For now, we will return to our simple models of local populations and incorporate the effects of competitors (Chapter 5) and predators (Chapter 6).

Table 4.1 Four metapopulation models (Gotelli 1991).

		Extinction	
		Independent	***Mediated by rescue effect***
Colonization	***External ("propagule rain")***	$\frac{df}{dt} = p_i(1-f) - p_e f$	$\frac{df}{dt} = p_i(1-f) - ef(1-f)$
	Internal	$\frac{df}{dt} = if(1-f) - p_e f$	$\frac{df}{dt} = if(1-f) - ef(1-f)$

Empirical Examples

THE CHECKERSPOT BUTTERFLY

Populations of the bay checkerspot butterfly (*Euphydryas editha bayensis*) occur in discrete patches that seem to be organized into a large metapopulation. The butterfly is somewhat of a habitat specialist; adult butterflies emerge in spring, and females prefer to lay their eggs on the annual plantain *Plantago erecta*. This host plant serves as a food source for the caterpillars, which feed for one or two weeks and then enter a summer diapause, or resting stage. Caterpillars resume feeding during the cool, rainy months of December to February, and then build cocoons. *P. erecta* grows in Northern California grasslands on serpentine soil rock outcroppings, which serve as potential population sites (Figure 4.3). Populations of the checkerspot butterfly have been studied in this area for over 30 years (Ehrlich et al. 1975).

Fluctuations in the weather can disrupt the life-cycle synchrony of the butterfly and its host plant, leading to local extinction. For example, at least three butterfly populations are known to have gone extinct following a severe drought in 1975–1977 (Murphy and Ehrlich 1980). Very small populations recorded in 1986 may represent successful recolonizations of empty sites (Harrison et al. 1988). The Morgan Hill site is a large patch of serpentine soil that supports a population of hundreds of thousands of butterflies. Because of its large size and the topographic diversity of the site, this population survived the drought and probably served as a source of colonists for empty patches.

The checkerspot metapopulation is similar, in some respects, to the island–mainland model, in which there is a persistent, external source of colonists. Although our simple metapopulation models assumed that all patches were identical, this was clearly not the case for the checkerspot butterfly. Populations were more likely to be found in sites that were close to the Morgan Hill population, had large areas of cool, north-facing slopes, and high densities of appropriate host plants (Harrison et al. 1988). For conservation purposes, preservation of the Morgan Hill population is probably essential because it provides colonists for other patches.

By their very nature, metapopulation studies require access to a lot of land. Although researchers have studied the checkerspot metapopulation for several years, work on many of the smaller patches can no longer be carried out. Attitudes of western land owners have changed; many are no longer willing to allow biologists onto their property to census the checkerspot butterfly

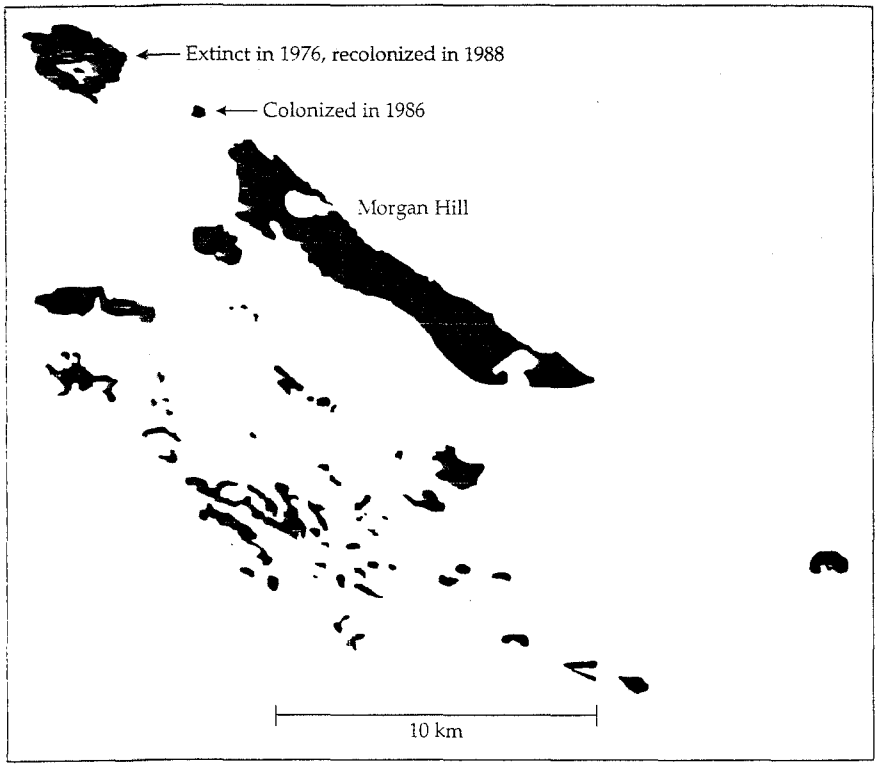

Figure 4.3 Distribution of serpentine soil grasslands in Santa Clara County, California. These habitat patches function as potential population sites for the bay checkerspot butterfly (*Euphydryas editha bayensis*). A large population of butterflies at the Morgan Hill site probably serves as a continual source of colonists for the other small patches, as in the simple island–mainland model. (After Harrison et al. 1988.)

(S. Harrison, personal communication). Some land owners fear that the discovery of an endangered species will deprive them of their property rights.

HEATHLAND CARABID BEETLES

Not all metapopulations occur in well-defined patches, as in the checkerspot butterfly example. Populations may be organized as a metapopulation even in the absence of discrete habitat patches. In the northern Netherlands, populations of carabid ground beetles have been studied by pitfall trapping for over 35 years (den Boer 1981). Radioactive marking revealed that most individuals moved a very limited distance. For example, 90% of the individuals of the beetle *Pterostichus versicolor* moved less than 100 meters a day.

Consequently, sites separated by even modest distances effectively contain different subpopulations that are connected by migration.

Figure 4.4a shows the size of 19 subpopulations of *P. versicolor* that were studied for 21 years. Although populations fluctuated asynchronously, there

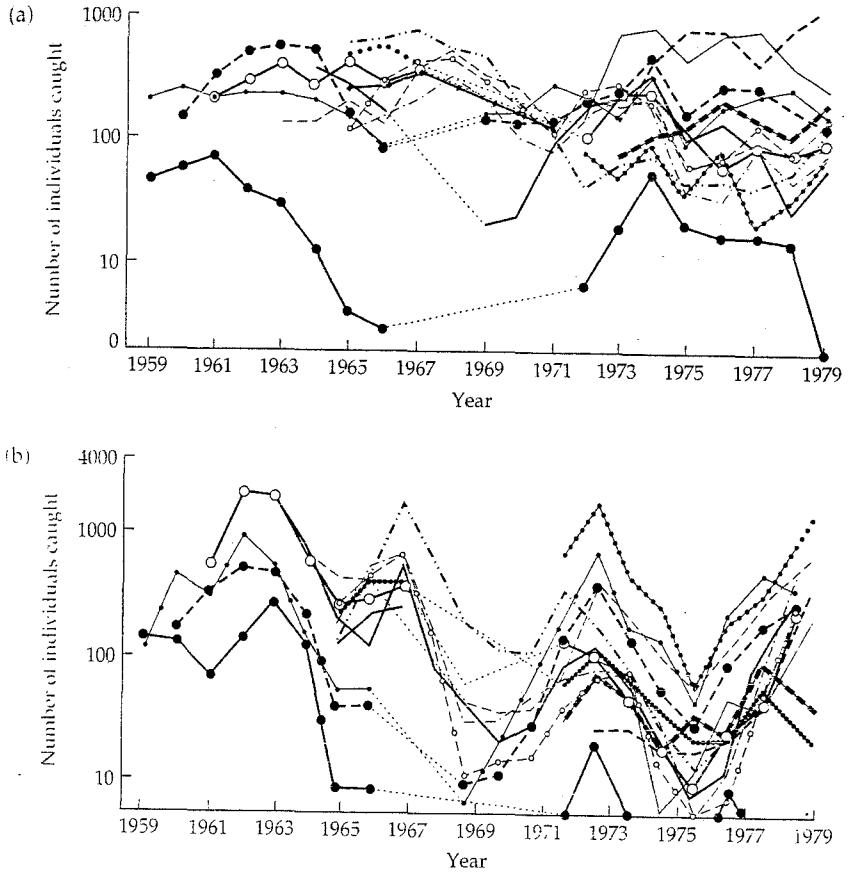

Figure 4.4 (a) Metapopulation dynamics of the ground beetle *Pterostichus versicolor* in heathlands of the northern Netherlands. Each symbol represents the track for a different subpopulation in the heath. Note the great variability in population dynamics and the relative rarity of local extinctions. Broken lines indicate gaps in sampling. Lines that touch the *x* axis indicate local extinctions. At each time period, some subpopulations are usually increasing, which may act as sources of migrants that prevent the extinction of declining subpopulations. (b) Metapopulation dynamics of the ground beetle *Calathus melanocephalus* in heathlands of the northern Netherlands. In contrast to *P. versicolor*, subpopulations of *C. melanocephalus* tend to fluctuate in synchrony. Consequently, there are no "source" areas to rescue declining subpopulations, so that local extinctions are more frequent. (After den Boer 1981.)

were almost no extinctions recorded during this time period. This is because, at any point in time, some populations were increasing in size and acting as **source populations** that prevented the extinction of other, declining **sink populations**. In contrast, the population fluctuations of the species *Calathus melanocephalus* were much more synchronous during this period (Figure 4.4b). As a consequence, conditions were sometimes uniformly bad for all populations. At these times, there were no source populations available, so population extinctions were much more frequent. Because each subpopulation of *C. melanocephalus* behaved similarly, the risk of extinction was high. Because each subpopulation of *P. versicolor* behaved differently, the metapopulation structure effectively spread the risk of extinction. We still don't understand why the population dynamics of these two beetle species are so different, but it is clear that metapopulation structure affects local extinction and perhaps long-term persistence.

Problems

4.1. You are studying a rare and beautiful species of ant lion (see cover). Populations of the ant lion live on a set of islands and on an adjacent mainland that serves as a permanent source of colonists. You can assume that the mainland is the only source of colonists and that extinctions on the islands are independent of one another.

a. If $p_i = 0.2$ and $p_e = 0.4$, calculate the fraction of islands occupied at equilibrium.

*b. A developer is preparing to pave over the mainland area for a new condominium complex. To appease local environmental groups, the developer promises to set aside the islands as a permanent "ant lion nature reserve." Assuming that $p_e = 0.4$ and $i = 0.2$, predict the fate of the island populations after the mainland population is eliminated.

4.2. An endangered population of 100 frogs lives in a single pond. One proposal for conserving the frog population is to split it into three populations of 33 frogs, each in a separate pond. You know from your demographic studies that decreasing the frog population from 100 to 33 individuals will increase the yearly risk of extinction from 10% to 50%. In the short run, is it a better strategy to retain the single population or to split it into three?

*4.3. Suppose a metapopulation has a propagule rain and a rescue effect. The parameters are $p_i = 0.3$ and $e = 0.5$. Forty percent of the population sites are occupied. Is this metapopulation expanding or shrinking?

* Advanced problem