

## Metapopulation ecology

- Metapopulations and spatial ecology
- MacArthur and Wilson and the equilibrium theory
- The Levins or classical metapopulation
- Extinction in metapopulations
- Metapopulation dynamics of two local populations
- Source-sink metapopulations and the rescue effect
- Non-equilibrium and patchy metapopulations
- Spatially realistic models
- Assumptions and evidence for the existence of metapopulations in nature

### 5.1 Introduction

On August 27, 1883 Krakatau, an island about the size of Manhattan located between Sumatra and Java, underwent a series of volcanic eruptions releasing as much energy as 100 megatons of TNT (Wilson 1992). Magma, ash, and rock flew 5 km into the air and fell back into the sea, creating a tsunami 40 m in height, washing away villages in Java and Sumatra, killing 40,000 people. Waves were still a meter high when they came ashore in Sri Lanka. A total of over 18 cubic kilometers of rock and ash was thrown into the air with dust and sulfuric acid aerosol reaching 50 km into the stratosphere, where their effects were seen as brilliant sunsets for several years thereafter. All of this airborne material produced "darkness at noon" in areas near the former Krakatau.

Only the southern end of Krakatau remained. This island, which became known as Rakata, was covered by pumice 40 m thick. The pumice had been heated to between 300 and 850 °C, and all living things had been destroyed; Rakata was a sterile island. Yet living things soon began colonizing this lifeless rock. Nine months after the explosion a visitor found a small spider spinning its web. In the fall of 1884, a year after the eruption, biologists found a few shoots of grass. By 1886 there were 15 species of grasses and shrubs; by 1897 there were 49 species; and in 1928 300 species of plants were found. In 1919 there were patches of forest; by 1929 most of the island was forested, forcing the grasses into small pockets (Wilson 1992).

What Wilson described was a successional sequence or "climax" forest. What Wilson's theory, is the two patch model of colonization. New species arrive through other process is local extinction. early in the twentieth century students of succession had noted that earlier successional stages that we would associate with *reticulatus*), was present is perhaps more to the point by 1920 there were 300 species that an "equilibrium" stage that number had been the actual composition between the 1920 and 1929 replaced by four new species bulbul (*Pycnonotus* sp.) on Rakata between 1920 and 1929.

The history of Krakatau is obviously subject to the same processes are continuously changing the composition of the island.

### 5.2 Metapopulations

Many of the populations have underlying assumptions contiguous habitats certain populations activities. Wildlife and increasingly is partially because of begun stressing the ecosystems. What is spatial variation patterns over time only have its common on present-day Krakatau Java and Sumatra mainland (Wilson 1992).

Spatial ecology (ii) metapopulations Landscape ecological studies

What Wilson described, as outlined in the preceding paragraphs, sounds like a typical successional sequence, proceeding from a community of colonizing species to a mature or "climax" forest. What we want to emphasize, as we consider the topic of metapopulations, is the two processes at work on Rakata. Obviously one of those processes is colonization. New species continually arrive on the island from the nearby mainlands. The other process is local extinction. Many species that arrived on this island, and were recorded early in the twentieth century, are no longer present. Again, this may not be surprising to students of succession. So-called climax species are supposed to outcompete and eliminate earlier successional species. But is that what happened? At least one animal species that we would associate with the more mature community, the reticulated python (*Python reticulatus*), was present as early as 1933, but was gone by the 1980s. The bird community is perhaps more to the point. In 1908, 13 species of birds were recorded on Krakatau; by 1920 there were 31 species; and in 1933, 30 species were found. Wilson (1992) believed that an "equilibrium" number for Krakatau was approximately 30 species of birds, and that number had been reached by about 36 years. More important, however, is that the actual composition of the bird community has not remained stable. During the interval between the 1920 and 1933 surveys, five species of birds went extinct on Krakatau, to be replaced by four new species (MacArthur and Wilson 1967). For example, the sooty-headed bulbul (*Pycnonotus aurigaster*) and the long-tailed shrike (*Lanius schach*) had become extinct on Rakata between 1920 and 1933.

The history of Krakatau illustrates two major points: (i) local populations are continuously subject to the twin processes of colonization and extinction; and (ii) communities are continuously changing. Even when the number of species in the community is static, the composition of the community is not.

## 5.2 Metapopulations and spatial ecology

Many of the population models we have examined, particularly the deterministic models, have underlying assumptions that natural populations are numerous, widespread, and occupy contiguous habitats. The reality is that these assumptions may never have been true for certain populations, and that the natural world is now increasingly fragmented due to human activities. Wildlife populations are now more likely to be small, restricted in distribution, and increasingly isolated from each other. Partially as a reaction to these realities and partially because of increasingly sophisticated theoretical developments, ecologists have begun stressing the importance of the spatial context in populations, communities, and ecosystems. What we can broadly call **spatial ecology** is the progressive introduction of spatial variation and complexity into ecological analysis, including changes in spatial patterns over time. Krakatau is an example of both temporal and spatial complexity. Not only have its communities and populations changed over time, but the community found on present-day Krakatau is still very different from that of the nearby mainland forests of Java and Sumatra. The local community of Krakatau remains distinct from those of the mainland (Wilson 1992).

Spatial ecology is distinguished by two different approaches: (i) **landscape ecology** and (ii) **metapopulation ecology**.

Landscape ecology usually focuses on a larger geographic scale than traditional ecological studies; it was founded largely by community- or ecosystem-oriented ecologists,

geographers, and landscape planners. Landscape ecology explicitly recognizes the heterogeneity or "patchiness" of the environment both spatially and over time. It provides a large-scale perspective that describes the physical structures of patchy environments as well as the movements of both individuals and resources among them. Generally, landscape ecologists focus at the community, as opposed to the population, level. Furthermore, landscapes have a more complex structure than usually allowed in simple metapopulation models, with habitat suitability being on a continuous scale, rather than simply "suitable" or "unsuitable" (Hanski 1999). Landscape ecologists do not usually work on population dynamics (Turner *et al.* 2001), but much of their work is relevant to metapopulations. For example, both landscape and metapopulation models often attempt to incorporate the roles of edge habitats, movements of individuals between patches via habitat corridors, spatial location of the patches, habitat fragmentation, landscape disturbance, and spatial and temporal variation in the quality of the habitat.

The metapopulation approach begins by stressing that local populations are influenced by immigration/emigration and extinction, as well as by birth and death processes. Until the 1960s, the idea that populations might routinely go locally extinct was rarely discussed in the literature. However, the population geneticist Sewall Wright (1940), as well as ecologists such as Andrewartha and Birch (1954), introduced the notions that populations are connected by migration and that local extinctions might be commonplace (Hanski 1999). The importance of immigration and emigration to the long-term persistence of a local population, however, was first emphasized by Levins (1970), who coined the term **metapopulation**. For Levins a metapopulation was a population consisting of many local populations. He asserted that all local populations have a finite probability of extinction, and long-term survival of a species was at the regional or metapopulation level (Hanski 1999). Beginning in the 1990s, as it became obvious that the natural world was becoming increasingly fragmented, the metapopulation approach became standard in the world of conservation biology. An understanding of metapopulations, the probabilities of local extinctions in different-sized natural reserves, and the rates of immigration and emigration between these preserves, became one of the fastest-growing research areas in population, community, landscape, and conservation biology. As currently defined, **metapopulations** are **regional assemblages** of plant and animal species, with the long-term survival of the species depending on a shifting balance between local extinctions and re-colonizations in the patchwork of fragmented landscapes.

Whereas in landscape ecology we begin with the assumption of complex environmental heterogeneity, in a simple metapopulation analysis, the landscape, from the perspective of a given species, is assumed to consist of discrete patches of suitable habitat, surrounded by unsuitable areas. All of these patches are of the same quality and size, and while these patches are isolated from each other there is no special recognition given to how far apart they are or any measure of ease of movement from one patch to another (connectivity). Nor are local population dynamics emphasized. The concern is simply whether a patch is occupied or not, the extinction rate on patches, and the overall colonization rate among patches. From this simple approach, more complex spatially realistic models have been developed to recognize differences in habitat quality and size, local population dynamics, and differences in connectivity among local patches.

Spatial ecology includes a variety of approaches, including so-called lattice models. In patch or lattice models, the habitats occupied by local populations are represented in continuous space or made up of a series of spatially subdivided cells or "lattice" segments.

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These models include explicit spatial locations for the habitats. In patch models the habitats have just two states, occupied or empty, and no effort is made to estimate the size of the population in the occupied patches. Cells change states according to simple rules, and stochastic extinctions and colonizations take place. Many of these simplifying rules can be relaxed in a spatially explicit variation of this approach known as the incidence function model, examined later in this chapter (Hanski 1999).

The spatial distribution of a species is based on environmental patchiness. However, the recognized patterns of spatial distribution (**clumped**, **random** or **regular**) only describe the current spatial pattern; they do not address the underlying causation of the pattern, or the long-term persistence of the population at that site.

The term "metapopulation" has been used for any spatially structured population and "metapopulation dynamics" has been used to refer to any population dynamics involving spatial patterns (Hanski 1998). Furthermore, as Harrison (1994) has pointed out, several different types of metapopulations exist: classical metapopulations, mainland-island metapopulations, non-equilibrium metapopulations, and patchy metapopulations. We will explore these later in this chapter.

As pointed out by Tilman and Kareiva (1997), we must recognize that an individual organism only interacts with its local environment and with the competitors and/or predators present in that local environment. Such realities have been largely ignored by ecologists in the past, particularly when deriving theoretical models for competition or predation. Both classical and modern studies of competition and predator-prey interactions can be easily integrated into a simple metapopulation (spatial) context. For example, envision the environment as a series of patches and apply the competitive-exclusion principle (to be elaborated in a later chapter). If we have a superior competitor that drives other species extinct on a given patch, the inferior competitors are only driven locally extinct. They can remain in the region as long as they can have a higher dispersal rate than extinction rate and there are empty habitat patches. Similarly, a predator may drive a prey species locally extinct, but the prey population remains regionally present as long as it continues to colonize empty habitat patches faster than its predator. Although this is an oversimplification of models presented later, consider the following two examples.

Huffaker (1958) worked with orange mites and their predators in the laboratory. He found that coexistence of the two species was impossible on any given orange. Here one orange represents a small homogeneous habitat or patch. Through the addition of spatial complexity, however, as well as barriers to limit the rates of movements between patches, the orange mite and its predator coexisted in the laboratory for many months. A higher dispersal rate and environmental complexity allowed the prey species to remain regionally present, even though it was continually driven locally extinct on a given orange once the predator arrived. Notice the parallels to epidemiological and host-parasite interactions. An unoccupied, but suitable, habitat patch is the equivalent of an individual susceptible to a parasite, yet not infected. An infected individual is the equivalent of an occupied habitat patch.

Spatial complexity can also have important effects on competitive interactions. For example, spatial complexity can help explain the coexistence of more species than expected based on the theory that the number of coexisting species should not exceed the number of limiting resources (Hutchinson 1961). As pointed out by Lehman and Tilman (1997), usually there is a trade-off, often expressed in terms of energetic investments, between competitive ability and colonization ability. While a superior competitor may take over

a given site, if the less competitive species is a better colonizer, it may simply escape to a new site before competitive exclusion can occur. For example, Hubbell *et al.* (1999) proposed that high tree diversity on Barro Colorado Island in Panama is due, at least in part, to the low dispersal ability in competitively dominant species. Through a combination of low local abundance, low dispersal, and chance events, many plant species are absent from the local neighborhood in which a tree is located. Many sites are colonized by “default” species that were not the best competitor for the site. For example, an individual tree sapling competes with only 6.3 neighbors on average. Thus, plants compete only with those individuals sufficiently nearby to shade them or whose roots overlap with theirs in the soil. In order to “win” locally, a tree must only compete with those species that have “shown up” in the local neighborhood. Inferior competitors “win” by default. Because winners are only the best competitors that happen to have colonized a specific site, this process can lead to an almost unlimited diversity (Tilman 1994, Hubbell *et al.* 1999).

While landscape ecology and metapopulation ecology have started at different scales and with different assumptions and traditions, these two branches both ask similar questions. Many landscape ecology courses include sections on metapopulations. An important future task will be the reconciliation of these two approaches and the establishment of common methodologies and principles.

### 5.3 MacArthur and Wilson and the equilibrium theory

Spatial ecology has its roots in the MacArthur and Wilson equilibrium (or dynamic) theory of island biogeography. MacArthur and Wilson (1963, 1967) brought a quantitative theoretical framework to the study of biogeography. Even before Darwin carried out his pioneering work on the Galapagos, islands and island examples have been of great importance in biology, and islands have been analyzed as natural laboratories and experimental systems. They are small, contained ecosystems in which certain species found in continental ecosystems may be missing. The lessons learned from examining islands can also be applied to those continental areas that are comparable to islands. That is, streams, lakes, tidal pools, caves, and mountaintops can be thought of as habitat islands in a "terrestrial sea." The approach of island biogeography has also been applied to host animals as habitat patches for parasites. Finally, as noted above, the natural world is increasingly fragmented, surrounded by roads, agricultural crops, shopping malls, industrial sites, and urban development. As conservation biologists became increasingly aware that wildlife preserves were essentially islands, a set of rules for the design of natural areas was inferred from the MacArthur and Wilson theory (Diamond 1975, Terborgh 1975, Wilson and Willis 1975, Willis 1984).

The basic principles derived from the MacArthur and Wilson theory are:

- 1 There is a relationship between habitat island area and the number of species found there (the species-area curve);
- 2 local extinction is a normal, common occurrence, particularly on small islands with small populations;
- 3 local diversity is based on an interplay between colonization from a "mainland" source of species and local extinction, resulting in an "equilibrium" number of species;

4 island size and number of species  
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The relationship between the number of children and the number of parents is one of the corners of the family. It has been discussed since the beginning of time, and it is still true that the number of children is a key factor in determining the number of parents.

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- 4 island size and distance from the source of species will affect the "equilibrium" number of species. That is, large islands that are close to the mainland will have more species than small islands far from the mainland.

The relationship between number of species on an island and the area of the island is one of the cornerstones of island biogeography theory. The species-area relationship has been discussed since the nineteenth century, and MacArthur and Wilson (1967) proposed that the number of species on an island could be approximated by the equation:

$$S = CA^z$$

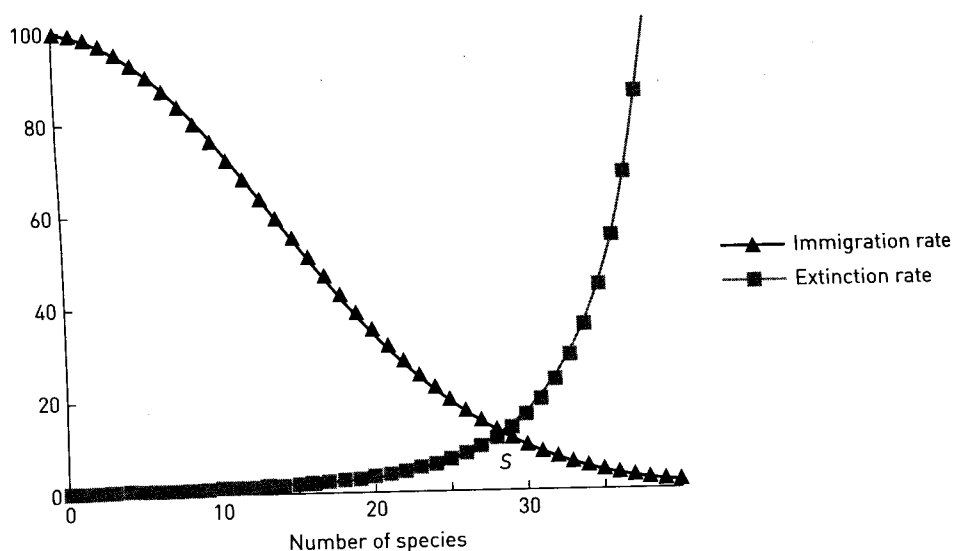
where  $S$  = the number of species on the island,  $A$  = the area of the island,  $C$  = a constant (the  $y$ -intercept, see below), and  $z$  = a constant which remains fairly consistent within a taxonomic group and/or the types of islands being considered.

The above equation can be log-transformed as follows:

$$\text{Log } S = \text{Log } C + z \text{ Log } A \quad (5.1)$$

This is an equation for a straight line with a slope =  $z$ , with  $\text{log } C$  as the  $y$ -intercept. Thus, if data are gathered on the area of islands of different sizes and on the number of species on each island, a regression of the log-transformed data will produce a linear equation with slope  $z$ . The slope is relatively consistent within a taxonomic group but also depends on the type of island system. That is, the  $z$ -value depends on whether we are dealing with true oceanic islands, recently isolated islands ("land-bridge" islands), or habitat islands. According to MacArthur and Wilson (1967),  $z$ -values range from 0.20 to 0.40 for oceanic islands, 0.1 to 0.25 for arbitrary portions of the mainland, and greater than 0.26 for habitat islands (Gould 1979, Quinn and Harrison 1988). Preston (1962) showed that a  $z$ -value 0.26 is expected when the log of species abundance versus the number of species has a normal distribution.

Gould (1979) pointed out that a slope of 0.25 is extremely common for species-area curves. What is of interest are those  $z$ -values differing significantly from 0.25. When we simply sample larger and larger areas of habitats not isolated from each other, the  $z$ -values are theorized to be smaller than the expected 0.25. When small areas are sampled they include a number of transient species passing through the area, raising the number of species. The result is a smaller-than-expected rise in the number of species with increasingly large sample areas. Thus, ants from non-isolated continental areas in New Guinea (Wilson 1961) have a  $z$ -value of 0.17, mammals from the Sierra Nevada in California have a  $z$ -value of 0.12 (Brown 1971b), and birds from the Great Basin of the USA a  $z$ -value of 0.17 (Brown 1978). By contrast, larger-than-expected  $z$ -values arise when islands contain great habitat diversity, with semi-isolated unique biota encountered as sample areas are increased. Examples include terrestrial invertebrates found in caves ( $z = 0.72$ , Culver *et al.* 1973), mites on cushion plants ( $z = 0.42$ – $0.69$ , Tepedino and Stanton 1976), and mammals on isolated mountaintops ( $z = 0.43$ , Brown 1971b, and  $z = 0.33$ , Brown 1978). Lawrey (1991, 1992) has suggested that pollution, by reducing interspecific competition, produces larger-than-expected  $z$ -values for lichen species on rocks of differing sizes. Whereas  $z$ -values varied from 0.16 to 0.21 for six undisturbed sites, a site disturbed by air pollution near the Capital Beltway in Maryland yielded a species-area curve with a  $z$ -value of 0.28.



**Figure 5.1** Immigration and extinction curves from the island biogeography model of MacArthur and Wilson (1967).  $S$  is the equilibrium number of species, where the two curves intersect.

Some scientists have asserted that as islands get larger the topography becomes more complex, there are more habitats, and therefore we have more species. In their study of red mangrove islands, however, Simberloff and Wilson (1969, 1970) found that species number increased with island size alone and was unrelated to habitat diversity.

The number of species found on an island, according to MacArthur and Wilson, was due to two contrasting processes of (i) **immigration** and (ii) **extinction**. Extinction was envisioned as a normal, locally common event, while new species were added through immigration from the mainland. Diversity was the result of the equilibrium between immigration and extinction. Furthermore, the theory indicated that once the "equilibrium" number of species was reached, the only constant was the **number of species** in the community, not the identity of the species involved (Fig. 5.1). Since extinction is a locally common process, there should be a regular "turnover" in the species found on the island.

The expected number of species on an island is affected not only by the area of the island, but also by the distance of the island from the source of species. Immigration rates are lower on smaller islands and on islands further from the "mainland" source of species. By contrast, immigration rates are higher on larger islands and on islands closer to the "mainland." Extinction rates are expected to be higher on small islands, since average population sizes are smaller (Wilson 1992).

The rate at which new immigrant species establish themselves on the island falls as the number of species on the island increases. As more species become established on the island, fewer individual immigrants will belong to a species not already present; moreover it will be harder for a new species to successfully colonize due to competition with the already established species. Species with high dispersal rates are those that arrive quickly, while those with lower dispersal rates arrive more slowly. Because of the proposed colonization-competition trade-off, the species with lower dispersal rates are likely more competitively dominant.

The extinction curves are present, the more the competition increases and the probability of extinction in a community will be saturated on the island, though species diversity is not.

The MacArthur and Wilson model of conservation biology is based on the spatial dynamics of species in a metapopulation biogeography model. Both the probability of extinction and the probability of immigration to extinction; and both the probability of extinction and the probability of immigration to extinction; and both the probability of extinction and the probability of immigration to extinction. A property of diversity is that it is a function of the number of habitats (or islands). A property of diversity is that it is a function of the number of habitats (or islands). Furthermore, island theory indicates that the probability of extinction is a function of the number of habitats (or islands). Furthermore, island theory indicates that the probability of extinction is a function of the number of habitats (or islands).

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#### 5.4 The Levins model

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- 1 The local population size, even though it is a function of the number of habitats (or islands).
- 2 extinctions, which are a function of the number of habitats (or islands).

The extinction curve rises as more species arrive on the island. The more species that are present, the more that can become extinct. But again, as more species are present, competition increases and the average population size per species declines, leading to an increased probability of extinction. Finally, if succession proceeds to a "climax" stage, the community will be saturated with species. At equilibrium, the number of species will be constant on the island, though some new species will continue to arrive while others will go extinct.

The MacArthur and Wilson equilibrium theory captured the imagination of ecologists, conservation biologists, and biogeographers, making it the leading paradigm for the spatial dynamics of species during the 1980s. It shares much of the conceptual framework of metapopulation biology. Both view nature as subdivided into discrete fragments of suitable habitat; both view local populations as subject to stochastic processes and prone to extinction; and both stress the importance of movements of individuals between habitats (or islands). A key difference is that island biogeography stressed the community property of diversity rather than focusing on the dynamics of individual populations. Furthermore, island theory was developed to explain patterns at large spatial scales as opposed to fragmentation of landscapes at small scales (Hanski 2002).

The MacArthur and Wilson model is now categorized as a **mainland-island metapopulation**. There is a constant source of species, the mainland. The mainland population is seen as permanent, with no chance of extinction. Furthermore, dispersal is one-way. Species move from the mainland to the island; the reverse is not significant. Finally, no movement from one island to another is included in this type of metapopulation.

#### 5.4 The Levins or classical metapopulation

According to the Levins model, metapopulation persistence is due to a stochastic balance between local extinction and re-colonization of empty habitat patches. The rate of change in occupied habitat patches is a function of colonization rates ( $c$ ) and extinction rates ( $\epsilon$ ) as shown in Equation 5.2 (Levins 1969).  $P$  is the proportion of patches occupied by the population under consideration.

$$\frac{dP}{dt} = cP(1 - P) - \epsilon P \quad (5.2)$$

As described by Hanski (2001), if we define  $P'$  as the number of habitat fragments occupied by the species (rather than the proportion), and define  $T$  as the total number of habitat patches available, the equation can be modified as follows:

$$\frac{dP'}{dt} = cP'(T - P') - \epsilon P' \quad (5.3)$$

Both of these models are deterministic descriptions of the rate of change of metapopulation size, even though the models are based on stochastic events. Assumptions include:

- 1 The local populations are identical and have the same behavior;
- 2 extinctions occur independently in different patches and therefore local dynamics are asynchronous;



- 3 colonization spreads across the entire patch network and all patches are equally likely to be "encountered;"
- 4 furthermore, all patches are equally connected to all other patches.

In the Levins model we are not concerned with population dynamics within each population. We do not attempt to assess the number of individuals in each patch; we simply record a patch as occupied or not occupied. For this reason we also do not assess the size or quality of the patches.

The equilibrium value of  $P$  can be obtained by setting  $dP/dt = 0$ . This produces the expected proportion of patches to be occupied and amounts to a carrying-capacity term such as is found in the logistic equation.

$$0 = cP(1 - P) - \epsilon P = P(c - cP - \epsilon)$$

Since  $P = 0$  is not an interesting solution, we have:

$$0 = c - cP - \epsilon, \quad \text{and} \quad \epsilon = c - cP$$

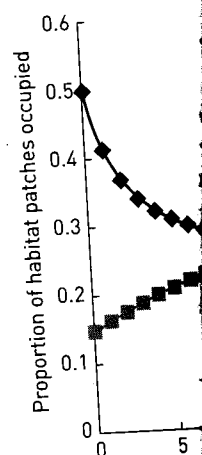
The equilibrium value of  $P$ , defined as  $\hat{P}$  and found by solving the above for  $P$ , is shown in Equation 5.4:

$$\hat{P} = \frac{c - \epsilon}{c} = 1 - \frac{\epsilon}{c} \quad (5.4)$$

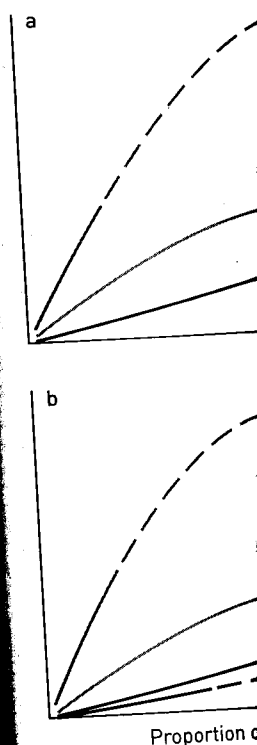
The implication here is that colonization must be greater than extinction or the equilibrium proportion of patches occupied will be zero, and the colonization rate must be greater than the extinction rate for persistence of the metapopulation. If we consider colonization a "birth" event and extinction a "death" event (thereby using  $c - \epsilon$  as the equivalent of the growth rate,  $r$ , in the logistic equation) and we use  $1 - \epsilon/c$  to represent a "carrying capacity" term (equivalent to  $K$  in the logistic equation) as mentioned above, we can model metapopulation dynamics as a modification of the logistic (Equation 5.5). No matter what the starting patch frequency is (assuming  $1 \geq P > 0$ ), over time it moves to the expected value based on  $\hat{P} = 1 - \epsilon/c$  (see Fig. 5.2).

$$\frac{dP}{dt} = (c - \epsilon)P \left( 1 - \frac{P}{1 - \epsilon/c} \right) \quad (5.5)$$

This simple model has helped ecologists develop insights into the consequences of habitat destruction and fragmentation. For example, imagine a fragmented landscape in which a fraction of the habitat patches is destroyed. The extinction rate is not affected, but the colonization rate is. This is because there are fewer local populations and fewer empty patches. If the patch connectivity is reduced, it can be modeled by reducing the value of  $c$ . Habitat destruction can therefore lead to a reduction in the proportion of patches that are occupied. Alternatively, if no patches are destroyed but they are reduced in area, this would result in lower average population sizes, which would increase the extinction rate. Simultaneously, colonization rate would be reduced due to the smaller population sizes in the occupied patches. The net result again is a reduction in the fraction of occupied patches (Fig. 5.3).



**Figure 5.2** Expected  $P$  from Equation 5.5. In this example,  $c = 0.5$  and the extinction rate  $\epsilon = 0.25$ , so the equilibrium  $P = 1 - \epsilon/c = 0.5$ .



**Figure 5.3** (a) The effect of a reduction in the colonization rate on the proportion of patches occupied. (b) The effect of a reduction in the extinction rate on the proportion of patches occupied. In both cases, the proportion of patches occupied increases over time.

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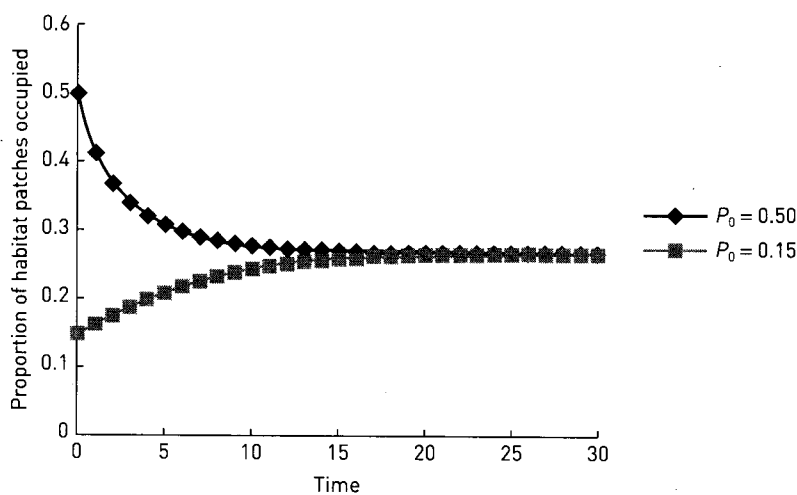
above for  $P$ , is shown

(5.4)

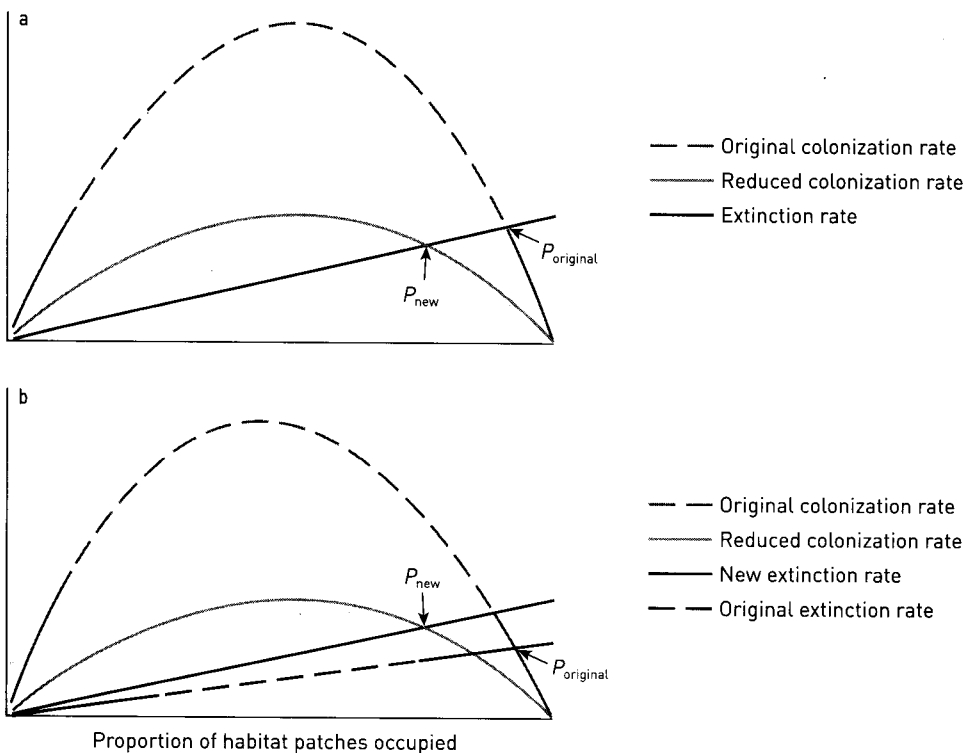
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**Figure 5.2** Expected proportion of habitat patches occupied, based on Equation 5.5. In this example  $P_0 = 0.50$  and  $0.15$ , the colonization rate  $c = 0.75$ , and the extinction rate  $\epsilon = 0.55$ . The expected proportion of patches occupied at equilibrium  $= 1 - \epsilon/c = 0.27$ .



**Figure 5.3** (a) The effect on patch occupancy of a lowered colonization rate due to a reduction in the number of habitat patches. (b) Expected changes in patch occupancy with lower colonization rate and increased extinction rate. Colonization rate is reduced by loss of habitat number; extinction rate is increased by reduction in patch area. Adapted from Hanski (1999).

**Table 5.1** Potential causes of local and metapopulation extinctions (Hanski 1998).

	Local extinction	Metapopulation extinction
Stochastic processes	(a) Demographic (b) Environmental	(a) Extinction-colonization interaction (b) Regional processes
Extrinsic causes	Habitat loss	Habitat loss and fragmentation

**5.5 Extinction in metapopulations**

In metapopulation dynamics, as well as in the MacArthur and Wilson theory, the extinction of a local population is not uncommon. But we are more interested here in the extinction of the metapopulation. Table 5.1 (Hanski 1998) summarizes the potential causes of both local and metapopulation extinctions.

We need only comment on the comparison of stochastic processes in local versus metapopulation extinctions. One of the assumptions for long-term metapopulation persistence is that the expected number of new populations generated by one existing population during its lifetime must be greater than one. That is, the replacement rate must be greater than one, as is true for a local population to persist. In a small metapopulation, however, all local populations may go extinct by chance. This is known as “extinction-colonization stochasticity” (Hanski 1998). This is an exact analogue to demographic, stochastic extinction of a local population (Chapter 1). This may happen even if the replacement rate is greater than one in both local populations and metapopulations. Regional stochasticity is due to processes such as large-scale weather patterns, which produce synchrony among the independent local populations. This effectively reduces the number of independent populations and makes metapopulation-level persistence less likely.

**5.6 Metapopulation dynamics of two local populations**

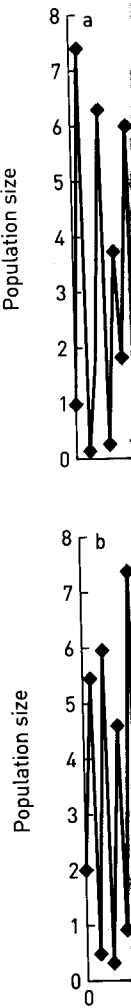
Recall that in the discrete-time population model, when  $r$  was set  $> 2.69$  (Fig. 2.19) the population underwent chaotic behavior (May 1974, 1976b). However, if two such populations are connected to each other by migration a number of interesting and unexpected changes occur (Hanski 1999).

In this example the Ricker model, is used:

$$N_{t+1} = N_t e^{r(1-\frac{N_t}{K})}$$

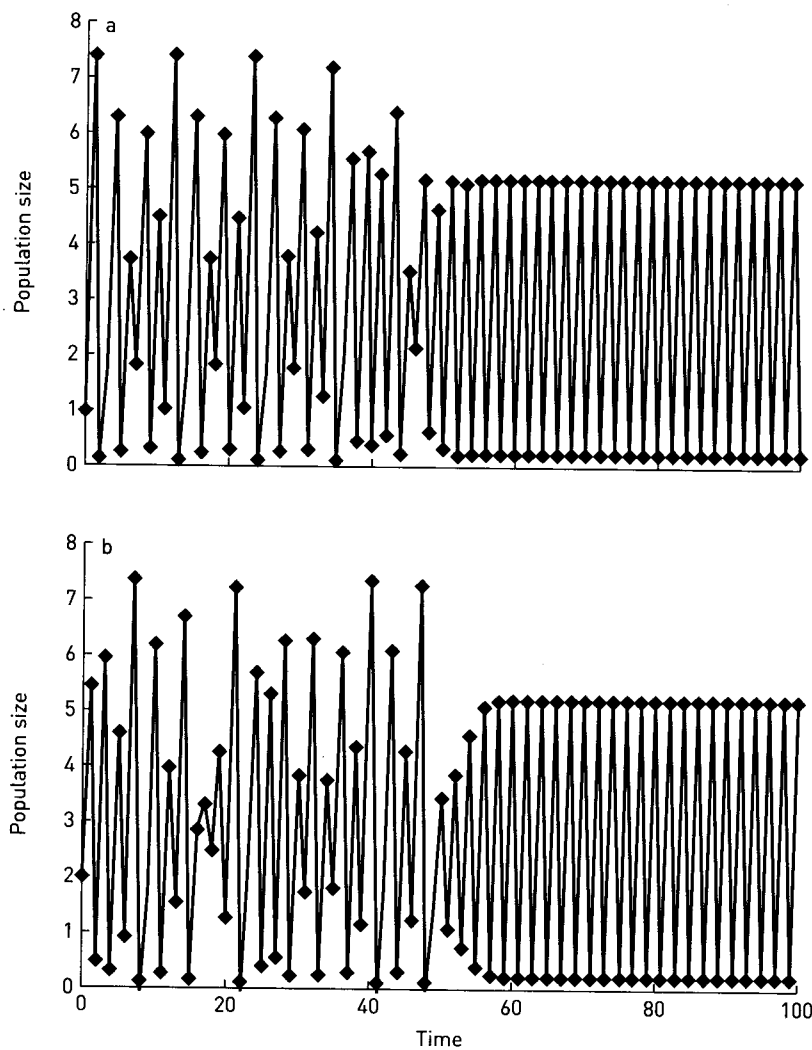
(5.6)

In populations one and two, shown in Fig. 5.4,  $r = 3$  and  $K = 3$ . Population one is initiated with one individual ( $N_0 = 1$ ), while for population two  $N_0 = 2$ . Each population and the metapopulation (Fig. 5.5) behave chaotically. The metapopulation is simply the sum of populations one and two. At time = 49 the two populations are connected by allowing 30% of the individuals to emigrate. The emigrants are divided equally between the



**Figure 5.4** Two local populations (a) Population one and (b) Population two at  $t = 49$ .

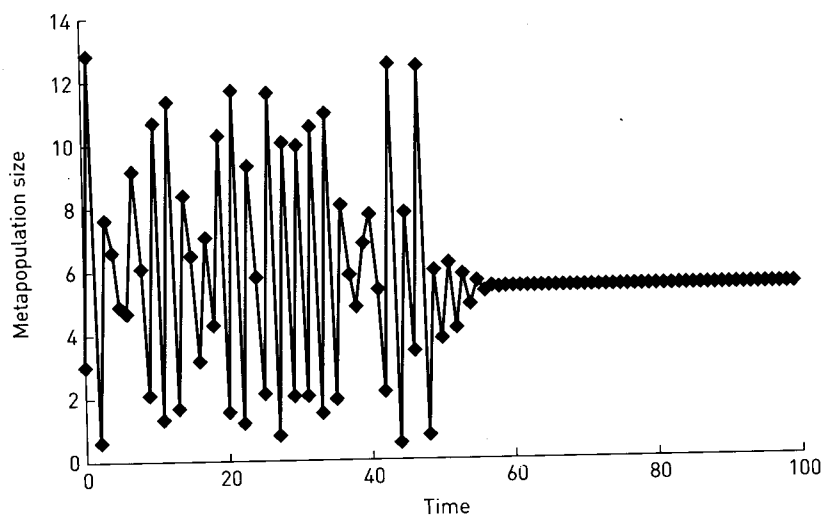
two populations. populations (Fig. 5.5) cycles out of phase. ilized (Hanski 1999). Gyllenberg *et al.* tion dynamics, ab izing effect. Simil population with a between local po populations them not to push this t



**Figure 5.4** Two local populations. (a) Population one:  $N_0 = 1$ ,  $r = 3$ ,  $K = 3$ . (b) Population two:  $N_0 = 2$ ,  $r = 3$ ,  $K = 3$ . The two populations are connected at  $t = 49$ .

two populations. The migrations calm the chaotic behavior, and by time = 55 the two populations (Fig. 5.4) have moved to a two-point limit cycle. The two populations go through cycles out of phase with each other, and the metapopulation (Fig. 5.5) is completely stabilized (Hanski 1999).

Gyllenberg *et al.* (1993) have confirmed that migration can help stabilize local population dynamics, although some mortality must occur during migration to have a stabilizing effect. Similarly, migration from a permanent (mainland) population or from a population with a low growth rate also has a stabilizing effect. Movement of individuals between local populations has, at least theoretically, a stabilizing effect on the local populations themselves as well as on the metapopulation. We are well advised, however, not to push this theoretical point too far in field populations (Hanski 1999).



**Figure 5.5** Metapopulation of populations one and two from Fig. 5.4. The two populations are connected at  $t = 49$ . The metapopulation is stabilized at  $t = 55$ .

### 5.7 Source-sink metapopulations and the rescue effect

The concept of source-sink metapopulations was put into the literature by Pulliam (1988), and is based on the fact that habitats are not uniform but differ in quality. High-quality patches produce large populations with positive growth rates, and are likely to be a source of emigrants. These high-quality areas, where  $r > 0$ , are known as **source patches**. Other habitat patches are of low quality, have small populations, and consistently have negative growth rates. That is, populations in **sink patches** have a negative  $r$  in the absence of immigration (Hanski 1999). If and when migrants from source populations arrive at sink patches, they become either founders of new populations, or new members of established populations. The **rescue effect** is based on the idea that emigrants from source areas regularly supplement these small, extinction-prone populations. If the expected size of the small population is increased through this supplementation it becomes less prone to, or is **rescued from**, extinction (Brown and Kodric-Brown 1977). In a true sink habitat a population would decline to extinction if cut off from its source population. A **pseudo-sink** population is one in which the population would decline to a lower equilibrium, but not go extinct, if cut off from its source population (Watkinson and Sutherland 1995). In practice it is difficult to distinguish between a true sink and a pseudo-sink population in the field.

The MacArthur and Wilson (1967) island biogeography theory, a mainland-island metapopulation, has much in common with source-sink metapopulations in that mainlands are large compared to islands and, in theory, not prone to extinction, while islands are small and there is always a finite probability of extinction. The mainland is the source, while the islands are, collectively, sink populations. While MacArthur and Wilson (1967) emphasized that extinction is a normal process in a community, they envisioned the mainland as a more or less uniform patch when compared to the island populations, and that

the mainland would function to occur on islands, the islands in a normal year (Elmhagen and Foster 1986a, 1986b).

One of the best illustrations of this is provided by the study of Island in Panama. They maintained populations over a 13-year period. The plot was a result of immigration.

Sink populations can be maintained. Assume that the source populations in size because of drought or fire. In this case, a sink (Gyllenberg *et al.* 1998).

### 5.8 Non-equilibrium

In examining the literature, that the term has also been used to describe **equilibrium metapopulations** with a high colonization rate. With the restoration of functional extinction.

By contrast, in a patchy subpopulations function that patchy population distinct breeding subpopulations between the extremes (Angerbjörn 2001).

### 5.9 Spatially realistic

The Levins model assumes that subpopulations function independently in different habitats. If the subpopulations were equally connected, from one population to another in spite of the importance of the spatial structure.

Most metapopulation models have no consequences to the reasonable assumption that individuals when a population of non-breeding males was or an existing group of butterflies and other insects deposition. Male and

the mainland would function as a source indefinitely. Moreover, while extinction was assumed to occur on islands, the island populations were also assumed to have positive growth rates in a normal year (Elmhagen and Angerbjörn 2001).

One of the best illustrations of the source-sink concept comes from the study by Hubbell and Foster (1986a, 1986b) of a 50-hectare plot of tropical moist forest on Barro Colorado Island in Panama. They mapped over 238,000 individual trees and shrubs of 314 species over a 13-year period. They found that at least one-third of the rare species were not self-maintaining populations. They were not reproducing effectively and their presence in the plot was a result of immigration from outside of the 50-hectare plot.

Sink populations can be important to the long-term survival of a source population. Assume that the source population is prone to chaotic behavior, or shows great fluctuations in size because of disease or sensitivity to environmental fluctuations such as drought or fire. In this case the source population itself could be rescued if connected to a sink (Gyllenberg *et al.* 1993).

### 5.8 Non-equilibrium and patchy metapopulations

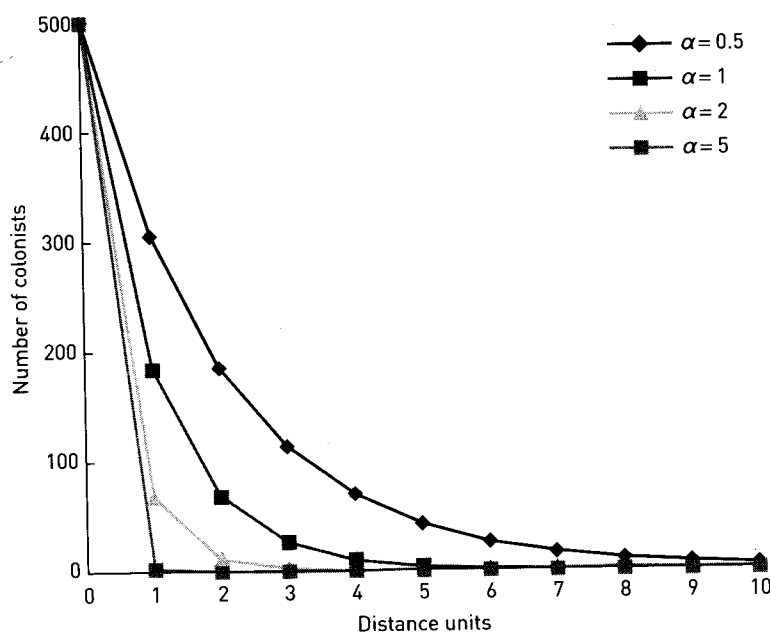
In examining the literature on metapopulation studies, Harrison (1991, 1994) found that the term has also been used to describe two other kinds of situations. In a **non-equilibrium metapopulation** the rate of extinction among the populations exceeds the colonization rate. Without some change in the dynamics of the system, including perhaps restoration of functioning habitat patches, the ultimate fate of such a metapopulation is extinction.

By contrast, in a **patchy population** the migration rate is so high that the so-called subpopulations function effectively as one single population. Hanski (1999) has asserted that patchy populations should be excluded from metapopulation theory since they lack distinct breeding subpopulations. The classical metapopulation of Levins is found between the extremes of patchy and non-equilibrium metapopulations (Elmhagen and Angerbjörn 2001).

### 5.9 Spatially realistic models

The Levins model assumed that local populations were identical; extinctions occurred independently in different patches; all patches were equally likely to be found; and patches were equally connected to each other. He did not try to describe how individuals move from one population to another, nor did he allow for differences in patch size or quality, in spite of the importance assigned to island size by MacArthur and Wilson.

Most metapopulation models also assume unconditional emigration. That is, there are no consequences to the source population from losing individuals. This seems to be a reasonable assumption in most populations since emigrants are often pictured as "extra" individuals when a population has reached or exceeded its carrying capacity. In many species non-breeding males venture away from the family group looking for an empty territory or an existing group that they may join in order to become breeders. Females of butterflies and other insects emigrate in order to find newly available host plants for egg deposition. Male and female dung beetles emigrate when the dung pile they were born



**Figure 5.6** Number of colonists arriving at different distances, based on a negative exponential model,  $C_i = \beta e^{-\alpha d_i}$ , and using different  $\alpha$  values.  $C_i$  = the number of colonists arriving at a distance  $d_i$  from the source population. In all cases  $\beta = 500$ .

into has become depleted. If the mortality rate of dispersers, however, is much higher than that of individuals who remain “home,” a very high population dispersal rate (large percentage dispersing) can lead to local, and sometimes metapopulation, extinction (Hanski 2002, J. Mickelberg, personal communication).

The rate and the scale of re-colonization of an empty habitat depend on the shape of the dispersal curve of the population. A simple model of animal movement is based on a random walk, using a coefficient of diffusion ( $D$ ) and a normal distribution for movements, the variance of which increases with time ( $2Dt$ ) (Okubo 1980). Studies of animal emigration, however, indicate that more individuals move very short and very long distances than predicted by random walks (Johnson and Gaines 1990). In metapopulation models emigration distances are usually modeled using a negative exponential function, which is a reasonable approximation of reality (Hanski 2002) (Eqn. 5.7, Fig. 5.6). Two characteristics determine the dispersal efficiency of a species. One is the number of individuals dispersing (here equal to  $\beta$ ) and the dispersal ability of each individual ( $\alpha$ ). Species differ a great deal in the amount of energy invested in reproduction each year. Obviously the more energy invested in reproduction, the greater the number of dispersal units. But for a given reproductive effort, species also differ in whether they produce a smaller number of large offspring or a larger number of small offspring. The smaller the dispersing unit, the greater distance it is likely to travel. Many highly dispersed organisms are so small that the wind can carry them hundreds or even thousands of miles. On the other hand, acorns only move as far as gravity or squirrels will take them. In Equation 5.7  $\alpha$  is directly associated with a greater colonizing ability per unit of dispersal, while  $\beta$  is associated with the number of colonists produced per individual from the source

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population.  $C_i$  is the colonization probability per unit time for population  $i$  and  $d_i$  is the distance from the source population.

$$C_i = \beta e^{(-\alpha d_i)} \quad (5.7)$$

where  $\alpha$  and  $\beta$  are site- and species-specific parameters.

What is most important to a metapopulation is the proportion of individuals that move long distances. The exact shape of the distribution of migration distances among emigrants is therefore of great importance, but it is very hard to estimate in most populations (Hanski 2002).

We will discuss one approach that has been proposed to make metapopulation models more realistic, the **incidence function model** (IFM) championed by Hanski and his colleagues (Hanski 1994a, 1994b, 1999, Hanski and Gilpin 1997). The IFM is a **stochastic patch model** in which the population in each patch has one of two states, presence or absence. The IFM includes: (i) a finite number of habitat patches; (ii) patches of different sizes (sometimes including differences in quality and shape); and (iii) each patch having a unique spatial coordinate so that interactions among patches are localized in space. Since habitat patches are simply occupied or not, there is usually no estimation of population sizes or dynamics within patches. The major virtue of the IFM is that it is constructed so that parameters can be estimated from field data. This allows the application of this model to real populations.

The IFM begins with the assumption that for an empty habitat patch,  $i$ , there is a constant probability,  $C_i$ , of re-colonization per unit time. If a patch is occupied, there is a constant probability,  $E_i$ , of extinction per unit time. One event, either colonization or extinction, is allowed per time period. The long-term probability of the patch being occupied is called the "incidence" or  $J_i$  (Eqn. 5.8). The incidence function model is based on discrete time intervals, and is a stochastic rather than a deterministic model (Hanski 2001).

$$J_i = \frac{C_i}{C_i + E_i} \quad (5.8)$$

There are a number of difficulties if we are modeling a true metapopulation with no "mainland" source of species. With no external mainland, metapopulation extinction is the only true steady state (Hanski 1999). However, a metapopulation may theoretically persist for very long periods of time.

Recall that in the rescue effect the probability of extinction on a habitat patch is reduced through immigration of individuals from other patches. In order to allow for the rescue effect, Hanski modified the probability of extinction between times  $t$  and  $t + 1$  by substituting  $(1 - C_i)E_i$  for  $E_i$ . This modified equation is:

$$J_i = \frac{C_i}{C_i + E_i - C_i E_i} \quad (5.9)$$

Hanski (1999) then derived a relationship between extinction probability,  $E_i$ , and the size of the patch area,  $A_i$ , using the basic reasoning of the species-area curve. That is, extinction probability depends on population size, which is a function of patch area. The general relationship is as expressed below (Eqn. 5.10) in which  $e$  and  $X$  are estimated from the



data. The value  $e$  is a parameter related to the probability of extinction per unit time in a patch of a given size. The parameter  $X$  is a measure of environmental stochasticity (Hanski 1999).

$$E_i = \frac{e}{A^X} \tag{5.10}$$

Colonization probability,  $C_i$ , is a function of the number of immigrants,  $M_i$ . In a simple mainland-island metapopulation, the colonization probability is a function of distance ( $d_i$ ) from the mainland, which was expressed above as Equation 5.7.

For a true metapopulation, however,  $M_i$  is the sum of individuals arriving from all of the surrounding habitat patches.  $M_i$  can be written as a summation for all patches:

$$M_i = \beta S_i = \beta \sum_{j \neq i} e^{(-\alpha d_{ij})} p_j A_j \tag{5.11}$$

In this equation  $d_{ij}$  represents the distance between patches  $i$  and  $j$ ;  $p_j$  is 0 for an unoccupied patch and 1 for an occupied patch; and  $A_j$  is the size of the patch. The summation term is represented by  $S_i$ , which becomes a measure of patch isolation or, to put it positively, patch connectivity. If population sizes ( $N_j$ ) are known for each patch,  $S_i$  can be written as:

$$S_i = \sum_{j \neq i} e^{(-\alpha d_{ij})} N_j \tag{5.12}$$

As above, the term  $\alpha$  describes how fast the immigration rate from patch  $j$  declines with distance. Hanski suggests that this term can be found through mark-recapture data.

If interactions among immigrants are negligible,  $C_i$  increases exponentially with  $M_i$ . However, there is often a sigmoid relationship between the number of immigrants and successful re-colonization by a given species. Therefore  $C_i$  can be written as:

$$C_i = \frac{M_i^2}{M_i^2 + y^2} \tag{5.13}$$

where  $y$  is a parameter fitted from the data. In the sections below the terms  $y$  and  $\beta$  are combined simply as  $y$  (Hanski 1999).

Once equations were developed for the dependence of extinction on patch size and colonization on patch connectivity, Hanski combined them into the usual form of the incidence function model:

$$J_i = \frac{1}{1 + \frac{ey}{S_i^2 A_i^X}} \tag{5.14}$$

As before,  $J_i$  is the probability that a patch,  $i$ , is occupied;  $y$  is a parameter related to successful immigration;  $A_i$  represents the area of the patch  $i$ ;  $X$  is the rate of change of

extinction per unit time with patch size (stochasticity); and  $S_i$  describes the connectivity of patch  $i$  (immigration rate. Equation 5.11).

If we manipulate and take the log of both sides of a linear relationship between  $\ln J_i$  and  $\ln S_i$ , we get a linear relationship between  $\ln J_i$  and  $\ln S_i$  variables, connectivity ( $S_i$ ).

Hanski (1999) has described this model and has applied the model to field data gathered from Kindvall (1995) found that the model's predictions about the relationship between patch occupancy and patch size were very good.

In Table 5.2, from Kindvall (1995), we see that the model's predictions about the relationship between patch occupancy and patch size were very good.

**Table 5.2** Results of field data for bush cricket *Metrioptera* *sp.*  $P$  is mean proportion of patches occupied. Predicted mean proportion of patches occupied. Adapted from Kindvall (1995).

Parameters	
Number of available patches	
Actual $P$	
Predicted $P$	
Multiplier of $X$	
for the rescue effect	
$\alpha$	
$X$	
$y$	
$e$	

extinction per unit time with increasing patch size (a measure of environmental stochasticity); and  $S_i$  describes the connectivity between patches, that is, the effect of distance on immigration rate. Equation 5.14 can be rewritten as:

$$J_i = \frac{1}{1 + e^{\ln(e\gamma) - 2 \ln S_i - X \ln A_i}} \tag{5.15}$$

If we manipulate and take natural logs of both sides of this equation we come up with a linear relationship between the expected patch occupancy ( $J_i$ ) and the two independent variables, connectivity ( $S_i$ ) and size ( $A_i$ ) of the habitat patches:

$$\ln\left(\frac{J_i}{1 - J_i}\right) = -\ln(e\gamma) + 2 \ln S_i + X \ln A_i \tag{5.16}$$

Hanski (1999) has described how to estimate all of these parameters from field data, and has applied the model to simulate metapopulation dynamics in butterflies (Hanski *et al.* 1995, Wahlberg *et al.* 1996), the American pika (*Ochotona princeps*) (Moilanen *et al.* 1998), and a number of other species. The basic information needed in order to apply this model in the field is simply the area of each habitat patch and the inter-patch distances ( $d_{ij}$ ). Subsequently, model parameters must be estimated. First  $\alpha$  is estimated from mark-recapture data or estimated from patch-occupancy data. The parameters  $\gamma$  and  $e$  are fitted to empirical data using nonlinear regression techniques. The value of  $X$  is fitted from the data and can be modified to include the rescue effect.

In Table 5.2, from Kindvall (2000), are the results of fitting the incidence function model to field data gathered from a fragmented population of the bush cricket *Metrioptera bicolor*. Kindvall (1995) found that using occupancy data from a single year did not result in realistic predictions about the metapopulation. When parameters for the IFM were estimated from patch occupancy over a five-year period, better results were obtained.

**Table 5.2** Results of fitting the incidence function model to occupancy data of the bush cricket *Metrioptera bicolor* for two areas of Sweden during the period 1989–94.  $P$  is mean proportion of available habitats actually occupied from 1990 to 1994. Predicted mean proportion of patches occupied is based on 100 replicates. Adapted from Kindvall (2000).

Parameters	Western area	Eastern area
Number of available patches	66	50
Actual $P$	0.82	0.71
Predicted $P$	0.80	0.62
Multiplier of $X$ for the rescue effect	0.05	0.001
$\alpha$	2.0	6.0
$X$	0.876	0.514
$\gamma$	7.278	2.571
$e$	0.072	0.029

**Table 5.3** The predicted and observed annual extinction and colonization rates for three species of shrews (*Sorex*) on small islands. Parameters for this mainland–island incidence function model were from 68 islands and applied to a different set of 17 islands. *X* and *e* are annual extinction parameters. *C* = annual colonization rate; *E* = annual extinction rate. Adapted from Peltonen and Hanski (1991), Hanski (1993).

Species	Body size (g)	Parameter estimates		Predicted		Observed	
		<i>X</i>	<i>e</i>	<i>C</i>	<i>E</i>	<i>C</i>	<i>E</i>
<i>S. araneus</i>	9	2.30	0.20	0.26	0.04	0.20	0.04
<i>S. caecutiens</i>	5	0.91	0.53	0.03	0.28	0.05	0.33
<i>S. minutus</i>	3	0.46	0.73	0.18	0.53	0.13	0.46

Kindvall (2000) compared the incidence function model to three other spatially realistic models, including a logistic regression model (Sjögren-Gulve and Ray 1996), and found the logistic regression model performed best in its ability to predict regional occupancy, local occupancy, and the number of colonizations and extinctions. Nevertheless he found the IFM did a reasonable job of predicting the actual outcomes for the bush cricket in Sweden.

The application of the IFM to mainland–island populations can be simpler since there are fewer parameters to estimate. One example is a study on the occurrence of small mammal populations on islands in lakes and in the sea (Peltonen and Hanski 1991, Hanski 1993). The IFM was based on the occurrence of three species of shrew (*Sorex*) on 68 islands. Using parameters estimated from this study, Hanski (1993) predicted the annual colonization and extinction probabilities on 17 additional islands. The observed and the predicted rates were well matched (Table 5.3). In this study only the extinction parameters (*X* and *e*) were estimated since colonization was from the mainland and was assumed not to differ among islands (Hanski 1999). The value *X* is inversely related to the strength of environmental stochasticity: a large value of *X* means weaker environmental stochasticity. The value of *X* is directly correlated with body mass in the shrews described in Table 5.3, as well as in birds from four different areas (Cook and Hanski 1995). What this implies is that species with larger mass (such as *Sorex araneus*) are less affected by environmental stochasticity as compared with species with a smaller mass (Hanski 1999). Table 5.3 also suggests that only *Sorex araneus* has a long-term metapopulation survivorship, since it is the only species with a *C* > *E*.

5.10 Minimum viable metapopulation size

As discussed in Chapter 1, conservation biologists introduced the concept of minimum viable population size (Soule 1980), although this approach has been replaced by various population-viability analyses. The MVP size was intended to estimate the minimum number of individuals necessary for a population to have a specific probability of surviving for a fixed period of time. When applied to metapopulations the analogous concept would

be defined as the persistence of the metapopulation. Hanski developed a stochastic model of the metapopulation.

If  $\hat{P}$  is the fraction of occupied habitat patches, then the metapopulation is considered to be viable if  $\hat{P} > 3$ .

For example, if the extinction rate is 100 times  $T_L$ , then the metapopulation is viable if the number of habitat patches is greater than 300.

5.11 Assumptions in nature

The different types of metapopulations (sink, patchy, and source) are common in nature. The rates, and so on, of different quality patches, and where the patches are located.

What are the assumptions in nature? We demonstrate that the assumptions of the metapopulation model are not always realistic. Population data, population persistence, come from different sources. The emphasis on population viability is on the bay checkers, on the other hand, metapopulation viability is in designing a conservation strategy (2002), and is being used in the design of a metapopulation (Leontopithecus). The personal communication with Hanski (1999) suggests that the assumptions of the metapopulation model are not always realistic.

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be defined as the minimum number of local populations necessary for the long-term persistence of the metapopulation. Gurney and Nisbet (1978) and Nisbet and Gurney (1982) developed a stochastic version of the Levins model with a finite number of habitat patches and local populations. In the analysis of their results they defined long-term persistence of the metapopulation,  $T_M$ , as at least 100 times the expected time of local extinction,  $T_L$ . If  $\hat{P}$  is the fraction of occupied patches at equilibrium, and  $H$  is the total number of habitat patches, Gurney and Nisbet (1978) found that the product of  $\hat{P}\sqrt{H}$  must be greater than 3:

$$\hat{P}\sqrt{H} > 3 \tag{5.17}$$

For example, if there are 50 habitat patches, this equation says that colonization and extinction rates must be such that  $\hat{P} > 0.42$  for a metapopulation to persist more than 100 times  $T_L$ . This relationship does not take into account the size and quality of the habitat patches, but does demonstrate that long-term metapopulation persistence benefits from a large number of habitat patches.

5.11 Assumptions and evidence for the existence of metapopulations in nature

The different types of metapopulations described above (mainland-island, classical, source-sink, patchy, and non-equilibrium) are all variations on the same themes. Local extinctions are commonplace, there is an equilibrium involving colonization and extinction rates, and so on. They differ in the levels of detail, whether they allow for patches to be of different quality, whether they allow for differing levels of connectivity between patches, and whether they include local population dynamics.

What are the general assumptions we are making in all of these models? How can we demonstrate that the long-term persistence of a species in a landscape is due to metapopulation, rather than local population, processes? One difficulty is that long-term population data on patch occupancy are hard to gather. For this reason, many studies of population persistence in a fragmented landscape, meeting the criteria for a metapopulation, come from short-lived, easily monitored organisms. Accordingly, there has been an emphasis on populations of butterflies such as the Glanville fritillary (*Melitaea cinxia*) and the bay checkerspot (*Euphydryas editha*) (Hanski 1999, Ehrlich and Hanski 2004). On the other hand, metapopulation theory was famously, though perhaps inappropriately, used in designing a conservation plan for the northern spotted owl (*Strix occidentalis*) (Boyce 2002), and is being implemented in the management of both black and golden lion tamarin (*Leontopithecus chrysomelas* and *L. rosalia*) populations in South America (J. Mickelberg, personal communication).

Assumptions that metapopulation dynamics are decisive to the structure of the regional population include (Hanski and Kuussaari 1995, Hanski 1999):

- 1 The species has local breeding populations in relatively discrete habitat patches. This condition stresses that the population is spatially structured and therefore most individuals interact with others only in the local habitat patch.

- 2 No single local population is large enough to have a longer expected lifetime than the expected lifetime of the metapopulation itself. This excludes mainland-island populations.
- 3 Empty habitat patches are common. In the Glanville fritillary butterfly study in Finland, for example, 70% of approximately 1600 habitat patches have been empty at a given time (Hanski *et al.* 1995).
- 4 The habitat patches are not too isolated to prevent re-colonization. Long-distance movements may be facilitated by habitat corridors or other mechanisms.
- 5 Local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely. With complete synchrony, the metapopulation only lasts as long as the local population with the lowest chance of extinction. The greater the asynchrony, the longer the metapopulation is likely to last. In a recent review of the literature, Elmhagen and Angerbjörn (2001) found eight studies (four insect species and four small mammal species) in which asynchrony of population dynamics among patches was confirmed.
- 6 Population turnover, local extinctions, and the establishment of new populations form the basis for metapopulation dynamics, and metapopulations persist despite population turnover. Elmhagen and Angerbjörn (2001), in a review of the literature, found 22 studies confirming turnover. See supportive data below.
- 7 Population size or density is significantly affected by migration. This is the basis for source-sink populations and the rescue effect (Pulliam 1988, 1996).
- 8 Population density, colonization rate, and extinction rates are all affected by patch size and isolation.
- 9 Metapopulations can affect competitive, predator-prey, and parasite-host interactions. These ideas were discussed at the beginning of this chapter and will be elaborated in later chapters.

Reviews of metapopulation studies by Elmhagen and Angerbjörn (2001) and Harrison (1991, 1994) found that many of these criteria are frequently not met in the published metapopulation literature. Nevertheless, there is an extensive literature, particularly from studies of butterflies, supporting most of these assumptions (Ehrlich and Hanski 2004).

Supportive field studies

- 1 Boycott (1930) studied freshwater mollusk populations in 84 ponds in England. Over a 10-year period he recorded 64 extinctions and 93 colonizations of 18 species.
- 2 In their study of arthropod populations on red mangrove islands, Simberloff and Wilson (1969, 1970) removed all arthropod species by fumigation. After re-colonization of the mangroves by the arthropods, they found an equilibrium of between 20 and 40 species per island, depending on island size. But the turnover rate of species was approximately 2% of the species pool per day.
- 3 As described at the beginning of this chapter, after the explosion on Krakatau the number of bird species on Rakata seemed to reach equilibrium at 30 by 1934. Yet a consistent turnover has continued.
- 4 Hanski *et al.* (2004) described an experiment with the Glanville fritillary in which 10 local populations, derived from 72 larval groups, were transported from the Finnish island of Åland to the island of Sottungia in August 1991. Sottungia is a 4 km by 2 km island containing 20 small meadows suitable for this butterfly, although there were none at the time of the introduction. An

**Table 5.4** The number of local populations and the number of colonizations of *cinxia* on Sottungia. Adapted from Hanski *et al.* (2004).

Year	Number of local populations
1991	10
1992	10
1993	10
1994	10
1995	10
1996	10
1997	10
1998	10
1999	10
2000	10

- 5 Long-term examination of the fact that the study of stochastic processes in habitat patches of the population of habitat patches.
- 6 Crone *et al.* (1991) studied the vole (*Microtus*) in Finland. The model proved to be a source of local extinctions for the persistence of the incidence of, this is a permanent

**Table 5.4** The number of surviving local populations, the number of extinctions, and the number of colonizations per year for the metapopulation of *Melitaea cinxia* on Sottungia island in the Baltic Sea off the coast of Finland. Extinctions + colonizations = turnover events. Larvae were transported in August 1991. Adapted from Hanski *et al.* (2004).

Year	Number of local populations	Number of extinctions	Number of colonizations	Total number of turnover events
1991	10	–	–	–
1992	5	5	0	5
1993	5	1	1	2
1994	6	2	3	5
1995	3	3	0	3
1996	6	0	3	3
1997	10	0	4	4
1998	14	0	4	4
1999	2	12	0	12
2000	11	0	9	9

examination of Table 5.4 shows that this metapopulation has persisted, in spite of the fact that none of the original 10 populations lasted for the entire 11 years of the study. These data confirm the persistence of the metapopulation as a stochastic balance between local extinctions and re-colonizations of available habitat patches. Note that we are only keeping track of presence or absence of the population in a habitat; we are not making an assessment of local population numbers or local population dynamics, and there is no assessment of habitat quality.

- 5 Long-term work on the same species of butterfly on the Åland archipelago (Nieminen *et al.* 2004) over an eight-year period found: (i) the number of extinct populations varied from 131 to 234 per year; (ii) the number of colonizations ranged from 97 to 230 per year; (iii) the total number of extant populations varied from 303 to 496 per year; and (iv) the number of empty patches varied from 749 to 3507 per year.
- 6 Crone *et al.* (2001) examined the six-year data gathered by Pokki (1981) on vole (*Microtus agrestis*) populations found on the Tvärminne archipelago in Finland. Extinction and re-colonization of local island subpopulations were common, and a spatially explicit model such as the incidence function model provided reasonable predictions of the structure and function of this metapopulation. However, contrary to assumptions, the mainland did not prove to be a significant source of dispersing animals; in fact, an important source of immigrants to the larger islands came from tiny, ephemeral populations found on small islands. While these small populations were unlikely to persist, they were an important source of immigrants to larger islands on the archipelago. Crone *et al.* also found that the parameters fitted to the incidence function models varied dramatically from year to year. Most importantly, this study suggests that the “rescue effect” can be turned around such that a small ephemeral population may help stabilize a larger, more permanent population.

### 5.12 Conclusions

Metapopulation biology and spatial ecology have provided a new framework for both population and conservation biology. Spatial locations of populations and the interactions among local populations have as great an effect as the traditional parameters of birth and death rates, age structures, and interspecific interactions. Although a metapopulation was originally just a "population of populations" (Levins 1970), many of Levins' simplifying assumptions have been relaxed in modern models. As we have seen, the persistence of the metapopulation is highly influenced by: (i) the number of patches; (ii) the size and quality of the patches; and (iii) the connectivity between the patches. Spatially explicit models attempt to encompass these variables.

We have not specifically discussed the topic of corridors between patches. The usefulness of corridors to metapopulation persistence has been widely discussed. The general idea is that, since movements between populations have the potential to stabilize both the local population and the metapopulation, a corridor between habitat patches would increase connectivity and facilitate these movements. Yet in spite of intuitive appeal and theoretical support, the benefits of corridors remain a controversial topic in metapopulation and conservation biology. Although corridors have not yet been proven irrefutably to be beneficial to wild populations, Laurance and Laurance (2003) concluded that the preponderance of available evidence is positive. They recommended that corridors be regarded as beneficial in fragmented landscapes unless specific local evidence suggests otherwise.

The metapopulation approach has challenged the dogma that populations only exist in locations where they are optimally adapted. Rather, we know that local populations go extinct on even the best-quality habitats, and that so-called sink populations hang on in areas of marginal habitat. Furthermore, most natural populations are small enough to be subject to stochastic extinctions. Metapopulations, in which populations in different patches have independent growth and decline dynamics, may therefore be necessary for the long-term persistence of the regional population (Hanski 1999). Foppen *et al.* (2000) have even demonstrated that sink populations can be essential to the preservation of the populations found in larger patches.

Within a decade of the publication of MacArthur and Wilson's theory of island biogeography it dominated conservation biology to the extent that "rules" of refuge design were based on it. In the 1990s there occurred a shift, and now metapopulation theory has replaced island biogeography as the major theoretical basis for conservation biology, although its applications to specific situations should not be undertaken lightly (Doak and Mills 1994). Metapopulation theory may be replaced by some other paradigm in the future. But the overall message is clear. Spatial dynamics matter.

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### 6.1 Introduction

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