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# Metapopulation BIOLOGY

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**Ecology, Genetics, and Evolution**

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# The Metapopulation Approach, Its History, Conceptual Domain, and Application to Conservation

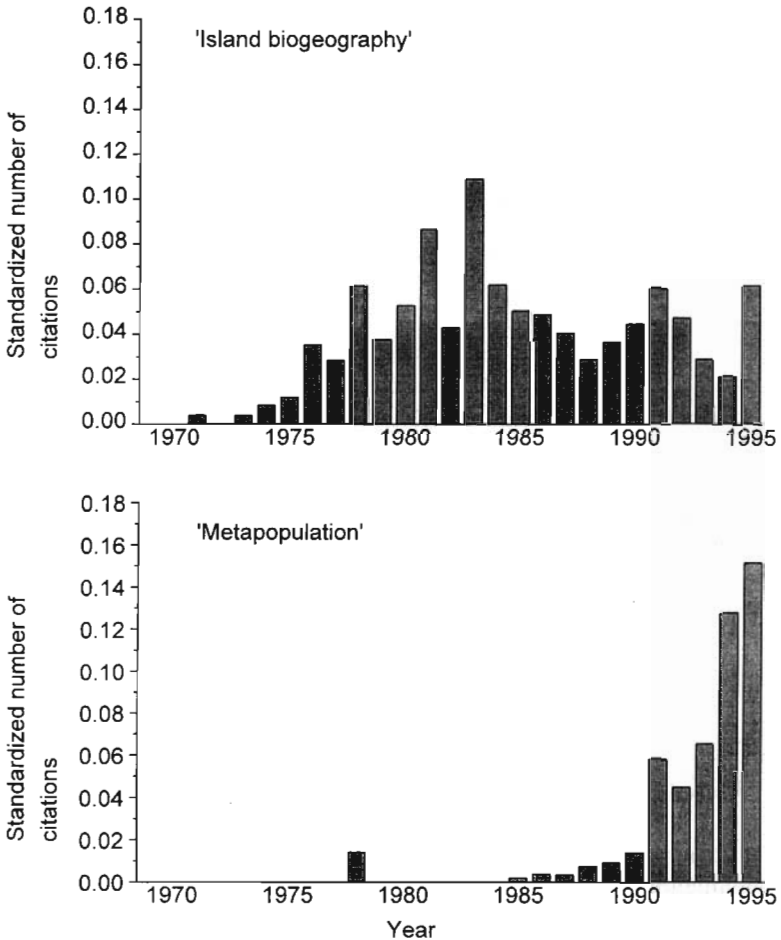
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## I. INTRODUCTION

At no period in the history of ecology has the spatial structure of populations and communities been entirely ignored, but the role that space plays in forming ecological patterns and in molding processes has been viewed very differently in different times (McIntosh, 1991). In the 1960s and 1970s, theoretical ecology was largely focused on issues other than spatial dynamics (May, 1976a), with notable exceptions (MacArthur and Wilson, 1967), and field ecologists tended to follow suit. Today, space is in the forefront and space is introduced in various ways into all fields of ecology and population biology more generally. Whether one is interested in processes occurring at the level of genes, individuals, populations, or communities, spatial structure is widely seen as a vital ingredient of better and more powerful theories, and good empirical work involving space is seen as a great challenge (Kareiva, 1990).

Five years ago, before the publication of the predecessor of this volume (*Metapopulation Dynamics: Empirical and Theoretical Investigations*, Gilpin and Hanski, 1991), the metapopulation concept was new to most biologists. Since then, literature on metapopulations has grown exponentially, with a doubling time of less than 2 years (Fig. 1). The metapopulation concept has by now been firmly established in population biology and beyond; we review and analyze in this



**FIGURE 1** Numbers of citations to the key words "island biogeography" and "metapopulation" in the BIOSIS data base in 1970–1995, standardized by the respective total number of papers in the data base.

chapter the spread of the metapopulation concept to conservation biology and applications.

What is the metapopulation approach? A more complete explication is given below, but in a nutshell the two key premises in this approach to population biology are that populations are spatially structured into assemblages of local breeding populations and that migration among the local populations has some effect on local dynamics, including the possibility of population reestablishment following extinction. These premises contrast with those of standard models of demography, population growth, genetics, and community interaction that assume a panmictic population structure, with all individuals equally likely to interact

with any others. Population biology has made productive use of such models for at least 100 years, but today there is a distinct need to account for the position of individuals and populations in space. This need has arisen from the intrinsic development of population biology as a science, but the trend has clearly been strengthened by the demand for professional advice on environmental issues typically involving space.

In the past few years, metapopulation studies have shed new light on such phenomena as patterns of distribution and population turnover dynamics in fragmented landscapes (Hanski, this volume; Harrison and Taylor, this volume; Thomas and Hanski, this volume; Smith and Gilpin, this volume; van der Meijden and van der Veen-van Wijk, this volume), landscape ecology (Wiens, this volume) and community structure (Holt, this volume), population viability and time to extinction (Gyllenberg *et al.*, this volume; Foley, this volume), coexistence of competing species, and of prey and their natural enemies (Nee *et al.*, this volume), evolution of migration rate and other life-history traits (Olivieri and Gouyon, this volume), ecological consequences of migration (Ims and Yoccoz, this volume; Stacey and Taper, this volume), unexpectedly high levels of inbreeding and low heterozygosity in natural populations (Hedrick and Gilpin, this volume), patterns of genetic differentiation (Giles and Goudet, this volume), adaptation (Barton and Whitlock, this volume), and coevolutionary processes (Frank, this volume). As is apparent from the citations, these developments are well represented in the chapters in this volume, which provide an excellent entree to the literature at large.

There are many advantages of a metapopulation approach, but success may also breed problems. As in any scientific field experiencing rapid growth, there is the danger of blurring of concepts. There is the temptation to view any system with any kind of patchiness at any spatial or even temporal scale as a "metapopulation." Harrison (1991, 1994b; Harrison and Taylor, this volume) cautions us about this tendency. Anticipating the kind of verbal entropy that has enveloped many terms in population biology, Hanski and Gilpin sketched in the 1991 volume the meaning of the term "metapopulation," highlighting issues of scale, hierarchy, and a requirement for some population turnover. We feel a need to dwell on the same issues in this chapter, and we provide a revised succinct glossary of the commonly used terms in the literature. First, however, let us examine briefly the history of the metapopulation concept.

## II. BRIEF HISTORY OF METAPOPOPULATION STUDIES

The metapopulation concept has a pedigree dating back to the early part of this century, but until recently this tradition played only a minor and episodic role in the intellectual advance of population biology. For a long time, the prevailing view was one emphasizing persistence and stability of local populations. or as McIntosh (1991) put it, "the great tradition of balance of nature, going back

to antiquity, imputed to nature homogeneity, constancy, or equilibrium and abhorred thoughts of extinction and randomness.”

In evolutionary biology, Sewall Wright (1931, 1940) had the insight that evolution might proceed rapidly in spatially structured populations, especially if there are local extinctions and recolonizations. Wright's shifting balance theory has remained an intriguing, imperfectly understood, and little tested model ever since (Barton and Whitlock, this volume). Wright's work may have stimulated interest in spatially structured populations in the first half of this century, represented for instance by studies of Boycott (1930), Diver (1938), and Lamotte (1951) on ecology and genetics of snail populations (for a more thorough discussion, see Hanski, 1996a). Pioneering quantitative studies in epidemiology (Ross, 1909, Kermack and McKendrick, 1927; see Anderson and May, 1991; Nee *et al.*, this volume) are now seen as closely linked conceptually and theoretically to metapopulation studies, but that connection remained without comment until recently (May, 1991; Lawton *et al.*, 1994; Nee, 1994).

The ecological implications of the metapopulation concept were not considered before 1954, when Andrewartha and Birch published their distinguished text on animal ecology. Drawing on their wide experience from insect population ecology, Andrewartha and Birch found the “dogma of density-dependent factors” unacceptable. They emphasized wild oscillations of populations, documented frequent local extinctions, but also recognized the possibility of reestablishment of populations at vacated localities. In brief, Andrewartha and Birch (1954) advocated the view that local population extinction was a common phenomenon: “spots that are occupied today may become vacant tomorrow and reoccupied next week or next year” (Andrewartha and Birch, 1954, p.87). However, why did their ideas fail to gain wider acceptance? We believe the reason is their nearly categorical rejection of the concept of density-dependent population regulation. The Andrewartha and Birch notion about population dynamics in space was largely ignored and eventually forgotten. The incipient metapopulation concept nonetheless had a quiet existence in the 1950s and 1960s, in works of Huffaker (1958), den Boer (1968), Ehrlich and Raven (1969), Gadgil (1971), and undoubtedly a few others. The MacArthur and Wilson (1963, 1967) dynamic theory of island biogeography has much in common with the metapopulation concept, even if MacArthur and Wilson were primarily concerned with multispecies communities, as we discuss below.

The term “metapopulation” was introduced in the works of Richard Levins in 1969 (1969a) and 1970. The word itself suggests a population of populations, with colonization and extinction of local populations in a metapopulation likened to births and deaths of individuals in a local population (hence the emphasis on population turnover in “classical” metapopulation studies). Levins's work marks the beginning of contemporary metapopulation biology. It is puzzling, though, that the early lead that Levins provided was followed by a period of nearly 20 years of recess (Fig. 1). We return to the possible reasons for this delay below, in the section on metapopulations and conservation biology.

### III. CONCEPTUAL DOMAIN AND METAPOPOPULATION APPROACHES

A fundamental assumption of the original metapopulation concept (Levins, 1969a) is that space is discrete and that it is possible and useful to distinguish between habitat patches that are suitable for the focal species and the rest of the environment, often called the matrix. In this respect the metapopulation approach is closely akin to the dynamic theory of island biogeography (MacArthur and Wilson, 1967) but differs from landscape ecology (Wiens, this volume). The metapopulation concept also presumes that the habitat patches are large enough to accommodate panmictic local populations, but not larger. Other fields of ecology are concerned with spatial patchiness, but either at a smaller (foraging theories; Krebs and Davies, 1984) or at a larger scale (e.g., much of landscape ecology: Forman and Godron, 1986; GAP analyses: Scott *et al.*, 1991; geographical ecology: Ricklefs and Schluter, 1993) than the scale of (panmictic) local populations. The concept of an ideal metapopulation *à la* Levins includes three other simplifying assumptions: habitat patches have equal areas and isolation, local populations in the metapopulation have entirely independent (uncorrelated) dynamics, and the exchange rate of individuals among local populations is so low that migration has no real effect on local dynamics in the existing populations: local dynamics occur on a fast time scale in comparison with metapopulation dynamics.

No real metapopulation completely satisfies all these requirements. However, the more specific assumptions, such as equal patch areas and isolation, can be relaxed without need for a major conceptual amendment. This is not unlike how the population concept is used in population biology: no real population completely satisfies all the criteria of an ideal, closed and panmictic, population. What really matters is the notion of discrete local breeding populations connected by migration. We suggest that if this assumption cannot be defended, some other approach should be used instead of the metapopulation approach; and conversely, the more distinct and smaller the local breeding populations are, the more useful the metapopulation approach is likely to be. Hanski and Gilpin (1991) used population turnover, local extinctions and colonizations, as the hallmark of true metapopulations. By this definition, the mainland-island systems studied in the dynamic theory of island biogeography and in recent metapopulation models (Gotelli, 1991; Hanski and Gyllenberg, 1993) would not count as metapopulations. Following the current usage of the term, we now include mainland-island structures among other metapopulation structures.

It has been suggested that "much" migration among local populations makes the metapopulation approach less useful (Harrison, 1994b). While it is true that the classical concept (Levins, 1969a) implicitly assumes a low migration rate, so low that migration plays no role in the dynamics of existing local populations, more recent theoretical (Hassell *et al.*, 1991a, 1994, Gyllenberg and Hanski, 1992; Nee *et al.*, this volume) and empirical work (Hanski *et al.*, 1995a,b) has made good use of the metapopulation concept even when some tens of percents of

individuals per generation leave their natal patch. An important issue here is the spatial scale of migration. Theoretical studies suggest that a low rate of long-distance migration has often about the same consequences as a high rate of short-distance migration (Nachman, 1991). Clearly, if migration rate is very high, say  $> 50\%$ , and if migration distances are not limited, a metapopulation approach is unlikely to be helpful. The fundamental criterion, however, is whether or not the metapopulation approach is useful in elucidating the questions in which we happen to be interested, not whether migration rate is high or low. From the perspective of traditional population biology, the question is whether the implicit assumption that migration makes no difference to the dynamics of the focal population is a useful approximation or not.

Our remarks have been directed at the population ecological properties of metapopulations. Genetic and evolutionary consequences of these metapopulation structures enlarge the biological domain of the metapopulation concept as described by Olivieri and Gouyon (this volume) and Barton and Whitlock (this volume).

In the previous metapopulation book, Hanski and Gilpin (1991) defined a set of key metapopulation terms in the hope of promoting a more uniform terminology. We repeat this exercise here, with a revised and expanded list of terms (Table I). This list is largely self-explanatory, but a few comments are warranted. The source-sink concept continues to cause confusion in the literature. Pulliam (1988) defined sources and sinks on the basis of whether emigration exceeds immigration, or vice versa, at equilibrium. This definition is useful for population genetic purposes, in emphasizing asymmetry in gene flow, which may have important consequences for genetic structure and adaptation (Barton and Whitlock, this volume; Giles and Goudet, this volume). The definition given in Table I, which is based on the expected population growth rate at low density, in the absence of intraspecific density dependence, may often be preferable for ecological purposes. In the latter case, sinks are populations that would go extinct in the absence of immigration (by Pulliam's definition, a sink population may decline to a low but positive equilibrium value in the absence of immigration; Watkinson and Sutherland, 1995). A third and potentially misleading sense in which the source-sink concept is often used is for a mixture of small and large habitat patches. Populations in small patches typically have a high risk of extinction, but they are not necessarily "sinks" in the sense of Pulliam (1988) or Table I; small populations have a high risk of stochastic extinction, even if the expected growth rate at low density and the expected equilibrium population size are positive (Foley, this volume).

## A. Modeling Approaches

The traditional approach to population biology assumes spatially unstructured populations. Modeling approaches to spatially structured populations can be divided conveniently into two classes, based on whether the model deals with

**TABLE 1** Metapopulation Terminology<sup>a</sup>

Term	Synonyms and definition
Patch	Synonyms: Habitat patch, (habitat) island, (population) site, locality Definition: A continuous area of space with all necessary resources for the persistence of a local population and separated by unsuitable habitat from other patches (at any given time, a patch may be occupied or empty)
Local population	Synonyms: Population, subpopulation, deme Definition: Set of individuals that live in the same habitat patch and therefore interact with each other; most naturally applied to "populations" living in such small patches that all individuals practically share a common environment
Metapopulation	Synonyms: Composite population, assemblage (of populations) [population (when "local populations" are called "subpopulations")] Definition: Set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible (but see nonequilibrium metapopulation)
Metapopulation structure	Synonyms: Metapopulation type Definition: Network of habitat patches which is occupied by a metapopulation and which has a certain distribution of patch areas and interpatch migration rates
Levins metapopulation	Synonyms: Classical metapopulation Definition: Metapopulation structure assumed in the Levins model: a large network of similar small patches, with local dynamics occurring at a much faster time scale than metapopulation dynamics; in a broader sense used for systems in which all local populations, even if they may differ in size, have a significant risk of extinction
Mainland-island metapopulation	Synonyms: Boorman-Levitt metapopulation Definition: System of habitat patches (islands) located within dispersal distance from a very large habitat patch (mainland) where the local population never goes extinct (hence mainland-island metapopulations do not go extinct)
Source-sink metapopulation	Definition: Metapopulation in which there are patches in which the population growth rate at low density and in the absence of immigration is negative (sinks) and patches in which the growth rate at low density is positive (sources)
Nonequilibrium metapopulation	Definition: Metapopulation in which (long-term) extinction rate exceeds colonization rate or vice versa; an extreme case is where local populations are located so far from each other that there is no migration between them and hence no possibility of recolonization
Turnover	Synonyms: Colonization-extinction events (or dynamics) Definition: Extinction of local populations and establishment of new local populations in empty habitat patches by migrants from existing local populations
Metapopulation persistence time	Synonyms: Expected life-time of a metapopulation Definition: The length of time until all local populations in a metapopulation have gone extinct

*(continues)*



TABLE I (continued)

Term	Synonyms and definition
Patch model	Synonyms: Occupancy model, presence/absence model Definition: A metapopulation model in which local population size is ignored and the number (or fraction) of occupied habitat patches is modeled
Levins model	Definition: The model presented by Levins (1969a; see Hanski, this volume)
Structured metapopulation model	Definition: A model in which the distribution of local population sizes is modeled
Incidence function model	Definition: A model of the stationary probabilities (incidences) of patches being occupied, generally assumed to be functions of the sizes and isolations of the patches
Spatially implicit metapopulation model	Synonyms: Island model Definition: Model in which all local populations are equally connected; patch models and structured metapopulation models are spatially implicit models
Spatially explicit metapopulation model	Synonyms: Lattice (grid) model, cellular automata model, stepping-stone model Definition: Model in which migration is distance-dependent, often restricted to the nearest habitat patches; the patches are typically identical cells on a regular grid, and only presence or absence of the species in a cell is considered (the model is called a coupled map lattice model if population size in a patch is a continuous variable)
Spatially realistic metapopulation model	Synonyms: Spatially explicit model (note that we make a distinction between spatially explicit and spatially realistic models) Definition: Model that assigns particular areas, spatial locations, and possibly other attributes to habitat patches, in agreement with real patch networks; spatially realistic models include simulation models and the incidence function model

<sup>a</sup> Modified from Hanski and Gilpin, 1991, and Hanski, 1996a.

interactions among two conspecific populations connected by migration, or with interactions among many local populations. The former approach is useful when the focus of the study is specifically on the effect of migration on local dynamics and one is willing to assume that populations are so effectively regulated that extinctions do not occur (Levin, 1974; Holt, 1985; Gyllenberg *et al.*, 1993). In metapopulation studies in the narrow sense, when there is population turnover, it is necessary to resort to modeling approaches assuming many habitat patches and local populations. Among these approaches, we distinguish between spatially implicit, spatially explicit, and spatially realistic approaches (Hanski, 1994c).

### 1. Spatially Implicit Approaches

Truly significant insights are often based on a critical simplification of what at first appears a hopelessly complex problem. The model that Levins (1969a,

1970) constructed to caricature metapopulation dynamics is an excellent example. Instead of attempting to extend a model of a single population to many populations connected by migration, Levins modeled the changes in the number of such populations, effectively ignoring what happens in each one of them and where in space they happen to be located (Hanski, this volume). For the latter reason, the Levins model and other related patch models (Table I) are spatially implicit; the habitat patches and local populations are discrete (and are generally assumed to have independent dynamics), but they are assumed to be all equally connected to each other. In spite of this simplifying assumption, which can be generally defended only for metapopulations close to steady state and with no strong spatial aggregation, the patch models allow us to analyze many interesting questions about metapopulation dynamics, starting with the conditions of metapopulation persistence in a balance between local extinctions and colonizations. The advantage of the spatially implicit approach is that it greatly facilitates the mathematical and conceptual analysis; the disadvantage is that it can be used to study only a subset of all interesting questions.

Thinking about the restrictive assumptions of the Levins model and other patch models, ecologists have asked what happens when local dynamics are included in the metapopulation model. What happens when the habitat patches are of different sizes and when the local populations have different extinction probabilities? What if migration rate is high enough to "rescue" local populations before extinction? What are the consequences of real spatial locations of local populations? What if extinction events are correlated over the entire metapopulation? What if there is spatial asymmetry and source and sink populations? Some of these questions have been explored in the context of spatially implicit models (Pulliam, 1988; Harrison and Quinn, 1989; Hanski and Gyllenberg, 1993; Gyllenberg *et al.*, this volume), but it comes as no surprise that at some point we have to turn to models that incorporate specific information on the spatial locations of populations. Incidentally, most analyses of metapopulation genetics (Barton and Whitlock, this volume; Hedrick and Gilpin, this volume) have been based on the Levins model, which is essentially equivalent to what population geneticists call the "island model." As in ecology, there is an increasing need to add space in a more explicit manner to metapopulation genetic models.

## 2. Spatially Explicit Approaches

Under the rubric of spatially explicit approaches are several related modeling frameworks, such as cellular automata models (Caswell and Etter, 1993), interacting particle systems (Durrett, 1989), and coupled map lattice models (Hassell *et al.*, 1991a). These modeling approaches assume that "local populations" are arranged as cells on a regular grid (lattice), with population sizes modeled as either discrete or continuous variables. The key feature that distinguishes spatially explicit approaches from spatially implicit approaches is localized interactions: populations are assumed to interact only with populations in the nearby "cells." Localized interactions can have profound dynamic consequences, such as very

long times before the metapopulation settles to a steady state (Hastings and Higgins, 1994) and spatially chaotic dynamics (Hassell *et al.*, 1991a; Nee *et al.*, this volume). The disadvantage is that the state of the metapopulation cannot be described simply by the fraction of cells occupied; an entire vector of presences and absences is needed. Such models require considerable computation. An advantage is that, since each cell on the grid has a constant area and constant spacing, the mathematical rules that govern local behavior are the same from cell to cell, and it is easy to write a computer program to model the dynamics.

Lattice-based models and raster-based GIS descriptions in landscape ecology share the same format of representing space. Thus it is possible to develop complex models that blur the distinction between spatially explicit and spatially realistic models (below). From raster-based description of habitat suitability, one can aggregate "cells" into patches on which local populations may exist, thus reverting to a patch-based metapopulation model for a dynamic analysis (Burgman *et al.*, 1993; Akçakaya, 1994).

### 3. Spatially Realistic Models

Spatially realistic models allow one to include in the model the specific geometry of particular patch networks: how many patches are there in the network, how large are they, and where exactly are they located? Including all this information in the model is necessary if one is interested in making specific quantitative predictions about the dynamics of real metapopulations. For instance, if we want to assess the likely consequences of destroying some particular patches in a patch network, we need a spatially realistic model. For obvious reasons, the spatially realistic approach is closely linked with empirical field studies.

The incidence function (IF) model (Hanski, 1994a,b, this volume) is perhaps the simplest spatially realistic metapopulation model. The IF model is conceptually related to the Levins model, but with the following critical differences: there is a finite number of habitat patches, and hence the model is stochastic in contrast to the deterministic Levins model; the patches are allowed to differ in area, which is assumed to affect local extinction probabilities; and the patches have specific spatial locations, which affect their probabilities of recolonization. Alternative spatially realistic approaches are based on extensive simulation of many local populations connected by migration (Hanski and Thomas, 1994; Akçakaya, 1994). Several generic models of this type are already available (Akçakaya, 1994; Sjögren Gulve and Ray, 1996). Not surprisingly, meaningful application of these models assumes much data. The extreme approach is to simulate the birth, movements, reproduction, and death of individuals (DeAngelis and Gross, 1992), but this approach, which can be used for any population structure, does not really take advantage of the metapopulation concept. An individually based modeling approach may nonetheless provide valuable insight into key processes affecting metapopulation dynamics, such as migration among populations (Kindvall, 1995).

## B. Empirical Approaches

In a standard ecological metapopulation study, a key initial task is to make a practical distinction between habitat and nonhabitat and to delimit the suitable habitat patches in the study area. Suitable habitat may be defined subjectively or with the help of statistical methods (Lawton and Woodroffe, 1991). An experimental approach may be used to test the accuracy of an existing habitat classification: experimental introductions to empty habitat should succeed (Harrison, 1989; Oates and Warren, 1990; Thomas, 1992; Massot *et al.*, 1994); introductions to nonhabitat should fail. Metapopulation studies focused on assemblages of extinction-prone local populations typically proceed to record the presence or absence of the focal species in the habitat patches and then to analyze the effects of various environmental factors on patch occupancy (Verboom *et al.*, 1991b; Thomas and Harrison, 1992; Hanski *et al.*, 1995a,b) and on the rates of extinction and colonization (Sjögren, 1991; Eber and Brandl, 1994; Hanski *et al.*, 1995b). Other field studies have been concerned with more permanent local populations, but ones whose dynamics are significantly affected by migration (Stacey and Taper, this volume). Experimental studies have attempted to demonstrate the predicted temporal stability of local populations in a metapopulation as opposed to that in isolated local populations (Murdoch *et al.*, 1996; Harrison and Taylor, this volume).

Landscape ecology (Forman and Godron, 1986; Turner, 1989; Wiens, this volume) and metapopulation ecology share a common focus on space and patchiness. The difference is primarily in the complex mosaic structure of real landscapes that is the object of landscape ecology (Wiens, this volume). In contrast, metapopulation studies typically assume that the patches which are used by the focal species are of the same type, though this assumption is made primarily for the sake of keeping the models reasonably simple (see Holt, this volume, for metapopulation models with two patch types). Empirical research in landscape ecology has been reluctant to use the population dynamic theory that metapopulation ecology purports to provide, even if in a rudimentary form, and consequently the two fields have developed largely independently. One trend that is beginning to change this situation is the use of GIS-based landscape descriptions in generic metapopulation simulation models (Akçakaya, 1994). Today, ecologists have access to huge data bases of digitized information about landscape structure, and the imminent arrival of low-cost global positioning systems will greatly facilitate further empirical research in this area.

It should come as no surprise that the bulk of current empirical research that is conceptually related to the metapopulation notion is conducted in conservation biology. We therefore devote the rest of this chapter to a more thorough scrutiny of the past and present links between metapopulation biology and conservation biology.

#### IV. METAPOPULATIONS AND CONSERVATION BIOLOGY

Conservation biology changed dramatically, beginning ca. 1975, from a heavy emphasis on habitat relationships of individual species to a focus on refuge design, guided by the dynamic theory of island biogeography and the genetic deterioration owing to drift and inbreeding (Simberloff, 1988). The two halves of this "new conservation biology" did not fit together well, as the former dealt with species richness of communities, while the latter aimed at the population level. Currently, a replacement of the island biogeographic component of conservation biology by metapopulation thinking is providing a more comfortable fit. Although the incorporation of metapopulation models into conservation biology has spurred important insights, it has also led to some misfocused proposals.

##### A. The Rise and Fall of the Theory of Island Biogeography

The theory of island biogeography (MacArthur and Wilson, 1963, 1967) quickly attracted much attention from ecologists (Fig. 1) by using simple mathematics to focus on an easily obtained statistic (species richness) and depicting a dynamic nature that is nonetheless readily understood because it is divided into small units, namely real or habitat islands (Simberloff, 1974, 1978a). The theory posits species richness on each island as a dynamic equilibrium maintained by continuing immigration of all species, balanced by ongoing local extinctions on the island, primarily owing to demographic and genetic stochasticity.

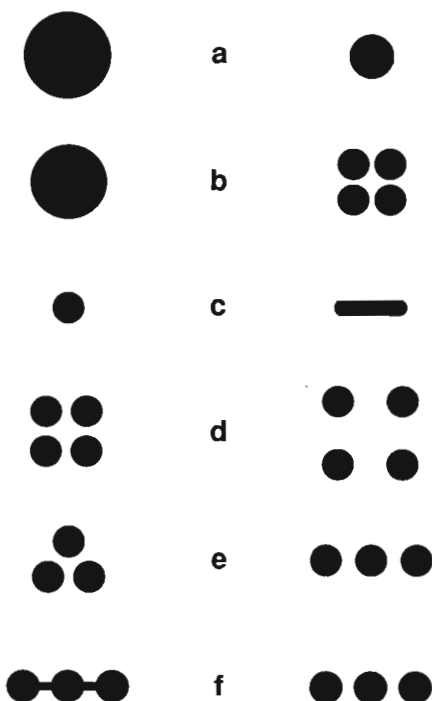
Clearly the island biogeographic theory shares key underpinnings with metapopulation models—the division of nature into discrete entities, with movement of individuals among relatively unstable local populations. There is also an apparent difference— island biogeographic theory treats communities, not individual species. Its key statistic is species richness. However, some island biogeographic models are formally composites of models for individual species, with the community-wide immigration and extinction rates being simply sums of the respective species-specific rates (Simberloff, 1969, 1983; Gilpin and Diamond, 1981). In these latter models, the underlying conception of what is happening in nature is just a mainland–island version of Levins's metapopulation concept (Hanski, this volume). However, even a species-based model of this type, and even one with migration from several sources, is still focused on a single island and on questions about the number of species and immigration and extinction rates on that island. A metapopulation model, even one in which the different sites and local populations are not modeled explicitly, focuses on the entire metapopulation of one or two species, using statistics such as the number of sites occupied.

In both types of models, an element of arbitrariness is just how much movement there is between sites for the models to remain useful. For metapopulations, the bone of contention is whether the movement is so frequent that one is dealing with a single population rather than a metapopulation, even if that population

may be so large that individuals are likely to interact with their neighbors only (Harrison, 1991). For island biogeographic models, the argument is whether groups of conspecific individuals on sets of islands are separate populations or just transient parts of one widely ranging population (Smith, 1975; Simberloff, 1976). The latter argument has recrudesced recently with important conservation implications. Pimm *et al.* (1988), extrapolating from records of breeding birds on small British islands, suggested guidelines for how many individuals should constitute propagules for reintroduction efforts based on the body size of the species. Aside from problems with the statistics of extrapolation (Tracy and George, 1992), Haila and Hanski (1993) saw a more fundamental flaw: the assumption that the birds on each island constituted a population, and their disappearance an extinction. In their view, all these birds are parts of wide-ranging, large populations and their disappearances from specific islands within the range are not population phenomena. Diamond and Pimm (1993) retorted that the birds of each island could be viewed as a population within a metapopulation.

Within about a decade (Fig. 1), the theory of island biogeography came to dominate much of conservation biology, with a series of nearly simultaneous papers (Terborgh, 1974, 1975; Diamond, 1975a; Wilson and Willis, 1975) all advocating a set of "rules" of refuge design ostensibly based on the theory (Fig. 2). The rules each suggest a refuge configuration that would maximize species richness, and the papers describing the rules apparently stemmed from lectures given by E. O. Willis beginning in 1971 (Willis, 1984). Although some of the rules in fact were not based on the theory (references in Simberloff, 1988); they became popular in conservation circles, particularly after their publication in 1980 in the first synthetic plan for dealing with a perceived disastrous wave of extinctions, World Conservation Strategy, jointly authored by the International Union for the Conservation of Nature and Natural Resources, the United Nations, and the World Wildlife Fund. With this imprimatur, it is unsurprising that these rules, and the theory that supposedly supported them, became the governing paradigm in conservation biology, reproduced in textbooks and published in newspapers. The dominance of the island biogeographic paradigm was so strong that even studies that today would be seen as metapopulation research were published as island biogeographic studies, with no mention of the term "metapopulation" (e.g., Fritz, 1979).

It was noted early that most ecological publications citing island biogeographic theory simply interpreted a species-area relationship in terms of the theory, when alternative explanations were also possible (Simberloff, 1974), and that there was little empirical evidence for continuing local extinctions of the sort envisioned by the theory (Lynch and Johnson, 1974; Simberloff, 1974). Further, as noted by Smith (1975) and Simberloff (1976), by defining the comings to and goings from local sites of individuals within continuous populations as "immigration" and "extinction," one could almost always claim that extinctions and colonizations were occurring, even if the theory really envisioned most recruitment to local populations as being by *in situ* reproduction rather than immigration.



**FIGURE 2** The “island biogeographic” rules for refuge design (after Wilson and Willis, 1975; International Union for the Conservation of Nature and Natural Resources, 1980). For each rule, the design on the left is seen as superior to the alternative on the right.

Nevertheless, ecologists on the whole tended to view the theory favorably until around 1980, when doubt about the existence of widespread local extinction became pervasive (Gilbert, 1980; Schoener and Spiller, 1987b; Williamson, 1989). The prevailing view now is that, in most systems, “turnover involves a subset of fugitive populations, with many others, mostly much larger, being permanent” (Schoener and Spiller, 1987b). The decline in citations of “island biogeography” (Fig. 1) reflects the declining faith in the theory. Though it is no longer seen as a model for much of nature, island biogeographic theory provided a theoretical perspective from which to view a number of patterns, such as the species–area relationship (Haila and Jarvinen, 1982).

The key conservation legacies of the dynamic theory of island biogeography were (1) the metaphor of a refuge as an island or spaceship, (2) interest in the fragility of the biota of individual refuges and causes of this fragility (Soulé and Simberloff, 1986; Simberloff, 1994a), and (3) the rules of refuge design (Fig. 2). The recognition that some of the rules, including the most widely debated one (SLOSS, single large or several small; Fig. 2b) are not related to the theory (Soulé and Simberloff, 1986, and references therein), lessened conservation interest in

the theory, while documented exceptions to some of the rules, including SLOSS, led to their fall from status of conventional wisdom. For example, the third edition of one of the most widely used introductory ecology textbooks, *Ecology* (Krebs, 1985, p. 559), reprinted the figure of the rules as popularized by the IUCN and described them as flowing from island biogeographic theory. The fourth edition (Krebs, 1994) omits the figure, makes no mention of the rules, and cites the criticism of the theory as "true but trivial" by Williamson (1989).

## B. Paradigm Shift

The waning of the theory of island biogeography as a dominant conservation paradigm in the late 1980s coincided with the burgeoning interest among biologists in the metapopulation concept (Fig. 1). As does Hanski (1989), Merriam (1991, p. 134) explicitly claims a paradigm shift: "Metapopulation models have largely replaced equilibrium island biogeography as a way of thinking about terrestrial habitat islands, fragmented habitats and heterogeneous terrestrial environments in general . . ." For other conservation biologists, the shift is tacit and consists simply of an assertion that nature is structured as metapopulations followed by discussion of what actions are required to preserve metapopulations (e.g., Noss, 1993). Perhaps most telling is *The Diversity of Life*, by Wilson (1992), a founder of the theory of island biogeography, in which species are typically seen as structured as metapopulations and the consequences of this structure for conservation are explored.

The causes of the shift are many. One must be the growing ecological literature, described above, doubting the verisimilitude of island biogeographic theory. However, scientific data and the weakness of a prevailing paradigm alone are unlikely to precipitate a paradigm shift (Kuhn, 1970; Haila, 1988), and we must seek other prevailing currents. It is worth recalling that, fundamentally, the theory of island biogeography can be construed as just a multispecies version of an analogous metapopulation theory, so it is hard to imagine objective scientific reasons for accepting one while rejecting the other.

One possible explanation is a shift among conservation biologists and ecologists from the conception of nature as an equilibrium world to that of a non-equilibrium one (Wiens, 1977, 1984; Chesson and Case, 1986). Island biogeographic theory is dynamic, of course, but the emphasis is on equilibrium species richness, hence the nickname, "equilibrium theory," and even the underlying immigration and extinction rates are seen as constant. Though metapopulation theories are not any more, or less, "equilibrium" theories than the theory of island biogeography, the emphasis in the latter on equilibrium species richness and in the former on population turnover may have created the sense of a conflict between an equilibrium and a nonequilibrium theory. The key point, of course, is that in both theories there is no equilibrium at the population level. However, the *modus operandi* of the island biogeographic theory is to ignore the changes in the presences and absences of individual species and to focus on the equilibrium



pattern of species richnesses; this theory is spatially implicit in our taxonomy. Yet two growing interests in conservation are spatially explicit models, to a large extent fostered by an increase in spatial data and the use of GIS, and maintenance of species that are destined to be locally ephemeral, such as fugitive species and early successional ones. The metapopulation theory fits well with these interests. Indeed, a critical difference between the models of MacArthur and Wilson (1967) and Levins (1969a) is the presence of a permanent mainland population in the former but not in the latter.

In addition to island biogeographic theory, the other main component of the "new conservation biology" is population genetics, particularly the study of drift and inbreeding in small populations (Simberloff, 1988). This research tended to shift the focus of conservation biologists from communities to species and populations. Ecological aspects of conservation began also to be seen in terms of populations rather than species—the role of demographic and environmental stochasticity in setting minimum viable population sizes is the prime example (Simberloff, 1988). Again, a focus on populations rather than on communities is bound to make island biogeographic theory seem less relevant.

Finally, metapopulation models rescued small sites from their devaluation by island biogeographic theory. The main ecological data interpreted in terms of island biogeographic theory were simply species–area relationships, showing that, all other things being equal, large sites tend to have more species than small ones. The first rule of refuge design (Fig. 2a) expresses this relationship as a mandate for conservation planners. The rules, and the theory, were widely used to argue that large refuges are needed and the elevated extinction rates in small ones will inevitably render them depauperate (e.g., Diamond, 1972; Soulé *et al.*, 1979). Indeed, to the extent that environmental stochasticity and catastrophes extinguish small populations, mathematical modeling suggested that even populations in enormous refuges, the size of the largest national parks in the United States, would be subject to collapse.

Conservationists eventually recognized that astute opponents could turn this emphasis on inviable small populations against conservation. For example, the refuge system of the small nation of Israel consists of some 200 reserves, many of which are very small. These are protected and managed to various degrees by the Nature Conservation Authority, and the Authority was under great pressure during the 1980s to abandon some small refuges, not because specific research showed declining populations within them but because island biogeographic theory, codified in the refuge design rules, shows that they will inevitably lose species (R. Ortal, personal communication, 1984).

This threat from island biogeographic theory to the maintenance of small reserves was forestalled in several ways. The species–area relationship was shown to have such wide confidence limits that an assertion of imminent faunal collapse could not be sustained (Boecklen and Simberloff, 1986). Some populations that had persisted as very small populations for millennia were adduced as cautions against taking the theory too literally (e.g., Walter, 1990). However,

the main salvation of small sites was the shift by conservationists to the metapopulation paradigm. In the Levins model, at least, small sites containing small populations were the only homes of a species and thus the proper locus of conservation concern. The model even suggests that a certain number of unoccupied sites is required for metapopulation persistence (Lande, 1988a; Hanski, this volume), thus relieving beleaguered conservation biologists from having to justify a refuge for a given species by confirmed residence. A famous example in which local extinction rates are high and a supply of suitable empty sites is necessary is *Pedicularis furbishiae*, the Furbish lousewort (Menges, 1990).

In sum, from a conservation standpoint, it is not surprising that citations of metapopulation studies increase exactly when those of island biogeography decline (Fig. 1). These trends represent a paradigm shift.

### C. Use and Misuse of the Metapopulation Concept in Conservation Biology

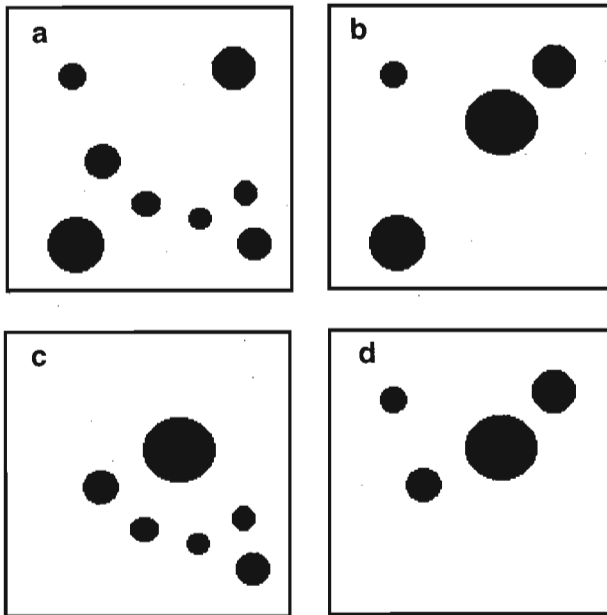
Hanski and Gilpin (1991) observed that "metapopulation ideas have recently become the vogue in conservation biology," and numerous conservation strategies are explicitly based on metapopulation models (references in Harrison, 1994b). The general effect has been to draw attention to landscapes and networks, as opposed to individual reserves in isolation, for which the island metaphor of island biogeographic theory is appropriate. This is a salutary development. Even if there were no significant interactions among populations in different refuges, it would be good to have multiple refuges simply as insurance against local catastrophes (Soulé and Simberloff, 1986). Doak and Mills (1994) and Harrison (1994b) argue that, even if most species are not structured as Levins-type metapopulations in nature, the rise of the metapopulation paradigm has served and continues to serve a useful function by forcing conservation biologists to gather data that are important to effective conservation strategies of individual species—movement rates from site to site, relative reproduction and mortality rates at different sites, and the like. This is precisely the view of Haila and Järvinen (1982) for island biogeographic theory.

The problems arise, for metapopulation models as for island biogeographic theory, when it is assumed without empirical evidence that all species, or all species in a large class, conform to some particular model (Doak and Mills, 1994; Harrison, 1994b). If a conservation strategy is based on metapopulation dynamics that do not exist, it can misfire. Thus, for example, Murphy *et al.* (1990) suggested that small-bodied, short-lived species with high reproductive rates and high habitat specificity typically constitute Levins metapopulations, but there are simply insufficient data to evaluate this claim (Harrison, 1991, 1994b). To focus automatically on metapopulation dynamics for such species would not constitute effective science. No wide-ranging generalizations are yet possible, because few data really demonstrate the existence of classical metapopulations. Harrison (1991) could cite only pool frogs (*Rana lessoniae*) in Sweden and waterflies (*Daphnia*) in rock pools as unequivocal cases (for some new examples, see Har-

rierson and Taylor, this volume). The endangered Glanville fritillary butterfly (*Melitaea cinxia*) in Finland is another good example (Hanski *et al.*, 1995a,b) and may represent many other butterfly species (Hanski and Thomas, 1994; Hanski and Kuussaari, 1995; Thomas and Hanski, this volume). In such instances, an understanding of metapopulation dynamics is crucial to effective conservation. Research is required on local extinction and migration rates and how these are affected by patch size and isolation (C. D. Thomas *et al.*, 1993; Hanski *et al.*, 1995b).

Harrison (1994b) suggests that the species most convincingly conforming to the Levins model occupy habitats that inevitably change because of succession (see also Thomas and Hanski, this volume). In many such species, the extinction of local populations is deterministic rather than stochastic, but this fact does not fundamentally undercut the Levins conception of metapopulation dynamics. The endangered Furbish lousewort, for example, requires a riverside habitat that is neither too little nor too heavily disturbed (Menges, 1990). However, any local population is ultimately destroyed by ice scour and bank slumping, so the metapopulation requires a supply of temporarily suitable sites that are not too isolated to be colonized. A metapopulation analysis (Menges, 1990) including observations on local extinction and recolonization suggests that the species is in decline rather than at equilibrium and that tempering of the disturbance (flow) regime will likely exacerbate the situation. Further, in this species as in the Levins scenario in general (Lande, 1988a; Hanski, this volume; Nee *et al.*, this volume), restriction of conservation measures to occupied sites only would be fatal. A static, nonmetapopulation view of nature would not have led to the recognition of the importance of currently unoccupied habitat. Much of the history of refuge establishment consists simply of locating apparently healthy populations and preserving their sites (Simberloff, 1988).

Metapopulation models have been used to deduce the minimum viable metapopulation (MVM) size under certain assumptions (Hanski *et al.*, 1996b). This concept is analogous to the minimum viable population (MVP) size (Shaffer, 1981), but with the critical difference that MVM involves both the minimum viable number of populations and the availability of suitable habitat patches (Hanski *et al.*, 1996b). In practice, use of these concepts may degenerate into specious "magic numbers." A more constructive approach is to use metapopulation models to rank alternative scenarios of landscape change in terms of persistence of a focal species. One may ask, for instance, whether the entire removal of one large habitat patch is more detrimental to a metapopulation than reducing the areas of several patches (Hanski, 1994a,b; Hanski *et al.*, 1996c; Wahlberg *et al.*, 1996; note the connection to the SLOSS rule, Fig. 2b). The theory of island biogeography inspired the rules of refuge design discussed above (Fig. 2). The analogous contribution from metapopulation theory is predictions about the relative performance of particular species in particular fragmented landscapes based on relatively simple but spatially realistic models (Fig. 3, Hanski, 1996b). There are two reasons to expect the latter sorts of predictions to be more helpful than the island bioge-



**FIGURE 3** Four examples of the same landscape fragmented in different ways (scenarios a to d). Spatially realistic metapopulation models, such as the incidence function model (Hanski, 1994a), can be used to rank the alternative scenarios in terms of the persistence time of the focal species. Note the conceptual link to the SLOSS rule (Fig. 2b).

ographic rules of refuge design. First, the rules of refuge design (Fig. 2) are static, even those actually flowing from the theory. For example, the fundamental concept in rule a (Fig. 2a) is the species–area relationship, which in applications is seen as meaning a fixed number of species in a fixed area. In contrast, the metapopulation predictions explicitly address the dynamics of species survival. Second, the rules of refuge design contrast fixed general alternatives (such as in Fig. 2b), whereas the spatially realistic metapopulation models practically force one to compare specific fragmented landscapes (Fig. 3).

We now turn to potential misuses of the metapopulation concept in conservation. To start with, if a species is structured as a mainland–island (Levitt–Boorman) metapopulation, population turnover in the peripheral “island” populations may be irrelevant to the persistence of the metapopulation as a whole, though the dynamics are crucial to the persistence of the peripheral populations (Doak and Mills, 1994; Harrison, 1994b, Simberloff, 1994b). More generally, emphasis on metapopulation models can potentially harm conservation by drawing attention away from single populations on the grounds that no one of these is crucial to a species’ persistence and it is the ensemble that matters (Harrison, 1994b).

Another example of the metapopulation concept used in misguided attempts

to deemphasize single populations is the hype surrounding movement corridors (though we observe that, strictly speaking, metapopulation models tend to emphasize connectance among habitat patches, not corridors). One rule of refuge design associated with island biogeographic theory is that a set of refuges connected by corridors will contain more species than an otherwise identical set without corridors (Fig. 2f). In the original formulation of this rule, the focus was on a community-level statistic, species richness, and corridors were assumed to increase this statistic by increasing immigration rate. However, for most proposed corridor systems, there is scant evidence that the corridors would be used for movement or that they would actually forestall extinction (Hobbs, 1992; Simberloff *et al.*, 1992). Even more troubling, investment in corridors can be expensive and can detract from efforts to protect particular populations that require a specific refuge that is not part of a network (Simberloff *et al.*, 1992).

Some examples of classical metapopulations in human-fragmented landscapes may represent transient, nonequilibrium situations, in which a previously more continuous population becomes divided into smaller units, with consequent local extinctions, but no functional metapopulation was created, merely an assemblage of populations all slowly declining to extinction. It seems likely that almost any gradual extinction would appear, during some parts of the decline, as a nonequilibrium metapopulation situation (Simberloff, 1994b). Even in this case, understanding its current dynamics can aid in the maintenance of the species in a fragmented or otherwise changed landscape (Harrison, 1991). In SLOSS terminology (Fig. 2b), a single large population might have been better, but if all we have left is several small ones, their interactions may be crucial to their survival. For example, the metapopulation analysis by Beier (1993) of cougars (*Felis concolor*) in the Santa Ana Mountains of California showed that the species currently exists as a collection of small populations loosely linked by riparian corridors, and his radiotelemetry data on movement combined with a simulation model suggested how loss of particular populations and corridors could affect the entire metapopulation. Data on sources and sinks in source-sink metapopulation can also be key to maintaining a species. A particular worry about nonequilibrium metapopulations in increasingly fragmented landscapes is that we might not recognize them as such (Hanski, this volume), which would give us a misleadingly rosy picture of the ability of species to persist in present landscapes.

Attempts to model the minimum number of populations necessary to maintain a viable metapopulation are hampered by assumptions that are hard to verify and data that are difficult to gather. These are, of course, problems with all population models that aim at quantitative predictions, and the problems become even more severe with spatially realistic models that might guide specific management plans (Doak and Mills, 1994). The history of conservation biology is marked by many examples of misused minima (Simberloff, 1988; Crome, 1993): as soon as a minimum is set for any variable, forces opposed to conservation use it to see how much of nature they can get rid of. Thus, as tentative and general as the MVM model is, someone may attempt to manage for a specific minimum based

on this model. As discussed above, a less controversial use of spatially realistic metapopulation models is simply to rank alternative management scenarios (Fig. 3) and to recognize that making long-term predictions about (meta)population persistence time in our rapidly changing world is practically hopeless.

The shift from island biogeographic to metapopulation thinking united ecologists and geneticists in focusing on populations. Genetic concerns have been prominent in the interest in metapopulations. Kimura and Crow (1963) first pointed out that occasional migration between local populations can maintain genetic variation better than would a single large population, essentially because drift is likely to fix different alleles in different populations. However, the situation becomes more complicated when we allow for local extinctions and recolonizations, and recently much effort has gone into modeling the way that such population turnover affects the maintenance of genetic diversity in metapopulations (Wade and McCauley, 1988; Hastings and Harrison, 1994; Barton and Whitlock, this volume). On theoretical grounds, one might expect species that naturally exist in metapopulations not to be prone to inbreeding depression because they lack genetic load (Harrison, 1994b), while local populations in a recently fragmented large population might be particularly susceptible to inbreeding depression because heterozygosity would quickly decline (Simberloff, 1988; Hedrick and Gilpin, this volume). Under the latter circumstances, maintaining movement among populations might seem particularly important, and indeed many management plans for declining populations call for measures to enhance population interaction, such as translocation and corridors, specifically to avoid inbreeding depression (e.g., U.S. Department of Agriculture, 1995). However, field evidence for inbreeding depression or other problems in recently fragmented populations is scarce (Harrison, 1994). Lande (1988b) argues more generally that the importance of genetic threats in conservation has been overblown. His view is that, in naturally small populations, the genes causing threatening inbreeding depression would have been selected out, while in recently reduced populations, ecological threats are more immediate. Despite this widely cited statement, genetic principles still underpin many viability analyses and management plans (Harrison, 1994b). Perhaps the very fact that genetic modeling is feasible ensures that it will be done, particularly if ecological modeling, even if potentially more useful, is more problematic. The latest round of papers (e.g., Lynch *et al.*, 1995) appears to strengthen the genetic argument, but the most urgent need is for relevant field studies.

Thompson (1996) contends that metapopulations may be crucial to the conservation of various coevolutionary interactions, such as those between pathogens or parasites and their hosts. In models, locally unstable population dynamics can be stabilized by the addition of metapopulation structure (Hassell *et al.*, 1991a; Nee *et al.*, this volume). In other cases, the metapopulation structure stabilizes evolutionary dynamics of the interaction. For example, under certain circumstances, the coevolutionary dialog between a pathogen and its host can lead to the extinction of the host, if a new virulence gene in the pathogen spreads rapidly enough. A metapopulation structure can then prevent the gene from eliminating

the entire species. Wild flax (*Linum marginale*) and flax rust (*Melampsora lini*) may be a natural example in which the host metapopulation structure serves this function (Burdon and Thompson, 1995). Frank (this volume) presents a thorough discussion of these issues.

The focus on metapopulations, combined with that on genetics, has led to the population and the species becoming the dominant levels of concern in conservation. It is striking that the recent explosion of interest in ecosystem management is quite antithetic to a primary interest in populations and to single-species management (Simberloff, 1996). In fact, a key motivation of ecosystem management is that research on species after species will be hopelessly expensive and inefficient, and so will management based on such research. Of course, both ecosystem management and metapopulation models share a concern with landscapes and regions, rather than highly local settings, and one could imagine a landscape with a distribution of habitat patches that would maintain many metapopulations simultaneously. Also, the emphasis in ecosystem management on maintaining processes rather than species (Simberloff, 1996) can accommodate concerns about the coevolutionary processes. Nevertheless, the research programs and primary goals of these two approaches differ fundamentally and they will surely compete for both research funding and influence in specific management plans in the future.

## V. CONCLUSIONS

The changing pattern of citations of the key words "island biogeography" and "metapopulation" represents a fascinating example of a paradigm shift in population biology. This example is the more striking because the respective theories are so closely related that whatever evidence can be mustered for, or against, one theory is likely to serve the same function with respect to the other theory. We have discussed in this chapter how it is largely the wider context that has made the difference. One apparently important issue is the spatial scale. The dynamic theory of island biogeography was originally developed to explain patterns at large spatial scales, whereas the metapopulation concept is associated with fragmentation of our ordinary landscapes. Though the difference is in perception only, it matters.

Metapopulation models have contributed important insights to conservation, and they have inspired field studies focused on collecting key data on demography and movement. Nonetheless, the temptation to apply the metapopulation approach blindly to systems for which there is no supporting evidence can be counterproductive. Metapopulation maintenance may be crucial to a limited range of species, probably dominated by those characteristic of successional habitats. The role of metapopulation dynamics in forestalling genetic deterioration is particularly unverified.