

Metapopulation dynamics: brief history and conceptual domain

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We review the early development of metapopulation ideas, which culminated in the well-known model by Levins in 1969. We present a survey of metapopulation terminology and outline the kinds of studies that have been conducted on single-species and multispecies metapopulations. Metapopulation studies have important conceptual links with the equilibrium theory of island biogeography and with studies on the dynamics of species living in patchy environments. Metapopulation ideas play an increasingly important role in landscape ecology and conservation biology.

KEY WORDS:—Metapopulation – colonization – extinction – population turnover – island biogeography – patchy populations – landscape ecology – conservation biology.

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INTRODUCTION

The term *metapopulation* arrived in the ecological literature in 1970, to describe a *population of populations*, an abstraction of the population concept to a higher level. The term was coined by Richard Levins, who formulated a simple model to investigate the basic dynamic properties of metapopulations. In a series of original and farsighted papers, Levins explored single-species dynamics in temporally varying environments, optimal pest control policies (Levins, 1969), group selection (Levins, 1970) and interspecific competition (Levins & Culver, 1971).

In this introductory paper and in the papers to follow, we take a broad look at *metapopulation dynamics* in almost all of its guises. With the qualifier 'dynamics', we emphasize the behaviour of a metapopulation over time. There are no static populations, and likewise there is no such thing as a static metapopulation, for it would be impossible to meaningfully attribute membership of local populations to a static metapopulation. Populations are defined as ensembles of interacting individuals each with a finite lifetime; metapopulations are ensembles of interacting populations with a finite lifetime, in other words expected time to extinction. The metapopulation concept is thus closely linked with the processes of population turnover, extinction and establishment of new populations, and the study of metapopulation dynamics is essentially the study of the conditions under which these two processes are in balance and the consequences of that balance to associated processes.

Our aim in this paper is to outline briefly the history of metapopulation ideas and the key conceptual links with related inquiries. We review the context in which Levins developed the metapopulation concept and we attempt to define and classify the key elements and terms in metapopulation dynamics. We then review the types of studies that have been conducted on single-species and multispecies metapopulations, including the ones in this volume, and examine the relationships between metapopulation dynamics, the equilibrium theory of island biogeography and the dynamics of populations living in patchy environments. Finally we turn to more practical issues, and pursue the links between metapopulation dynamics and landscape ecology, and between metapopulation dynamics and conservation biology.

THE METAPOPOPULATION IDEA QUANTIFIED

Back to Levins in 1969. Did he create a new concept or did he merely label an idea that had been in use before? Many biologists had thought about local extinctions and recolonizations of vacant habitat patches. Sewall Wright (1940) was acutely sensitive to the evolutionary implications of patchy population structure. The milestone ecology text by Andrewartha & Birch (1954) advocated vigorously what would now be called a metapopulation perspective to population dynamics, with local populations frequently becoming extinct and vacant sites being recolonized. In subsequent decades, this point of view remained little developed in the mainstream population dynamics literature, partly perhaps because the work of Andrewartha & Birch (1954) became identified as the losing side in the controversy about the role of density-

dependent and density-independent factors in (local) population dynamics. Two years prior to Levins's paper, MacArthur & Wilson (1967) published an entire theory centred around the extinction and colonization processes, as determinants of species diversity on islands. Den Boer's (1968) much-cited paper on "spreading of risk" pioneered ideas about metapopulation regulation of species with unstable local populations. In the late 1960s, Ehrlich & Raven (1969) refocused attention to population processes.

Despite these earlier investigations, Levins did, in our opinion, define something new. He distinguished between the dynamics of single populations and a set of local populations, and he introduced a variable to describe the latter, $p(t)$, which in Levins's model denotes the fraction of habitat patches occupied by the species at time t . He encapsulated the relevant individual and population processes in two key parameters, e and m , which set the rates of local extinction and colonization of empty patches, respectively. He wrote an equation for the rate of change in p , and thereby specified the conditions under which p would be greater than zero. Levins's model is,

$$dp/dt = mp(1-p) - ep, \quad (1)$$

with the equilibrium value of p given by $\hat{p} = 1 - e/m$ (for further discussion see Hanski, 1991). What Levins did with equation (1) was to provide a simple model for metapopulation dynamics, analogous to the logistic model as a paradigm of local population growth. In fact, the Levins model and the logistic model are structurally the same, which may be seen by rewriting equation (1) in the equivalent form

$$dp/dt = (m-e)p[1-p/(1-e/m)]. \quad (2)$$

The difference $m-e$ thus gives the rate of increase of p in a small metapopulation (when p is small), while $1-e/m$ is the equivalent of local 'carrying capacity', the stable equilibrium point towards which p moves in time. As a conceptual and mathematical tool, the Levins model was something new in population ecology, and a necessary first step towards further quantitative research in this area.

THE ROOTS OF THE LEVINS MODEL

Levins's (1969) metapopulation model was motivated by and applied to a pest control situation over a large region, within which local populations would fluctuate in asynchrony. One of the main results was the realization that the abundance of the species, in the sense of a smaller or larger value of p , is reduced by increasing temporal variance in the extinction rate. Thus Levins (1969) recommended that control measures should be applied synchronously throughout a large region. It is ironic that this very first interesting facet of metapopulation dynamics was overlooked by many for 20 years, until in the late 1980s, with a renewed interest in metapopulations, much work was directed to the same question under the rubric of 'correlated environmental stochasticity', and in the context of conservation biology (Quinn & Hastings, 1987; Gilpin, 1988, 1990; Harrison & Quinn, 1989; Hanski, 1989, 1991).

Apart from the population dynamic issues involved in pest management, Levins had another and a more theoretical reason to develop the metapopulation concept and its corresponding mathematical model: group

selection of altruistic traits. Without a model describing the balance of extinctions and colonizations, no exploration of the significance of genetics on these processes was possible. Levins (1970) wanted to know whether a gene that was disadvantageous in a single population could prevail in a larger system of many populations, in other words in a metapopulation. This would be possible if the gene lowered the rate of local extinctions, and it would be interesting if the gene did so with a high cost to itself. Levins ended up with a pessimistic view on group selection for altruism. He showed that it was likely only if there was a sharp increase, in effect a step function, in local extinction probability with increasing frequency of the alternative allele, the selfish gene, at the locus. However, a few years later, Gilpin (1975), utilizing the non-linear dynamics of a predator-prey metapopulation, showed that there were conditions under which group selection was possible.

The general controversy over the evolution of altruism remains unsettled, and there are alternative models that can explain the same phenomena. Some models of altruism have no spatial structure whatsoever, and are based on behaviour directed towards kin or towards individuals with whom there have been previous positive interactions (Hamilton, 1964; Trivers, 1971). But two other models assume a patchy spatial structure, and interestingly enough they highlight the two main directions towards which population ecologists have developed ideas related to Levins's metapopulation concept. The model of Boorman & Levitt (1973) assumed a large central population that never suffered extinction, surrounded by a set of small local populations, in which the altruistic gene much affected extinction probability. Initial gene frequencies were set by founder effects. Those small populations that had more altruists would last longer and would send more genes back to the mainland population. This sort of 'mainland-island' metapopulation structure is the one typically envisioned in island biogeographic studies (see below).

Another important model of the maintenance of altruistic behaviour is due to David Sloan Wilson (1975, 1980), who utilized a patchy spatial structure to drive the gene frequency away from the locally selfish state. Wilson's model is not, however, based on the metapopulation concept, because he assumed "local populations", in fact just groups of individuals, that were formed and always dissolved within each generation. Nonetheless, it is interesting to question the relationship between metapopulation dynamics and such small-scale patchy distributions of individuals (see below).

METAPOPOPULATION TERMINOLOGY

Ecology is plagued with terms and concepts that all ecologists recognize but which are not used in a consistent manner, perhaps because of the varying experiences of different ecologists with particular systems. Examples include the niche, community and metapopulation. The problem is more than mere semantics: vague use of terms leads to lumping and splitting of significant ecological phenomena, and it hinders our attempts to understand what is going on in the real world.

We find it useful to make a conceptual distinction between three spatial scales as described in Table 1. The local scale refers to the scale of local populations, within which individuals move during their routine daily activities, interact with

TABLE 1. Three spatial scales

<i>Local scale</i>
The scale at which individuals move and interact with each other in the course of their routine feeding and breeding activities
<i>Metapopulation scale</i>
The scale at which individuals infrequently move from one place (population) to another, typically across habitat types which are not suitable for their feeding and breeding activities, and often with substantial risk of failing to locate another suitable habitat patch in which to settle
<i>Geographical scale</i>
The scale of species' entire geographical range; individuals have typically no possibility of moving to most parts of the range

other individuals, and within which most individuals are born and die. *Metapopulations are systems of such local populations connected by dispersing individuals* (Table 2). We do not use the term metapopulation for the set of habitat patches which are potentially or actually occupied by local populations, but for the set of local populations themselves. We do not restrict the term metapopulation dynamics to only those systems that may be approximated by the Levins model, but to any set of local populations with turnover. In the Levins model, which assumes that all habitat patches are similar, it is natural to define the size of a metapopulation as the number (or fraction) of occupied patches. A metapopulation is said to be small when the number of local populations it consists of is small. A metapopulation may be small either because there is only

TABLE 2. Metapopulation terminology

Term	Synonyms and definition
Patch	<i>Synonyms:</i> Habitat patch, (population) site, locality <i>Definition:</i> The area of space within which a local population lives
Local population	<i>Definition:</i> Set of individuals which all interact with each other with a high probability
Turnover	<i>Synonym:</i> Colonization-extinction dynamics <i>Definition:</i> Extinction of local populations and establishment of new populations in empty habitat patches by dispersers from existing local populations
Metapopulation	<i>Definition:</i> Set of local populations which interact via individuals moving among populations
Characteristic time scale of metapopulation dynamics	<i>Definition:</i> $T_m = 1/e_{\min}$, where e_{\min} is the lowest extinction rate among local populations
Metapopulation persistence time	<i>Synonym:</i> Expected lifetime <i>Definition:</i> The length of time until all local populations in a metapopulation have become extinct
Occupancy model	<i>Synonyms:</i> Patch model, scalar state model <i>Definition:</i> A model in which local population size is ignored and the fraction of habitat patches occupied is modelled. Levins's (1969) model is an occupancy model
Metapopulation structure	<i>Synonym:</i> Metapopulation type <i>Definition:</i> System of habitat patches which is occupied by a metapopulation and which has a certain distribution of patch sizes and interpatch distances
Structured metapopulation model	<i>Synonym:</i> Vector state model <i>Definition:</i> A model in which the distribution of local population sizes is modelled

a small number of suitable habitat patches in the environment, or because only a small fraction of the patches is occupied. Unfortunately, this terminology is not very suitable for metapopulations in which there is much variation in the size of habitat patches.

Two issues frequently complicate classifications such as the one outlined in Table 1: the scaling is not discrete but continuous, and it is hierarchical. Delimitation of local populations is often subjective, unless the environment consists of discrete habitat patches—which is the situation that has prompted metapopulation thinking and to which metapopulation thinking most naturally applies. If the environment is uniformly suitable for a species, and if local populations are delimited by isolation rather than by habitat boundaries, one is less likely to observe population turnover, the hallmark of genuine metapopulation dynamics. This is not to say that it would not be useful to examine regional (or ‘metapopulation’) dynamics also in these cases. In a broader perspective, metapopulation dynamics emphasizes the role of emigration and immigration in population dynamics, and these processes can be important regardless of the type of spatial population structure.

Metapopulation structure may be hierarchical, a large ‘local’ population consisting of smaller and more strictly local populations, in which interactions among individuals are more evenly distributed. Thus the ‘mainland-island’ metapopulation structure implicit in island biogeographic studies (below) may be only apparently different from the Levins structure, in which all habitat patches are of the same size. The mainland ‘population’ may persist for a long period because of the close proximity of the local populations it comprises (Harrison, 1991). On the other hand, individuals in many local populations tend to aggregate at resource patches, and such small-scale spatial structure may affect population persistence and other population-level phenomena.

In summary, it would be misleading to try to draw sharp boundaries between different kinds of spatially structured populations, but it is still useful to try to identify the different kinds of mechanisms that operate in population dynamics at different spatial scales.

SINGLE-SPECIES METAPOPOPULATIONS: BEYOND THE LEVINS MODEL

The very simplified Levins model is a valuable theoretical device, but understanding the dynamics of real metapopulations requires models with greater realism and, especially for management purposes, models that lead to more precise predictions. As Levins (1966) clearly realized, no model can simultaneously satisfy the quest for generality, realism and precision.

Going beyond a model that considers only the scalar state variable p complicates matters greatly. Therefore, it is useful to consider modifications of the Levins model that retain this simplification, as reviewed by Hanski (1991) in this volume. In particular, Hanski examines the cases where there is a feedback relationship between the fraction of patches occupied and the probability of local extinction. Such coupling occurs as there is an empirically observed relationship between p and the size of local populations, which in turn reflects the relationship between the rates of local and metapopulation dynamics (Hanski, 1983). Another way of saying the same is to talk about a “rescue effect” (Brown & Kodric-Brown, 1977), or how immigration decreases the probability of local

extinction. The rescue effect is explicitly included in Hanski's (1985) three-state extension of Levins's (1969) two-state model. As discussed by Hastings (1991) in this volume, Hanski's (1985) model clearly demonstrates the dynamical complications in the form of alternative stable equilibria that may occur when immigration is allowed to affect the growth rate of existing local populations (see also Hanski, 1991). Hastings (1991) also examines more general metapopulation models in which the size distribution of local populations is explicitly modelled.

The work by Verboom, Lankester & Metz (1991) in this volume also deals with the internal structure of local populations and connects the Levins model to stochastic processes within each local population, modelled explicitly with probability transition matrices. Another recent extension of the Levins model is due to Lande (1987), who combined it with standard demographic models, and interpreted "habitat patches" as units of space corresponding to individual territories. Incidentally, Lande's (1987) work was motivated by a management problem in conservation biology: how to save the endangered spotted owl in the fragmented old-growth forests of north-western United States. For an extension of Lande's model to interspecific competition see Hanski & Kaikusalo (1989).

In the real world, where different local populations may occupy habitat patches of varying sizes, and where colonization has a component that depends on the distance the colonists have to travel, the phenomenological Levins model falls short of giving a realistic description of most metapopulations. Sjögren's (1991) case study of a frog metapopulation provides an example. Ray, Smith & Gilpin (1991) investigate metapopulation models which assume nearest-neighbour (stepping-stone) dispersal. In these models the presence or absence of particular local populations is critical, as an extinct population can only be colonized from a local population adjacent to it in space. Ray *et al.* utilize this model to consider the role that details of dispersal behaviour may have in metapopulation dynamics.

Regardless of the mathematical and conceptual structures that are used, the key processes in metapopulation dynamics are extinction and colonization, the focus of four papers in this volume. The extinction of local populations has been considered from many angles. Harrison (1991) reviews local extinction events in the metapopulation context, while Sjögren (1991) discusses some real-world complications in a case study of a frog metapopulation. Hansson (1991) discusses the different categories of animal movement and relates them to the dispersal process. Ebenhard (1991) extends the original work of MacArthur & Wilson (1967) on the establishment of arriving individuals at a habitat patch, the colonization process.

The dynamics of local populations are affected by two kinds of stochasticity, labelled as demographic and environmental stochasticity by May (1973). An analogous dichotomy between two types of stochasticity may be defined for metapopulation dynamics, called the immigration-extinction and regional stochasticities, respectively, by Hanski (1991). Hanski (1991) demonstrates how all the four kinds of stochasticity play a distinct role in metapopulation dynamics.

METACOMMUNITIES

If two or more species are confined to the same set of habitat patches, they form a *metacommunity*, a community of metapopulations. Even if these species do

not interact, a metacommunity is an interesting concept, for we can describe not only the fraction of habitat patches occupied by each species, but can also produce probability distributions for their joint occupancies. Barbara Taylor (1991) makes some explorations along these lines in this volume.

If the species do interact as competitors, as predator and prey, or as facilitators in successional processes, then the presence of one species in a patch may influence the extinction probability or the colonization probability of another species, thereby influencing its regional distribution. Community ecologists are interested in interspecific associations and coexistence. The degree to which these phenomena can be explained by metapopulation structure is an important question, exemplified by the recent discussion on the possible role of metapopulation dynamics in host-parasitoid interactions (Murdoch, Chesson & Chesson, 1985; Reeve, 1988; Taylor, 1988).

In this volume, Caswell & Cohen (1991) introduce a general model which extends the Levins model to include all the above cases. Their model is constructed as a non-linear Markov transition matrix. All possible forms of ecological interaction are incorporated into the sign structure of the transition matrix. Case (1991) and Bengtsson (1991) study metacommunities of competitors. Bengtsson reviews his exemplary studies of *Daphnia* in rock pools, while Case develops new theory on the change in community structure as species assort themselves in a metacommunity.

This volume has three chapters on predator-prey metapopulations. Both Nachman (1991) and Sabelis, Diekmann & Jansen (1991) have worked with predator-prey metapopulations in biological control programs. In this volume, Nachman (1991) describes a case study from a greenhouse involving a plant-infested mite and its acarine predator. Sabelis *et al.* (1991) explore theoretically the consequences of various elements of the predator-prey interaction to metapopulation stability. Andy Taylor (1991) presents a review of the empirical literature on predator-prey systems with a supposed metapopulation structure. As with the single-species studies (Harrison, 1991), he finds only a few cases that fit the structure of the Levins model.

METAPOPULATIONS AND ISLAND BIOGEOGRAPHY

The metapopulation idea is related to the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), as there are the same fundamental processes at work: colonization and extinction. There is one major difference. In island biogeographic models, there is a mainland which is the source of colonists and immune to extinction, and only populations on the surrounding islands show turnover. In the Levins model, the source of colonists is the currently extant set of local populations, which is in a constant state of turnover and may itself decay to extinction. A single-species version of the MacArthur & Wilson (1967) model, analogous to equation (1), for changes in the fraction of *islands* occupied, is

$$dp/dt = m(1-p) - ep. \quad (3)$$

The equilibrium value of p in this model is $\hat{p} = m/(m+e)$, which is always positive for islands with any turnover.

Although Levins's metapopulation model and the equilibrium model of island biogeography are occasionally contrasted as two entirely different approaches, equations (1) and (3) actually define the two end points along a continuum of metapopulation structures. As Harrison (1991) discusses in her paper, most metapopulations exhibit much variation in the size (or quality) of habitat patches, which is reflected in the sizes of local populations. Some local populations are much larger and have a much lower extinction probability than others, functioning as 'small' mainlands. Most metapopulations in the real world are likely to have an intermediate behaviour between the Levins model and the genuine mainland-island model of equation (3).

The mainland-island population structure is occasionally confused with the source-sink structure. In the latter, some habitat patches support populations with growth rate balanced by emigration (source populations), while other habitat patches are less favourable, and have populations that would become extinct if the positive effect of immigration on local growth rate were to be eliminated. An apparently similar difference may occur between 'mainlands' and 'islands' due to stochastic factors, but the difference between source and sink populations is, by definition, due to some deterministic habitat differences. The source populations need not be larger than sink populations, and often they are not (Pulliam, 1988).

In island biogeographic models, the focus is in the populations of a single island or habitat patch. The state of these populations is studied as a function of island area and isolation from the mainland. Since each island is ideally a realization of the same process, it is possible to describe the probability of the presence of a species on an island as a function of its area. With a large set of islands an *incidence function* (Diamond, 1975) can be drawn for each species. From such curves, of which Hanski (1991) and Barbara Taylor (1991) give examples in this volume, it is possible to infer, under certain circumstances, relative or even absolute rates of extinction and colonization (Hanski, 1991).

A realistic single-species metapopulation model, in which area of habitat patches and distances among patches are variable, may be formulated from the island biogeographic model by making every occupied patch a potential mainland for any locally empty patch. Such models, as discussed by Gilpin (1987), are too complicated to study analytically. Gilpin (1986) and Gilpin & Ray (1990) have developed numerical computer models that can be run on microcomputers. Such models may be fitted to real world situations, to make predictions of the dynamics of these systems. The programs are available from the authors with the submission of a blank disk and a return envelope.

METAPOPOPULATIONS AND PATCHY ENVIRONMENTS

For some ecologists, any set of individuals that shows an aggregated spatial distribution, regardless of the scale at which aggregation occurs (Table 1), comprises a metapopulation. With this definition, practically any population becomes a 'metapopulation', because almost without exception spatial distributions are aggregated at all spatial scales (Taylor, Woiwod & Perry, 1978). Although it seems useful to us not to extend the metapopulation concept to patchy distributions of individuals at the local scale, it is important to observe that many processes operate in a parallel fashion in both patchy distributions of

individuals within populations and in metapopulations. We shall refer below to two models of coexistence of competitors as an example (a similar analogy could be developed for single-species and predator-prey models).

Competition models with independently aggregated spatial distributions of competitors, called the aggregation (Ives, 1988) or variance-covariance models (Hanski & Cambefort, 1991), demonstrate how intraspecific aggregation, by amplifying intraspecific competition, may allow two or more species to coexist on the same, limiting resource (Hanski, 1981, 1987a; Atkinson & Shorrocks, 1981; Ives & May, 1985; Shorrocks & Rosewell, 1987). Observational and experimental results on insects breeding in decaying mushrooms (Shorrocks & Rosewell, 1986, 1987; Ståhl, Ribeiro & Hanski, 1989), carrion (Hanski, 1987b; Kneidel, 1985; Ives, 1988) and dung (Hanski & Cambefort, 1991) support the predictions of these models (for a review see Ives, 1988).

At the metapopulation level, the occupancy models of Levins & Culver (1971) and Horn & MacArthur (1972), which were further developed and analysed by Slatkin (1974) and Hanski (1983), demonstrate how two similar competitors, which cannot coexist locally, may nonetheless coexist as competing metapopulations. Empirical support for this model is presented by Bengtsson (1991). Fundamentally, in both the variance-covariance and metapopulation models coexistence is based on heterogeneous distributions of individuals. But this comparison also illustrates the use of reserving distinct terms for processes occurring at different spatial scales: although in both cases coexistence is due to habitat heterogeneity amplifying intraspecific competition, the mechanisms are very different. In the variance-covariance model, the key mechanism may be played by the oviposition behaviour of females with larvae developing in patchy and ephemeral microhabitats. In the metapopulation model, the key mechanisms are rates of competitive exclusion and relative dispersal abilities of the species. We thus draw a conceptual boundary between models describing aggregated distributions of species in patchy environments, in which all individuals disperse via a common pool in each generation, and metapopulation models, which have a hierarchical population structure.

METAPOPULATIONS AND LANDSCAPE ECOLOGY

Landscape ecology has many superficial similarities with the set of topics that we have just described. It uses much of the same language, and it is interested in many of the same questions, as metapopulation studies: survival of species, communities and (possibly) ecosystems in fragmented habitats; how to distinguish the matrix, or the distinction between habitat patches and their surroundings; origin, size and shape of habitat patches; the role of habitat corridors in facilitating dispersal and hence maintaining viable metapopulations, etc. (Forman & Godron, 1986). Landscape ecology is particularly concerned with the human role in landscape development and management. Synthetically, it brings together expertise and viewpoints within and from beyond the biological and ecological sciences.

Despite these parallels, there are profound differences between the metapopulation studies we have outlined in this chapter and the present practice of landscape ecology. The exploration of metapopulations is based on the solid foundation of the well-studied behaviour of local populations. Metapopulation

studies have developed deductively, through extensive use of mathematical models and, as the papers in this volume attest, with extensive checking of these advances against observational data and experimental systems. Landscape ecology, on the other hand, is holistic in approach and takes as its object of study the entire landscape. Its methodology at this time is mainly descriptive, and the relevant components and landscape processes are categorized under a hierarchical scheme. Nonetheless, given their common concepts and terminology, the fusion of metapopulation studies and landscape ecology should make for an exciting scientific synthesis.

METAPOPOPULATIONS AND CONSERVATION BIOLOGY

Metapopulation ideas have recently become the vogue in conservation biology, and with most environments becoming increasingly fragmented, it seems clear that much of the metapopulation research in the future will be motivated by and applied to conservation biology. This volume touches two major issues in conservation biology, the population dynamic and genetic consequences of habitat fragmentation and reserve design.

Many species with a formerly continuous spatial distribution are being turned into possible metapopulations by habitat fragmentation. The dynamics of such fragmented populations needs to be understood so that relevant management remedies may be attempted to prevent total extinction. The problems involved in the management of old coniferous forests in north-western United States to save the spotted owl *Strix occidentalis* is a well-known example.

A species confined to a newly fragmented habitat does not necessarily function as a metapopulation, for it may have so poor a dispersal ability that a local population, once extinct, will remain extinct. Brown's (1971) study of mammals on mountaintops is an example: most species seem to be in a slow decline to total extinction. In such cases management may step in to provide artificial colonization, in which case the models of metapopulation dynamics become most relevant. Rolstad (1991) covers a different problem related to habitat fragmentation, namely how different species experience a fragmented environment differently. This question is related to the issue of environmental grain, a concept which Levins introduced in his 1968 book, *Evolution in Changing Environments*. Where an individual routinely moves between habitat fragments within its lifetime, we are concerned with patchy distribution of individuals, not with metapopulations. The same environment may be experienced differently by different organisms, making the conservation issues the much harder.

The decade-old SLOSS controversy, should reserve design emphasize a Single Large habitat patch Or Several Small patches, is fundamentally a metapopulation question when the reserve is being designed for one or a few focal species. Even at the level of species diversity, there are metacommunity aspects to the design problem such as those explored in the papers by Barbara Taylor (1991) and Caswell & Cohen (1991).

A metapopulation structure has important genetical consequences. For instance, the loss of heterozygosity can be greatly accelerated if the species has a Levins-type metapopulation structure. Gilpin (1991) extends the work of Maruyama & Kimura (1980) and Ewens (1989) to calculate the effective population size N_e for metapopulations. N_e can be substantially lower for a

metapopulation than for the same number of individuals in an undivided population. Gilpin believes that cases of strikingly low heterozygosity are best explained by the metapopulation scenario.

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