APPENDIX 4.2

Long-term growth rate with catastrophes

For a population growing exponentially with catastrophes, the population size in generation T just before the next catastrophe is

$$\begin{aligned} N_{t+T} &= \sum_{k=0}^{T-1} (1 + R_{t+k}) N_t \\ &= (1 + \tilde{R}_t)^T N_t, \end{aligned} \qquad (4.2.1)$$

where $(1 + \tilde{R}_t)$ is the geometric mean of $1 + R_t$ over this time interval. If a fraction p of individuals dies in each catastrophe, then N_{t+T+1} is a binomial random variable with parameters N_{t+T} and $1 - p$. If catastrophes occur independently with probability γ in each generation, then T is a geometric random variable and

$$\begin{aligned} \mathrm{E}\,[\ln (N_{t+T+1})] &= \sum_{T=0}^{\infty} \gamma (1-\gamma)^T \{T \ln [(1 + R_t)] + \ln N_t + \ln (1-p)\} \\ &\approx \ln N_t + \ln (1-p) + \left[\ln (1+\rho) - \frac{1}{2}\left(\frac{\sigma_r}{1+\rho}\right)^2 \right] / \gamma, \end{aligned} \qquad (4.2.2)$$

assuming γ is small enough that we can approximate $(1 + R_t)$ with its expectation. Because catastrophes are assumed to occur independently of one another, the long-term growth rate will be negative if and only if $\mathrm{E}\,[\ln (N_{t+T+1})] < \ln N_t$, or equivalently

$$\ln (1+\rho) < \frac{1}{2}\left(\frac{\sigma_e}{1+\rho}\right)^2 - \gamma \ln (1-p)$$

which will occur if, approximately,

$$\rho < (1/2)\sigma_e^2 - \gamma \ln (1-p),$$

where σ_e^2 is the variance in ρ that occurs in intervals between catastrophes.

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The metapopulation paradigm: a fragmented view of conservation biology

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ABSTRACT

In the past, single-population approaches have dominated ecology and evolutionary biology. However, populations are not isolated either in time or space, but are connected by among-population processes such as migration and gene flow. While this concept is not new, until recently, there have been relatively few studies that have explicitly investigated the effects of spatial structure on demographic and genetic processes in the context of conservation. The metapopulation framework explicitly recognises and provides a conceptual tool for dealing with the interactions of within- (e.g. birth, death, competition) and among-population processes (e.g. dispersal, gene flow, colonisation and extinction). The ever-growing diversity of empirical and theoretical studies that demonstrate the importance of spatial structure in determining ecological and evolutionary trajectories also indicates that long-term conservation programmes need to focus on regional rather than local within-population persistence. In this regard, it is important to realise that ultimately all populations are ephemeral, and therefore colonisation processes must also be preserved. Clearly, not all species whose populations have undergone fragmentation fit the definition of a metapopulation. Nevertheless, a metapopulation approach to conservation biology is likely to provide a useful tool for developing management strategies as it addresses genetic, species and community effects of fragmentation in a single framework, thereby making explicit questions regarding extinction, population connectedness, species behavioural patterns and the survival of coevolved systems. In essence, a metapopulation perspective ensures a process-oriented, scale-appropriate approach to conservation that focuses attention on among-population processes critical for persistence of many natural systems.

THE METAPOPULATION PARADIGM: AN INTRODUCTION

Traditionally, ecological studies of natural systems have been dominated by a focus on single populations, or several populations sampled at a single point in time. Reflecting this, much of the theory associated with population dynamics, genetics and interspecific interactions (e.g. competition, predation) has been framed in the context of single-population deterministic models, in part because of the usefulness of tractable mathematical formulations for stability analysis. However, notwithstanding their narrow focus, these single-population approaches have been invaluable in disentangling interactions between various within-population demographic and genetic processes, and their impact on ecological and evolutionary dynamics.

Despite the practical emphasis on single populations, ecologists and evolutionary biologists have long been intrigued with understanding the processes that lead to patterns of abundance and distribution at a range of spatial scales (e.g. Andrewartha & Birch, 1954), beginning with the early work of Wallace, and including the development of the influential theory of island biogeography (MacArthur & Wilson, 1967; see Quammen, 1996 for a recent discussion and review). The recognition that spatial structure might influence species persistence in interspecific interactions has also resulted in a range of studies, including Huffaker's classic experiments on mites (Huffaker, 1958), and theoretical work on spatial models of predator–prey interactions (Hassell & May, 1988; Taylor, 1988, 1990; Hassell *et al.*, 1991; Wilson & Hassell, 1997) and competition (Comins & Hassell, 1987). In contrast, population geneticists and evolutionary biologists have shown particular interest in spatial structure with respect to the way in which among-population processes of gene flow and migration might influence genetic change and evolution (e.g. shifting balance theory: Wright, 1940, 1943; island model: Wright, 1951). More recently, the importance of colonisation and extinction processes for regional persistence and population genetic structure have also come under investigation (Slatkin, 1977; Wade & McCauley, 1988; Whitlock & McCauley, 1990; Gilpin, 1991; Thrall *et al.*, 1998). This has led to the development of a whole range of biologically realistic spatiotemporal modelling approaches (Kareiva, 1990; Czárán & Bartha, 1992; Durrett & Levin, 1994; Gilpin, 1996; Tilman & Kareiva, 1997; Bascompte & Solé, 1998).

Indeed, it is now widely recognised not only that most species are patchily distributed in nature, but that in many cases, populations occupying these patches are ephemeral (e.g. Andrewartha & Birch, 1954; Antonovics *et al.*, 1997; McCauley, 1997*a*). Following the work of Richard Levins (1969, 1970), these ideas have been broadly embraced by a single conceptual framework (metapopulations), incorporating the idea that local populations (or communities) are connected by among-population processes, and these processes can potentially affect, and be affected by, within-population demographic and genetic processes. Hanski (1991) defined a metapopulation as a system of local populations (the scale at which individuals move and interact with each other on a regular basis) connected by dispersing individuals (in plant metapopulations, this would also include gene flow through pollen or seeds). A crucial component of the definition of a metapopulation *sensu stricto* is its emphasis on colonisation/extinction processes whereby all local populations have a significant probability of extinction (Moilanen & Hanski, 1998). However, population size is an important determinant of extinction probabilities, and therefore differential probabilities of extinction (e.g. island–mainland situations) are likely to be more generally the case. Correlated environmental effects may also be important in some systems, leading to similar extinction probabilities at some spatial scales greater than that of local patches (Harrison & Quinn, 1989). As a consequence of these caveats, the metapopulation concept should perhaps be broadened to include any system where colonisation/extinction dynamics play a significant role in the dynamics and persistence of a species or community (Hanski, 1998). The metapopulation approach has been widely publicised in two recent edited volumes (Gilpin & Hanski, 1991; Hanski & Gilpin, 1997).

There is some debate about what types of genetic structures might be found in metapopulations, especially where population turnover is an important feature of the dynamics (Harrison & Hastings, 1996). In general, theory suggests that among-population genetic structure will depend on the nature of among-population dispersal (Whitlock & McCauley, 1990; McCauley, 1991), with genetic differentiation of populations being magnified in proportion to the probability that colonists are drawn from a single source. Empirical studies explicitly relating these colonisation/extinction processes to genetic variation are scarce. However, McCauley and co-workers (McCauley, 1994; McCauley *et al.*, 1995) found that the genetic structure of local populations of the plant *Silene alba* was enhanced by colonisation and extinction processes, with relatively little mixing of individuals from multiple source populations and greater divergence in younger populations. Other work on the metapopulation dynamics of *S. alba* has also demonstrated significant rates of population turnover in this system (Antonovics *et al.*, 1994; Thrall & Antonovics, 1995). Similarly, studies on a metapopulation of *S. dioica* indicated that colonisation played an important role in determining the genetic structure of populations, although colonising propagules were derived from many, rather than few source populations (Giles & Goudet, 1997*a*, *b*). In contrast, counter to classical metapopulation model predictions, Dybdal (1994) found that even though colonists in tidepool populations of copepods were likely to be drawn from only one or a few sources, younger populations were less differentiated than older ones. He postulated that this might be due to the fact that colonists were actually less likely to be drawn from older populations. It is still largely an open question as to how genetic outcomes should depend on the type of metapopulation structure and life-history features of the organisms involved (Thrall & Burdon, 1997).

The extent to which any natural systems depend on a balance between colonisation and extinction processes for persistence has also been questioned (Harrison, 1991, 1994). However, when broadly defined as the interaction between within-population processes and among-population movement, metapopulation dynamics are inevitably a feature of all natural systems (Antonovics *et al.*, 1994; Husband & Barrett, 1996). Indeed, there is now a wide range of empirical studies that have demonstrated the importance of among-population demographic processes, ranging from insects and other invertebrates (Addicott, 1978; Bengtsson, 1989; Hanski *et al.*, 1994) through to amphibians (Gill, 1978; Sjögren, 1991*a*; Driscoll, 1998), mammals (Paillat & Butet, 1996; Moilanen *et al.*, 1998) and plants (Menges, 1990; Ouborg, 1993*a*; McCauley, 1994; Overton, 1994; McCauley *et al.*, 1995; Husband & Barrett, 1996), as well as host–pathogen interactions (Antonovics *et al.*, 1994; Burdon *et al.*, 1995; Thrall & Antonovics, 1995; Grenfell & Harwood, 1997; Burdon & Thrall, 1999). Eriksson (1996), however, suggested with respect to plants that long-lived species with clonal propagation or extensive seed banks may be much less dependent on the balance between colonisation and extinction required for regional persistence in a metapopulation. Certainly, metapopulation dynamics are likely to be much more apparent in annual plants or other short-lived species, but it is inevitable that population turnover will be a feature of most systems at some spatial or temporal scale. In fact, studies on a wide range of organisms, including predator–prey, host–parasitoid and plant–herbivore systems, provide solid evidence that local population extinction is not infrequent in nature (Sabelis & Diekmann, 1988; Fahrig & Merriam, 1992; Merriam & Wegner, 1992).

ECOLOGICAL AND GENETIC NEIGHBOURHOODS: THE IMPORTANCE OF REGIONAL SPATIAL STRUCTURE

Landscapes at many spatial scales are becoming increasingly fragmented as a result of human intervention – an activity that further emphasises the importance of understanding spatial processes. In this context, it should also be noted that 'metapopulation-like' situations can be created by habitat degradation as well as outright fragmentation. Such processes will be a permanent feature of many (if not all) ecosystems for the foreseeable future, and are rapidly becoming of significant concern among conservation biologists (Fig. 5.1), in large part because of the greater risk of extinction faced by small isolated populations. Given the enormous impact that fragmentation can have on genetic structure, ecological and evolutionary dynamics, and therefore population persistence, it is of paramount importance that strategies for conservation management also acknowledge this fundamental process. Moreover, stochastic and historical effects operating at local scales will often produce misleading (and in some cases erroneous) conclusions; one very real effect of fragmentation is to increase the likelihood that local populations will be in a non-equilibrium state (Olivieri *et al.*, 1990). Thus, understanding the causes and consequences of genetic and demographic processes at the within-population level requires that neighbouring demes also be taken into account because of gene flow and migration. Such considerations may have practical as well as theoretical implications, e.g. with respect to establishment of artificial populations for conservation purposes. A cogent demonstration of this was recently provided by a study showing that gene flow from diploid populations of an endangered daisy (*Rutidosis leptorrhynchoides*) into nearby re-established tetraploid populations was causing high levels of chromosomal abnormalities and reduced seed set (Young & Murray, in press).

For these reasons, a compelling argument can be made that viable long-term conservation programmes must place greater emphasis on regional persistence than has been done in the past. In this regard, it is crucial to realise that ultimately all populations are ephemeral, and hence for any species to have a long-term future, colonisation processes must also be preserved. In other words, this means setting aside areas of suitable habitat where species are not currently found, as well as maintaining existing populations. This is the core of the relevance of the metapopulation concept for conservation, where there is a continuum from large essentially 'global' systems through to an opposite extreme of many single, unconnected populations or habitat fragments (Fig. 5.2).

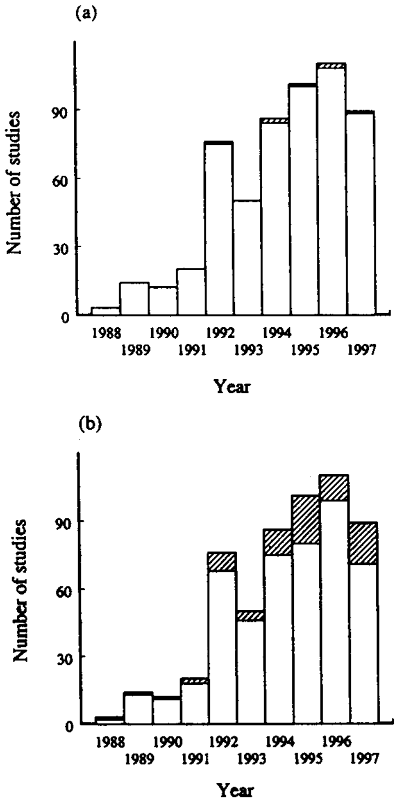

Fig. 5.1. Year-by-year account of the total number of conservation biology studies (empty bars) and the total number of studies incorporating both conservation biology and (a) metapopulation theory (hatched bars) and (b) fragmentation (hatched bars). Data obtained from searches of *Current Contents* (CAB – Abstracts) for 1988 to 1997, using terms 'conservation biology', 'conservation biology and metapopulation' and 'conservation biology and fragmentation'. Note that the 1997 search is up to and including October.

Identifying fragmented systems that have long-term viability

Perhaps the most important conservation issue that the metapopulation approach can usefully address is to identify conditions in which fragmented systems can persist as 'habitat area is lost and the remaining habitat becomes ever more fragmented' (Hanski, 1998). In order to integrate recent work on spatial structure and metapopulation dynamics into conservation practices, we need to become better informed as to how demographic and ecological processes are affected by fragmentation in natural systems (there are several excellent case studies in the present volume that address some of these issues). For example, how can we utilise knowledge about the impact of fragmentation to manage biodiversity effectively? Specific concerns that relate to spatial structure and fragmentation include the

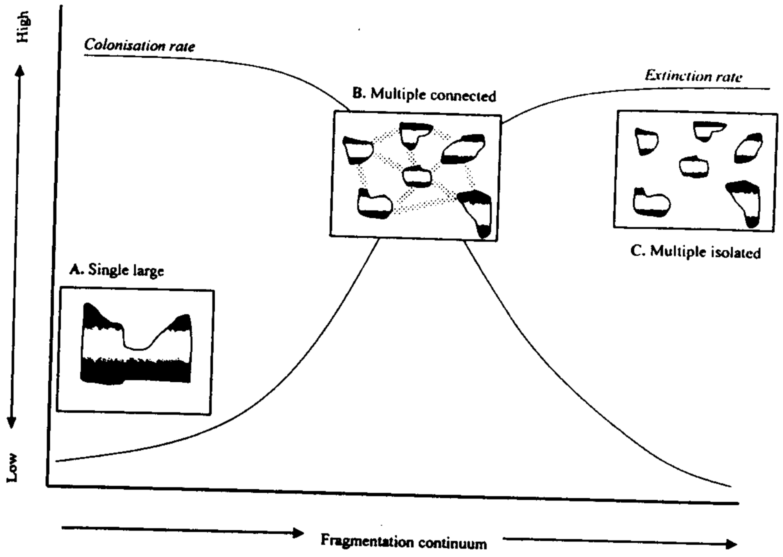

Fig. 5.2. Schematic diagram of the relationship between the continuum of species and community fragmentation and the relative importance of among-population processes for the dynamics. Where individual species or communities fit on the metapopulation axis is determined by a complex of factors including (but not limited to) life-history features that influence dispersal, colonisation and extinction phenomena. Note that even large natural areas (inset A) are rarely homogeneous, and thus among-patch movement will still play an important role in the dynamics. Inset B depicts the level of fragmentation at which the balance between colonisation and extinction processes can potentially result in long-term regional persistence. Conservation efforts centred on preserving such processes may thus provide the best chance of maintaining biodiversity, especially given that fragmentation is becoming a dominant feature of most landscapes.

loss of genetic diversity through genetic drift and inbreeding effects which may lead to increased extinction rates, and even system collapse (Gilpin & Soulé, 1986; Lynch *et al.*, 1995*a*, *b*; Thrall *et al.*, 1998). As a case in point, increased risk of extinction due to inbreeding effects has recently been demonstrated in a fritillary butterfly metapopulation (Saccheri *et al.*, 1998). In general, the importance of genetic and demographic stochasticity will depend on the type of metapopulation structure (i.e. stochastic effects will be relatively more important in systems composed primarily of small populations; Holsinger, Chapter 4, this volume).

Other issues relate to how various kinds of fragmentation processes might influence the relative persistence of species with different life histories. This will be a particularly important consideration in situations where the focus of conservation efforts is on species or communities that can function in a metapopulation situation. Some authors have also suggested that consideration should be given to how rates of spread of diseases depend on the degree of connectedness of patches across the landscape (Simberloff, 1988; Hess, 1994, 1996*a*, *b*). Whether pathogen or parasite movement should be taken into account when designing networks of habitat patches has not, to our knowledge, been critically addressed, although several theoretical studies have focused on how among-population connectedness influences pathogen dynamics and persistence (Thrall & Antonovics, 1995; Grenfell & Harwood, 1997; Thrall & Burdon, 1999).

The metapopulation paradigm provides a useful conceptual framework within which to address such questions, as it explicitly acknowledges that local populations are not isolated either in time or space. Furthermore, while fragmentation has certainly contributed to increased extinction rates in small populations, metapopulation theory tells us that even in fragmented systems, many species may have the ability to persist if individual patches are connected by dispersal (Moilanen & Hanski, 1998). While real-world metapopulations are unlikely to match several of the assumptions of the original Levins model (e.g. homogeneity of habitat quality and patch size, equal probability of dispersal to any site), increasing numbers of researchers are employing a range of descriptive, experimental, theoretical and computer-simulation approaches to ask how ecological and evolutionary processes are influenced by the incorporation of spatial structure in natural systems. These studies range from empirical work on small mammals inhabiting archipelagos to biologically realistic computer simulations of host–pathogen interactions that are integrated with empirical studies. In fact, much of the recent theoretical work on metapopulations has centred on exploring the consequences of departures from the classical Levins models. In the context of conservation, the most important of these are considerations of the interactions that occur between within- (e.g. birth, death, competition) and among-population (e.g. dispersal, gene flow, colonisation and extinction) processes, and how altering these may impact on species persistence.

Carrying out metapopulation studies in a conservation context

While all metapopulations (by definition) consist of spatially structured sets of habitat patches, not all fragmented ecosystems show the minimum requirement of stochastic extinction–recolonisation dynamics that fit the definition of a metapopulation (Hanski, 1994*a*). Therefore, it also follows that not all species in recently fragmented systems will have evolved to persist in a metapopulation situation. Nevertheless, a metapopulation approach to conservation biology is likely to provide one of the most useful tools for developing management strategies that optimise among-population processes critical for persistence of many natural systems. For example, Hanski (1994*b*) outlines methods for estimating the risk of metapopulation extinction and stochastic steady state. This approach can be used to investigate the likelihood of different outcomes when a fraction of patches is removed from the system (a possibility that is all too pertinent to conservation biology). Hanski's approach is based on simple metapopulation models which allow for estimation of colonisation and extinction probabilities from empirical patch occupancy data (often the very data that is most readily available from field studies). Hanski (1994*b*) illustrates this with an example from a metapopulation of fritillary butterflies (*Melitaea cinxia*) that assesses the 'relative importance of each patch for persistence of the metapopulation'. Similarly, Day & Possingham (1995) used a stochastic metapopulation approach to examine the spatial structure of populations of malleefowl, *Leipoa ocellata*, in southern Australia. With their model, they were able to quantify how further habitat loss (and consequent alterations in patch arrangement) would influence metapopulation extinction probabilities.

How do we approach the seemingly daunting task of carrying out metapopulation-type studies? Both practical issues associated with sampling multiple sites across time and also aspects of the species biology that determine relevant spatial scales for within- vs. among-population interactions must be taken into account (Antonovics *et al.*, 1994). As noted by Husband & Barrett (1996), one needs to consider the distribution of a species within its geographic range, the discreteness of habitats occupied and dispersal capability – these all play a role in determining connectivity and therefore what constitutes a local population. Demographic and genetic information may provide other criteria for defining local populations and metapopulations (Husband & Barrett, 1996); in this regard the concept of ecological and genetic neighbourhoods (Antonovics & Levin, 1980) is likely to provide a useful starting point. It is also possible to study metapopulation dynamics experimentally, using 'model' species that are easily manipulable in laboratory situations, such as bacteria and protozoa (Burkey, 1997), or where artificial populations can be readily established and maintained in the field (Thrall & Antonovics, 1995). However, in many cases, especially where endangered species are involved, experimental manipulation may be excluded and inferring metapopulation processes such as colonisation/extinction rates from pattern data becomes essential (Hanski, 1994*a*).

Both implicit and explicit modelling approaches have been developed to investigate spatial issues (Hanski, 1994*b*); the former include analytically tractable but often somewhat unrealistic theoretical models based on Levins's original concept, as well as more complex structured metapopulation models (e.g. Verboom & Metz, 1991), while the latter are often centred around biologically realistic, but analytically less friendly computer simulations. Both theoretical and computer-simulation studies have a special role to play as they also allow the investigation of many questions related to spatial scale that are not tractable empirically. Thus, these approaches have focused particularly on local vs. regional dynamics and their longer-term coevolutionary effects. Spatially explicit simulations have also proved useful as predictive tools for investigating the consequences of varying patch number and arrangement within reserves, and thus may be of assistance in identifying, not only how many, but which patches should be kept in a system. It is encouraging that in many cases, useful information may be derived from models based entirely on patch area and isolation (Moilanen & Hanski, 1998), both factors for which information is readily available.

LESSONS FOR CONSERVATION FROM METAPOPULATION STUDIES

Genetic effects

There are several general problems that have been raised with respect to increasing fragmentation and the consequent loss of connectivity among local populations. Notable among these are issues relating to genetic structure, for example, concerns over the loss of genetic diversity and inbreeding effects (Lacy, 1987; Gilpin, 1991; Thrall *et al.*, 1998). While a subject of intense interest among conservation biologists, empirical studies explicitly relating metapopulation dynamics (i.e. population turnover) to genetic fitness are almost non-existent, and non-conclusive. However, Richards (1997, and Chapter 16, this volume) has clearly demonstrated that smaller, more isolated populations of the plant *Silene alba* have higher levels of inbreeding, manifested as reductions in seed germination rates. Importantly, experimental work showed that fitness in these populations could be significantly enhanced by increased gene flow from other populations (Richards, 1997) – one of the criteria suggested by Harrison (1994) as a justification for using metapopulation models. Similarly, Young *et al.* (1999, and Chapter 19, this volume) found in the daisy *Rutidosis leptorrhynchoides* that the degree of correlated paternity was negatively related to population size and positively correlated with isolation, indicating the possibility of biparental inbreeding effects. Stochastic population simulations based on several years of demographic data for *R. leptorrhynchoides* also hint at a negative relationship between persistence time and the level of correlated paternity (Young *et al.*, Chapter 20). In contrast, work on a metapopulation of pool frogs (*Rana lessonae*) in northern Sweden indicated that while higher levels of population turnover resulted in reduced heterozygosity, this did not translate into lower fitness (Sjögren, 1991*a*, *b*). On several grounds, it has been argued that extinction of small populations is likely to occur for demographic or environmental reasons long before inbreeding effects will become important (Lande, 1988; Holsinger, Chapter 4, this volume). Clearly, this is an issue that is still far from resolved. However, in species with strong self-incompatibility systems, genetic effects may be manifest at a far earlier stage, effectively reducing population size very substantially (Young *et al.*, Chapter 20).

Species and community effects

Other important concerns relate to the maintenance of diverse species assemblages and communities. Under what conditions can fragmented systems maintain their integrity with respect to species composition? Much has been written about one single aspect of this issue, and that is with respect to fragment size in relation to effects on community structure [i.e. single large or several small (SLOSS); see Quammen, 1996 for a general review of this debate]. For example, long-term large-scale experiments in the Amazon basin (Lovejoy & Bierregaard, 1990) were explicitly focused on addressing this question. A great many researchers have argued both for and against particular sizes and numbers of reserves on economic, political and biological grounds, and it may well be that metapopulation theory can aid in determining optimal spatial structuring of patches. However, while fragment size is clearly important, it does not take into account issues of connectedness and the need to preserve colonisation processes at the among-population level for both ecological and genetic reasons.

Metapopulation viability

A wide range of recent studies that explicitly use the metapopulation framework has already indicated a number of important features of fragmented systems that are crucial to conservation biology. Firstly, various empirical studies have provided evidence that both population size and isolation can affect demographic and genetic parameters (Barrett & Kohn, 1991). For example, small populations of *Eucalyptus albens* (white box) have been shown to have less genetic diversity than large ones, this effect being more pronounced in more isolated sites (Prober & Brown, 1994). Similar results have been obtained in studies of the roadside weed *Silene alba* (Richards, 1997, and Chapter 16, this volume). Secondly, whether due to demographic, genetic or environmental causes, local patches often go extinct, which is a major reason for the simple rule that we should be preserving as much habitat as possible. In this regard, one of the most important lessons to be learned from metapopulation models is that 'currently unoccupied habitat fragments may be critical for long-term persistence' (Hanski, 1998). At the same time, both empirical and theoretical studies of metapopulations indicate that even though local extinction is common in a system, regional persistence may still be possible.

Paradoxically and deceptively, simulation studies have demonstrated the possibility that in many cases, metapopulations below the colonisation/extinction balance (and hence on the path to annihilation) can still have a high percentage of occupied sites at any particular point in time (Hanski, 1998). This may occur during the lag phase before past habitat destruction becomes manifest as declining numbers of populations in remaining areas, and begs the critical question of how we will know when we have passed a threshold. This highlights the importance of identifying 'indicator variables' in relation to species and community characteristics that can provide clues to the current and potential future state of fragmented systems (Brown *et al.*, 1997; Thrall *et al.*, 1998). It also shows quite clearly the potentially misleading nature of 'snapshot' studies taken at a single point in time or restricted to one or a few populations.

As noted by Hanski (1998), based on simple models, several important general conclusions can be drawn about how metapopulations respond to processes of fragmentation. Firstly, because among-population connectivity is lost in a non-linear fashion, gradual loss of habitat can result in a sudden shift from a positive equilibrium to regional extinction. Secondly, metapopulation decline in response to fragmentation occurs with a time-lag, sometimes referred to as the 'extinction debt' (Tilman *et al.*, 1994), which basically means that current extinctions are happening because of past habitat destruction. Thirdly, the equilibrium number of suitable but unoccupied patches existing in a metapopulation before fragmentation will be equal to the colonisation/extinction threshold. All of these factors highlight the difficulty of determining precisely when a system has passed the threshold for collapse, and moreover emphasise the fact that, in all likelihood, this point will be reached well before a decline in population numbers is obvious (Gutiérrez & Harrison, 1996; Thrall *et al.*, 1998).

On the positive side, the corollary to these observations is that metapopulation theory also suggests several obvious ways in which the likelihood of regional persistence can be enhanced: these include increasing the number of habitat patches, increasing the degree of clumping of these patches, increasing variance in patch size (e.g. moving towards a core–satellite structure) and increasing connectivity (Harrison & Fahrig, 1995; discussed in Wiens, 1996).

PRACTICAL APPLICATIONS OF METAPOPULATION THEORY

In the previous sections, we have argued for the general importance of understanding spatial structure, and taking it into account when implementing conservation strategies. How can we use knowledge about the effects of fragmentation to manage biodiversity? In practical terms this may translate into understanding how metapopulation extinction is a function of the number, size, quality and connectivity of habitat patches in the system (Drechsler & Wissel, 1998). Are there situations where such approaches have been implemented?

One clear example of how metapopulation thinking has been useful in a practical sense is with respect to the northern spotted owl in the northwestern United States (Gutiérrez & Harrison, 1996; Noon & McKelvey, 1996). As has been widely publicised, old-growth forests in this region have been heavily logged, leaving only discrete fragments in which spotted owls can persist. The application of metapopulation modelling to the conservation of spotted owls has led to a management approach that emphasises patch size and spacing consistent with persistence in a metapopulation (Wiens, 1996). Other examples include the Florida scrub jay (Stith *et al.*, 1996), kangaroo rats (Price & Gilpin, 1996), greater gliders in Australia (Possingham *et al.*, 1994) and pool frogs in Sweden (Sjögren-Gulve & Ray, 1996). In contrast, there appear to be relatively few examples where metapopulation thinking has been explicitly applied to conservation of plant species (but see Menges, 1990, 1991*b* with respect to Furbish's lousewort *Pedicularis furbishae*) although a wide range of studies has focused on genetic and demographic consequences of fragmentation in plant populations (e.g. Richards, 1996; Young & Brown, 1998).

Will we ultimately be reduced to artificially dispersing individuals among reserves? It has been suggested that knowledge of metapopulation dynamics may allow us to perform the functions of dispersal and recolonisation of locally extinct habitat patches, and that the metapopulation approach may also be able to guide conservation efforts in terms of optimal numbers and placement of translocated plants and animals, as well as genetic sources (McCullough, 1996). This may be of particular importance if we accept the argument that as suitable habitat areas become ever more isolated, and intervening areas increasingly hostile due to further development, most species will require help to move among patches (Simberloff, 1988).

Another area where metapopulation theory may inform conservation biology is in restoration ecology, where the realisable goal is often to regenerate a semi-natural system (in the sense of containing a subset of the original community). In a practical sense, it may well pay to identify and focus on species that have at least some potential to persist in a metapopulation-like situation. Biologically realistic metapopulation simulations should prove useful in identifying general characteristics that such species are likely to possess.

SPATIAL AND BEHAVIOURAL INTERACTIONS TO CONSIDER

Extinction thresholds

A major and increasingly urgent problem for conservation biologists is understanding to what extent systems can be fragmented, and the number of individual populations lost, before collapse occurs (whether for genetic, demographic or environmental reasons). This issue clearly relates to the concept of minimum viable metapopulations, defined as the 'minimum number of interacting local populations necessary for the long-term persistence of the metapopulation' (Hanski *et al.*, 1996*a*). Understanding factors that influence extinction risks in endangered metapopulations is an important component of management (Drechsler & Wissel, 1998). In this regard, it is important to develop a conceptual framework that allows some predictive power with respect to how spatial structure (e.g. core–satellite vs. many small populations) interacts with biological factors to determine persistence thresholds. Theoretical work on metapopulations certainly shows that thresholds for persistence exist, and at the most basic level this translates into a balance between extinction and colonisation processes (Levins, 1969, 1970). However, exactly how any threshold depends on various life-history features (e.g. dispersal capability, life span, the existence of seed banks in plant metapopulations) is not well understood. Indeed for most species we have very little knowledge of either their dynamics or their dispersal ability (Wiens, 1996). However, there are some theoretical studies that relate dynamics in metapopulations to dispersal (e.g. Herben & Söderström, 1992; Olivieri *et al.*, 1995). In the context of island biogeography, studies of colonisation ability in relation to life history suggest that the best colonisers are those that are generalists or are self-fertile; with respect to mammals, size appears to be positively correlated with colonisation ability, but the opposite has been shown to be true for insects (see Ebenhard, 1991 for a review). There is no reason to believe these general patterns will not be applicable in fragmented environments. However, ultimately at some spatial scales most organisms have limited dispersal, and therefore beyond that distance, increasing isolation brings a decreasing probability of colonisation. This provides an upper limit to the extent of fragmentation (with its almost inevitable dual effects of increased isolation and habitat loss) that is possible while yet maintaining the metapopulation.

Ascertaining what factors determine the conditions under which extinction rates exceed colonisation rates is essential to developing a true appreciation of the vulnerability of individual species (Harrison & Quinn, 1989; Frankel *et al.*, 1995). When integrated across multiple species this has direct links to the concept of conservation at the community level (i.e. metacommunities: Hanski & Gilpin, 1991*a*; Wilson, 1992). Within a single community type, species may have very different disturbance requirements or dispersal distances (e.g. consider the range of fruit-dispersal mechanisms in tropical forest tree species) leading to different extinction thresholds. While it may be possible to determine extinction thresholds for a range of single-species metapopulations, this may grossly underestimate the threshold required to maintain the intact community. Identifying extinction criteria for those organisms that are highly mobile may provide a conservative estimate of the total amount of habitat necessary to preserve particular community types (Frankel *et al.*, 1995), although it will still be necessary to understand how loss of connectivity within conserved regions impacts less vagile species (or those with more specialised requirements). A major challenge for the future is then to develop the concept of minimum community thresholds – otherwise, fragmentation may lead to qualitatively different communities, with drastically altered coevolutionary interactions and characteristics (e.g. with respect to ecosystem function).

A further complexity is that distance-independent extinction (correlated environmental variation) could lead to correlated extinction probabilities for conspecific populations (Harrison & Quinn, 1989). Such a possibility effectively reduces the number of demes in a metapopulation, as well as global persistence time, yet most metapopulation models still assume that local populations experience completely independent extinction (Harrison & Quinn, 1989). The very real potential for correlated environmental variation at spatial scales greater than single-habitat patches clearly indicates the need for management strategies that conserve as many habitat/environment types as possible, so as to maximise the probability of regional persistence.

Movement of pests, pathogens, parasites and predators

While, in general, metapopulation modelling has indicated that increased connectivity will lead to increased persistence at the regional scale (e.g. Harrison & Fahrig, 1995), some authors have suggested that there may also be negative consequences, at least in highly connected networks. For example, increased ability to move among populations may also facilitate the spread of infectious diseases and parasites (Dobson & May, 1986; Simberloff, 1988; Hobbs, 1992; Hess, 1994, 1996*a*, *b*). In fact, Simberloff (1988) has gone so far as to suggest that fragmentation may actually have the positive effect of reducing disease. Indeed, positive correlations have been found between disease incidence and the disease status of neighbouring populations in two natural plant–pathogen systems (Burdon *et al.*, 1995; Ericson *et al.*, 1999). Whether or not this is a real issue is an open question as there may well be trade-offs between the positive effects of increased ability of the host to move among patches and the negative effects of disease. Indeed, using simple Levins-type models, Hess (1994, 1996*a*, *b*) showed that there may be intermediate levels of connectedness that are optimal. However, these results do not take into account the fact that increased movement will also result in greater movement of resistance genes, and may also aid in disease avoidance, nor do they incorporate other aspects of coevolutionary interactions between host and pathogens. For example, recent empirical studies of a protozoan parasite (*Ophryocystis elektroscirrha*) of monarch butterflies with different patterns of migration suggest that life history and population structure may interact to determine disease prevalence, and the evolution of virulence (S. Altizer, unpublished data); parasites in non-migratory host populations were generally more virulent and disease prevalence was higher than in migratory populations. Overall, we would argue that disease is generally unlikely to provide a novel threat for species that have been artificially fragmented, as increasing connectivity is not likely to lead to the introduction of diseases that were not present in pre-fragmented times.

With respect to predation, increased connectivity may assist the movement of predators from one prey population to another. A classic illustration of this is given by the loss of native species on oceanic islands when predators such as rats and cats have been introduced (Simberloff, 1988). In a metapopulation context, a particularly good example is provided by the decline in frogs (*Rana muscosa*) as a consequence of the spread of introduced predatory fish in streams and drainage ditches that connect populations (Bradford *et al.*, 1993). Furthermore, where corridors are narrow it has been argued that they may often act as 'demographic sinks' doing more harm than good (Soulé & Gilpin, 1991). Thus, the effective degree of connectivity with respect to species persistence may be quite different from the perceived level if factors such as predation and behavioural complexities (see below) are not taken into account.

Behavioural issues

It has been suggested that increasing connectivity could lead to loss of individuals because of movement into suboptimal habitats (Hobbs, 1992). As a cautionary note, patterns of species behaviour may also alter model predictions and thresholds for extinction. For example, in a study of Columbian ground squirrels (*Spermophilus columbianus*), Weddell (1991) showed that squirrels did not disperse to new patches but settled near other individuals. Thus, social attraction can lead to reduced probabilities of patch colonisation, making the system more sensitive to fragmentation than would be otherwise expected. It seems likely that this will be a general issue for social species. Of critical importance for many species will be distinguishing between habitat patches used for different purposes (e.g. breeding vs. feeding). Moreover, movement among patches may often be non-random with respect to identity – e.g. young males leaving home territories to find mates. The extent to which such types of behaviour alter predictions for metapopulation dynamics is unknown. Overall, metapopulation management models for animals need to consider behavioural complexities (e.g. requirements for periodic migration: Hobbs, 1992) that would reduce the effective number of habitat patches, or change regional persistence thresholds. Other ecological features that apply to plants as well as animals, such as competitive interactions among species, may also be important factors to consider (Tilman *et al.*, 1994; Wiens, 1996).

Conservation of coevolutionary processes

Coevolutionary interactions between different organisms ranging from symbiotic (e.g. mycorrhiza fungal – plant and rhizobia bacterial – plant associations) to totally parasitic (e.g. fungal and viral diseases of plants and animals) are being increasingly recognised as both sources of biodiversity in their own right and as fundamental ecosystem processes that affect both population and community structure and function. However, conservation of these associations may be particularly complicated as the survival of one or both players is often inextricably tied to the continued existence of their partner(s). Examples of this phenomenon are myriad, including very many micro-organisms and invertebrates associated with plants.

Following the spatial pattern of their major component, coevolutionary associations typically occur as a series of individual, co-occurring populations distributed patchily across the landscape. As Thompson (1994, 1997) has pointed out, across this range of populations that represents a species' presence in an area (metapopulation) there are likely to be 'hotspots' of coevolutionary activity as well as others in which change is occurring far less rapidly. These hotspots may reflect a range of phenomena – both biological (e.g. enhanced recombination in the genome of either player through hybridisation with other ecotypes or species) and physical (e.g. sites that particularly favour the development of parasites) – that act as sources of variation in the metapopulation as a whole, and which consequently provide the driving force for continuing evolutionary change. A priori identification of such sites of high coevolutionary activity is very difficult if not impossible. Yet they must be maintained if such interactions are to continue to develop and change.

Increasingly, empirical evidence from coevolutionary studies is highlighting the diversity of responses achieved as coevolutionary partners respond to each other in different demes of single metapopulations. Thus in the interaction between *Linum marginale* (native Australian flax) and *Melampsora lini* (flax rust), the size of *Linum* and *Melampsora* populations, their ephemerality and their genetic structure often vary markedly between closely adjacent demes of a single metapopulation (Burdon & Jarosz, 1991; Burdon & Thrall, 1999). This interpopulational diversity provides a long-term 'insurance' for the continued existence of the association as individual local populations flicker in and out of existence. Equally importantly, though, the unpredictable changes in both the direction and intensity of selective interactions that occur as a result of these changes mean that we cannot predict the long-term trajectory of such associations nor can we expect to maintain them simply by preserving one or two populations. Indeed, recent increasingly sophisticated computer-simulation modelling clearly indicates the lack of clear predictive correlations between the behaviour of interactions at the level of the individual deme and that at the metapopulation level (Thrall & Burdon, 1999).

Failure to conserve such interactions within metapopulation arenas will inevitably lead to their eventual collapse. In many instances, this may result in the extinction of the antagonist. When this is a viral or fungal pathogen such a loss may raise little public concern (Dobson & May, 1986). However, what if the antagonist driven to extinction is a moth or spectacular butterfly? Or even a specialised variety of bird? Moreover, because of the unpredictable nature of interactions, we cannot say a priori what might be the long-term consequences of the extinction of individual players in coevolutionary plays. Micro-organisms are frequently ignored by ecologists and conservation biologists, but their potential as powerful selective forces shaping the demography and genetics of their hosts is well documented in their use as biological control agents.

CONCLUSIONS AND FUTURE DIRECTIONS

As noted at the beginning of this chapter, much of population ecology has focused on studies of single populations, and has further assumed that dynamics in local populations are deterministic, with local stability a viable outcome. It is of considerable concern that this view may have influenced the development of conservation management practices centred around preserving existing populations and/or patterns across the landscape. However the metapopulation perspective has highlighted the fact that local populations are, in fact, ephemeral, thereby emphasising the need to ensure that long-term conservation planning focuses on spatial scales larger than the single population. Moreover, we would argue that, generally speaking, there needs to be a frameshift towards conserving process rather than patterns (patterns are also ephemeral). In the context of studies on the ecology of mosses, Herben & Söderström (1992) specifically note that the 'primary aim in the protection of species living on temporary, patchy habitats is to identify and preserve the conditions that enable the dynamic process to operate'. We concur wholeheartedly and argue that this applies to all species, although the relevant spatial and temporal scales will vary in different situations. In fact, this argument could be extended to preserving coevolutionary processes rather than species themselves – ultimately, nothing is permanent except change! The importance of emphasising regional persistence applies equally to many different levels of organisation, ranging from metapopulations of a single species (or coevolutionary interaction) through to entire communities and ecosystems.

The bottom line is that fragmentation results in two fundamental changes across the landscape: firstly, it leads to increasing isolation of habitat patches, and secondly, it results in a decrease in the total amount of available habitat (Simberloff, 1988). The metapopulation paradigm explicitly recognises and provides a conceptual tool for dealing with the interactions of within- (e.g. birth, death, competition) and among-population processes (e.g. dispersal, gene flow, colonisation/extinction). The ever-growing diversity of studies that demonstrate the importance of spatial structure in determining ecological and evolutionary trajectories also makes clear that conservation biology must focus on regional persistence and not local within-population persistence. Simply put, it is just not good enough to put fences around existing populations as all local sites are ephemeral at some temporal scale. Rather, we must explicitly recognise the importance of colonisation/extinction processes. Unfortunately, while the importance of spatial structure is now generally recognised, it is still only rarely incorporated into population viability analyses (Harrison, 1994).

But, given the fact that most reserves are already far too small to support intact communities, and in the context of the ever-increasing destruction of habitat with the simultaneous decrease in the number and size of larger reserves, does a metapopulation perspective really provide any greater hope than any other approach? It would be relatively easy to advocate the rather pessimistic perspective that since (1) maintaining many small patches is both more time-consuming and expensive than single large reserves, and (2) small patches will go extinct anyhow, we should simply let the small reserves go and focus on the largest remaining areas. Simberloff (1988) has suggested that the metapopulation paradigm does provide some encouragement in that it has demonstrated that a partially connected system of many small patches can indeed have long-term viability. Thus, if it is to have value for conservation, the clear challenge for metapopulation theory in the immediate (and foreseeable) future is to enable managers (1) to determine when there is sufficient between-patch migration for persistence under realistic conditions (and if not, how this could be achieved), and (2) to guide efforts in maintaining appropriate numbers and placement of currently unoccupied patches in a state that they could become occupied again and not just overrun by weeds. Integration of management efforts within a regional metapopulation framework is invaluable in that it forces a process-oriented, scale-appropriate strategy to conservation.