

Local extinction in a metapopulation context: an empirical evaluation

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Metapopulations are classically viewed as sets of populations persisting in a balance between local extinction and colonization. When this is true, regional persistence depends critically upon parameters influencing extinction and colonization rates, e.g. the number of habitat patches and populations, the rates and patterns of interpatch migration, and propagule establishment probabilities. A review of relevant empirical literature identifies few metapopulations which fit this description well. Instead, three qualitatively different situations are found to be more common: (1) mainland-island and source-sink metapopulations, in which persistence depends on the existence of one or more extinction-resistant populations; (2) patchy populations, in which dispersal between patches or sub-populations is so high that the system is effectively a single extinction-resistant population; (3) non-equilibrium metapopulations, in which local extinction occurs in the course of a species' overall regional decline. This suggests a modified view of metapopulation dynamics in which local extinction is more an incidental than a central feature.

KEY WORDS: Extinction – metapopulations – persistence – dispersal – colonization – population dynamics.

CONTENTS

Introduction	73
Definition and causes of local extinction	75
Local extinction in a metapopulation context	77
Mainland-island and source-sink metapopulations	77
Patchy populations	81
Non-equilibrium metapopulations	82
Classical metapopulations and intermediate cases	83
Summary	84
Acknowledgements	85
References	85

INTRODUCTION

Although the theory of single-species metapopulation dynamics is well developed (see review in Hanski, 1991), and metapopulation ideas have permeated many areas of ecological and evolutionary theory, many empirical questions remain to be answered about how metapopulations function. The extinction of local populations is a central aspect of most metapopulation models and ideas. This review examines local extinction from an empirical perspective,

comparing the role it is given in metapopulation theory with evidence from relevant field studies.

Field observations of local extinctions, especially in plant and insect populations, were an important early stimulus to the ideas which later became known as metapopulation theory (Andrewartha & Birch, 1954). From such observations, it was argued that species may persist as regional ensembles of transient populations, through dispersal and (re-)colonization of vacant habitats. Such a 'shifting mosaic' mode of demographic persistence was proposed by some theorists as an alternative to stabilizing or regulatory factors acting within local populations (Andrewartha & Birch, 1954; Ehrlich & Birch, 1967; see also Ricklefs, 1979).

Mathematical theory in this area began with the model by Levins (1969, 1970). Hanski (1991) and Hastings (1991) review the development of metapopulation models. Levins's and other simple metapopulation models depict an either finite or infinite set of populations, all of which are subject to extinction with equal and temporally independent probabilities. More complex models (e.g. Hastings & Wolin, 1989) incorporate such refinements as spatially structured dispersal and continuous rather than binary population dynamics within patches. However, most retain the feature of Levins's (1969, 1970) model that local extinction affects all populations, more or less equally. This is true as well in the majority of models concerned with the regional coexistence of locally unstable combinations of competitors or predators and prey (e.g. Horn & MacArthur, 1972; Slatkin, 1974; Hastings, 1978; Hanski, 1983).

There are important implications to this extinction-centred view of metapopulations. If all populations are subject to extinction, regional persistence depends critically upon colonization. In turn, persistence depends on the parameters controlling colonization rates, such as the number of vacant patches and extant populations, the rates and patterns of dispersal (Hansson, 1991) and propagule establishment probabilities (Ebenhard, 1991). Another key determinant of metapopulation persistence is the degree of temporal independence among local populations in their chances of extinction (Harrison & Quinn, 1989; Gilpin, 1990).

Other metapopulation models present modified views of the role and importance of extinction. The mainland-island metapopulation structure of Boorman & Levitt (1973; see Fig. 1B) contains a central population, immune to extinction, which supplies colonists to transient marginal populations. In the model by Hanski (1985) local populations may alternate between susceptibility and resistance to extinction. In a different vein, metapopulation models by Roff (1974), Chesson (1981) and Roughgarden & Iwasa (1986; Iwasa & Roughgarden, 1986), emphasize spatio-temporal variability in population dynamics, rather than extinction and colonization. These models assume such a high degree of dispersal between the patches on which recruitment and growth take place that local extinction is unlikely to occur. Similarly, Levin (1974) and Comins & Noble (1985) find that competitors or predators and prey can coexist in a fugitive fashion without local extinction; coexistence is facilitated by the spatially localized nature of competitive exclusion and/or predation, combined with limited dispersal.

This brief review of theory provides a background against which to contrast the empirical evidence on local extinction in metapopulations. Although the

causes of local extinction will be briefly discussed, below, more emphasis will be placed on its consequences, especially with respect to demographic persistence. First, it will be necessary to define local extinction and to distinguish among the various ways the terms 'extinction' and 'metapopulation' are used in the literature.

DEFINITION AND CAUSES OF LOCAL EXTINCTION

'Local extinction' is sometimes used to denote the disappearance of a species from any arbitrarily defined sampling plot (e.g. den Boer, 1970). At the other end of the scale, it may signify a species' extirpation from any region less than its entire range (e.g. Chew, 1981). Here, local extinction is defined more narrowly as the disappearance of a population, where the term population is used in the demographic (Ehrlich, 1965) or genetic (Wright, 1969) sense. Admittedly, this definition presents practical difficulties, since not all species are organized into discrete, identifiable groups within which 'nearly all' mating, reproduction and interactions take place. In considering metapopulation dynamics, one possible definition of a local population is the minimal unit which once extirpated, may remain extinct for more than one or a few generations. This at least serves to exclude sub-populations so tightly coupled to others that their 'extinction' is likely to be followed immediately, e.g. within one generation, by 'recolonization'.

The causes of local extinction may be stochastic or deterministic. The stochastic aspects of extinction have been categorized by Shaffer (1981) as demographic, genetic and environmental stochasticity, and catastrophes. Stochastic local extinction has received a great deal of theoretical attention, beginning with MacArthur & Wilson's (1967) work on island colonization. More recently it has become a central theme in conservation biology (Shaffer, 1981; Wright & Hubbell, 1983; Shaffer & Samson, 1985; Gilpin & Soulé, 1986; Simberloff, 1988). Only a brief summary of theory and relevant empirical work is attempted here.

Demographic stochasticity (MacArthur & Wilson, 1967; Richter-Dyn & Goel, 1972; Gilpin & Soulé, 1986; Ebenhard, 1988, 1991) concerns the changes in population size caused by randomness in the order of occurrence of births and deaths. Theory suggests that this only adds significantly to the risk of extinction in populations which are below a relatively small threshold size (MacArthur & Wilson, 1967; Richter-Dyn & Goel, 1972), though the exact magnitude of the threshold depends on specific demographic traits of the species (Ebenhard, 1988, 1991). Because of the existence of a threshold, it might be expected that demographic stochasticity will play a more significant role in the success or failure of colonizing propagules, and the final extinction of declining populations, than in the extinction of established populations. Empirical studies of demographic stochasticity mainly concern colonization (e.g. Crowell, 1973; Ebenhard, 1988 and references therein).

Genetic stochasticity refers to the loss of heterozygosity through drift and the loss of fitness due to inbreeding. Empirical work connecting these genetic processes to the demography of small populations is almost non-existent. However, theory predicts that genetic stochasticity enhances the risk of extinction mainly in populations that have recently declined in size and that

lack histories of severe fluctuations. In species that are naturally subject to frequent population turnover, genetic stochasticity is expected to affect persistence relatively little (Gilpin, 1987, 1991; Lande, 1988; Sjögren, 1991).

Environmental stochasticity is temporal variation in the net rate of population growth, driven by variation in external factors such as weather or food supply. The magnitude of population variability depends on life-history traits that determine how well reproduction and mortality are buffered against environmental change. Theory predicts that in species with highly variable rates of population growth, even large populations have short expected lifetimes (Leigh, 1981; Goodman, 1987). Studies of insular faunas confirm this prediction: after correcting for different population sizes, the species with the greatest variability in population growth rates are the most prone to extinction (Leigh, 1981; Karr, 1982; Schoener & Toft, 1983; Pimm, Jones & Diamond, 1988).

When the environmental events causing populations to fluctuate are infrequent and severe, or so-called catastrophes, risks of extinction are only weakly dependent on population size (Ludwig, 1976; Hanson & Tuckwell, 1978, 1981; Gripenberg, 1985). Environmental catastrophes which have been observed to cause local extinction in insects include droughts (Ehrlich *et al.*, 1980; Thomas, 1984), aberrant freezes (Ehrlich *et al.*, 1972; Strong, Antolin & Rathbun, 1990) and fires (Cryan & Dirig, 1978; Givnish, Menges & Schweitzer, 1988).

Of the various stochastic causes of local extinction, environmental stochasticity and catastrophes are probably the most important in natural metapopulations, based on both the balance of empirical evidence (below) and the theoretical expectation that they can affect populations of a large range of sizes. Environmentally-driven local extinction raises a potential problem for metapopulation theory. Many of the environmental factors which cause population fluctuations and extinction act at a regional scale. Weather is the most obvious example. It is likely to affect all populations in a metapopulation simultaneously, and thus to create temporal correlation in their chances of extinction. Correlated local extinction (or 'regional stochasticity', Hanski, 1991) can sharply reduce the expected persistence time of metapopulations (Harrison & Quinn, 1989; Gilpin, 1990).

Direct evidence on correlated extinction in metapopulations is very limited. However, Pollard, Hall & Bibby (1986) examined 10-year relative abundance data for British butterflies, and documented that conspecific populations often fluctuate in synchrony. Ehrlich *et al.* (1972) and Ehrlich *et al.* (1980) observed the extinctions of multiple conspecific butterfly populations in two environmental catastrophes, a spring freeze and a drought respectively.

Thus, local extinction in many species is caused by large-scale environmental events. Theory suggests that in such circumstances, classical metapopulations are unlikely to persist. This enhances the potential significance of refuges, habitats in which certain populations are protected from catastrophes and act as sources for recolonization (see below), to persistence in such cases. Also, many species are adapted to large-scale adversity through 'escape in time' strategies, such as environmentally cued seed dormancy in plants or facultative diapause in insects (for a review of the latter, see Hanski, 1988). These adaptations have the effect of making local, as well as regional, extinction less likely.

Deterministic local extinction characterizes species of temporary habitats, such

as successional vegetation. These species continually disappear from local habitats as these become unsuitable. However, whether these local disappearances can be usefully regarded as local extinctions, in the sense defined above, depends critically upon the lifetime of the habitat and the frequency and range of individuals' movements (this issue is also discussed below under 'Patchy Populations'). The other major source of non-random local extinction is human pressures on species and their habitats (Ehrlich & Ehrlich, 1981).

LOCAL EXTINCTION IN A METAPOPOPULATION CONTEXT

There are far fewer case studies of local extinction in a metapopulation context than of local extinction *per se*. Of the empirical studies that have quantified patterns of local extinction in multiple populations, nearly all come from the field of island biogeography (see reviews in Schoener, 1983; Diamond, 1984). The sets of insular populations in these studies are not maintained by mutual recolonization, but by repeated immigration from a mainland. Apart from island studies, most cases of extinction reported in the literature are single observations from which little can be deduced about metapopulation structure, such as where colonists come from and how often (e.g. Washburn & Cornell, 1981; Svensson, 1985).

Studies documenting rates and patterns of local turnover within entire, closed population systems are limited in number. However, examining the available literature, it is possible to identify several major types of metapopulations, in terms of the different roles which they imply for local extinction. I have categorized these as follows (see also Hanski & Gilpin, 1991): (1) Mainland-island and source-sink metapopulations (Fig. 1B), the distinction between which is clarified below. Local extinctions occur mainly among a subset of populations, the islands or sinks, and have little effect upon regional persistence since the extinction-resistant mainland or source populations are the major providers of colonists. (2) Patchy populations (Fig. 1C), which are distributed over a patchy and/or spatiotemporally variable habitat, but in which high rates of dispersal effectively unite the patches into a single demographic entity. There is thus little potential for the extinction of discrete local populations. (3) Non-equilibrium metapopulations (Fig. 1D), among which recolonization is either absent or insufficient to balance extinction. Local extinction occurs as part of an overall regional decline, usually a product of the reduction, fragmentation or deterioration of the habitat. (4) Classical metapopulations (Fig. 1A), sets of conspecific populations persisting in a dynamic regional balance between extinction and colonization, as represented by the standard metapopulation models. There appear to be relatively few cases conforming well to this description; I will speculate on the reasons for this, after illustrating each of the types of metapopulation with examples.

Mainland-island and source-sink metapopulations

In the equilibrium theory of island biogeography (MacArthur & Wilson, 1967), local extinction affects the distribution of local populations, but not the regional persistence of the species. Extreme differences in patch sizes make some terrestrial metapopulations very similar in their dynamics to true mainlands and

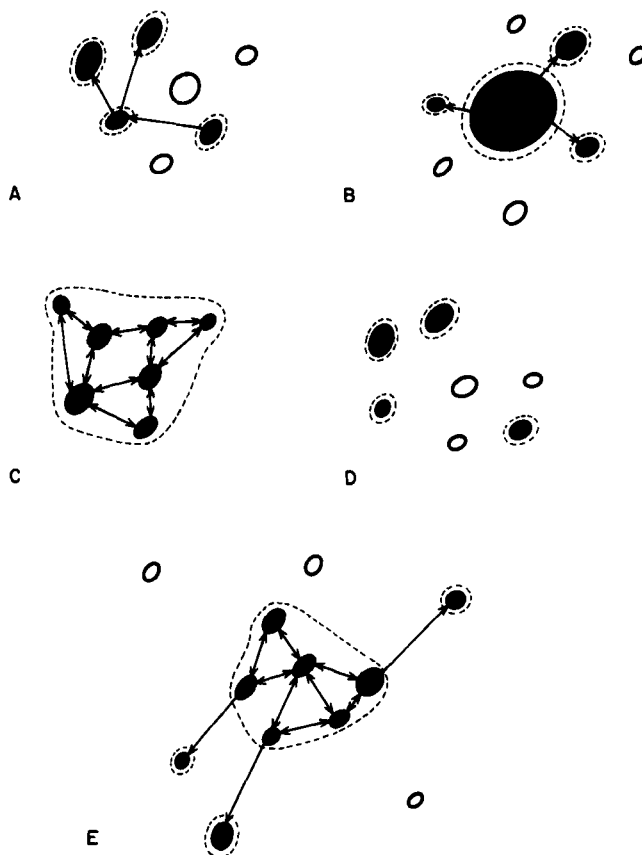


Figure 1. Different kinds of metapopulations. Closed circles represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate the boundaries of 'populations'. Arrows indicate migration (colonization). A, Levins metapopulation. B, Core-satellite (Boorman-Levitt, 1973) metapopulation. C, 'Patchy population'. D, Non-equilibrium metapopulation (differs from A in that there is no recolonization). E, An intermediate case that combines B and C.

islands. One example is the metapopulation of the Bay checkerspot butterfly (*Euphydryas editha bayensis* Boisduval) that I studied (Harrison *et al.*, 1988; Harrison, 1989). It consisted, in 1987, of a population of on the order of 10^6 adult butterflies on a 2000-ha habitat patch, and nine populations of 10–350 adult butterflies on patches of 1–250 ha. Of 27 small habitat patches in the region which were found to be suitable, only those closest to the large patch were occupied (Fig. 2). This pattern of patch occupancy could not be explained by differences in habitat quality. Instead, the distance effect appeared to indicate that the butterfly's capacity for dispersal is limited, and that the large population acts as the dominant source of colonists to the small patches. From this and other evidence, it appears that persistence in this metapopulation is relatively unaffected by population turnover on the small patches.

Thus, local extinction may be frequent and yet may be relatively trivial in terms of regional dynamics, as Williamson (1989) has previously noted. For this to be true, there need not be a mainland population of extreme size. High variance in patch or population size means that most local extinctions will

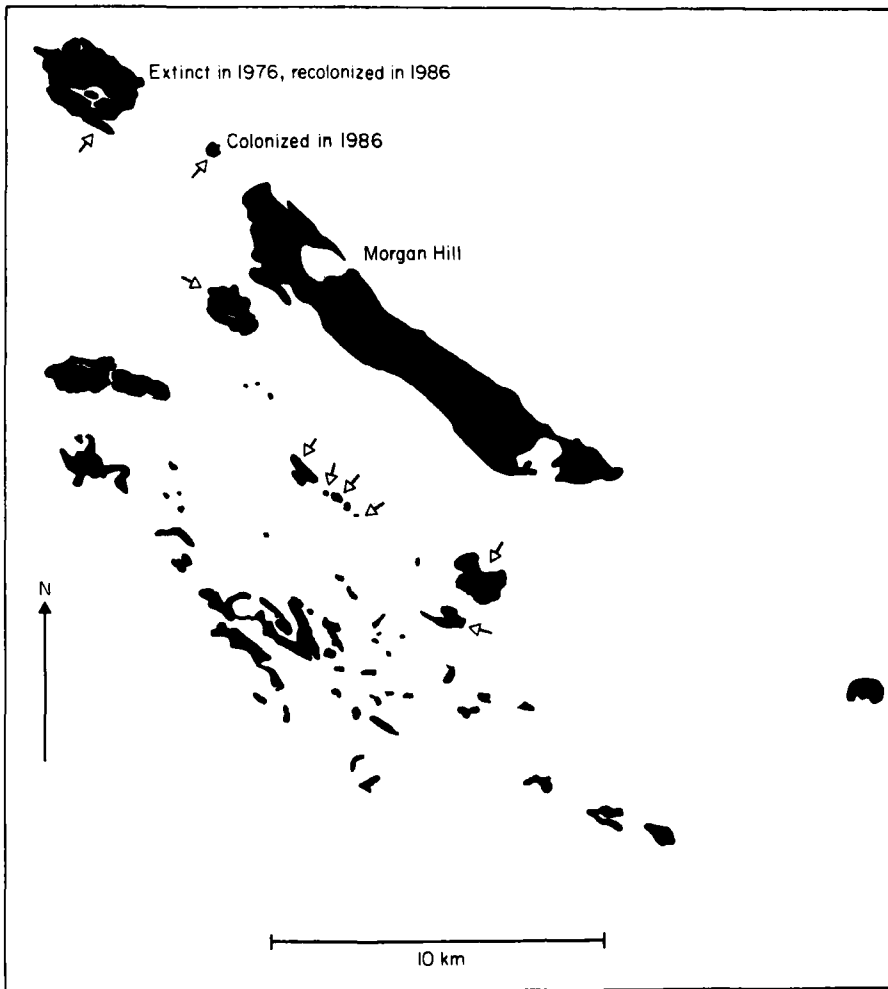


Figure 2. Metapopulation of the Bay checkerspot butterfly, *Euphydryas editha bayensis* (from Harrison *et al.*, 1988). The black areas represent patches of the butterfly's serpentine grassland habitat. The 2000-ha patch labelled 'Morgan Hill' supported a population of in the order of 10^6 adult butterflies in 1987. The nine smaller patches labelled with arrows supported populations of in the order of 10^1 – 10^2 butterflies in that year. Eighteen other small patches were found to be suitable but unoccupied.

probably be unimportant, as they will tend to strike the smallest populations with the least influence on the metapopulation. Schoener & Spiller (1987) found this to be the case in Bahamian orb spider metapopulations. In populations of five spider species on 108 islands (distant from the continental mainland), which were monitored for 5 years, local extinction affected only the 10–40% (depending on species) smallest populations. Many of the larger populations appeared to be effectively immortal, in that their expected lifetimes (were these populations isolated) would be much longer than the timescale of interisland dispersal.

Metapopulation dynamics have seldom been quantified as directly and thoroughly as in the study of Schoener & Spiller (1987). However, it is probably common for metapopulations to contain similarly high variation in population

and patch size and to function as constellations of mainlands and islands. The Solomon Archipelago, on which avian colonization-extinction dynamics were studied by Gilpin & Diamond (1976, 1981), spans a five-to-six order of magnitude range in island size. A population size range of up to three orders of magnitude was reported by Thomas (1984) in a review of population studies of endangered British butterflies. Fritz (1979) estimated lifetimes ranging from 2 to 100 years for the local populations in a spruce grouse metapopulation, based on patch sizes, bird densities and a demographic model. In the Concho water snake, Soulé & Gilpin (1991) noted a mainland-island effect caused by variation in local densities of river riffles.

High variation in local population size may arise for other reasons than patch size, including chance. Metapopulations of aphids on fireweed (Addicott, 1978) consisted of ensembles of local colonies, lasting in total for the duration of the summer growing season (4–8 aphid generations). The majority of colonies were much shorter-lived than the metapopulation as a whole, but a few were large enough to last the entire season, leading Addicott (1978) to conclude that metapopulation persistence did not depend on the ongoing founding of new colonies. The variation in colony size appeared to be produced by chance factors in the process of colony establishment.

From the point of view of regional dynamics, it is not the variation in patch or population size *per se* that is significant so much as the variation in the persistence of local populations. Heterogeneity in the quality of the habitat may have this effect. In the source-sink systems discussed by Pulliam (1988) there is a net flow of migrants from persistent populations in good habitats ('sources') to populations in inferior habitats which act as sinks. The difference between these and mainland-island metapopulations lies in the nature of the peripheral, extinction-prone habitats. While islands are merely smaller than mainlands, sinks are qualitatively different from sources, being unsuitable in some way for survival and reproduction.

An example of a source-sink metapopulation is the checkered white butterfly (*Pieris protodice* Boisduval & LeConte) in the Central Valley of California (Shapiro, 1979). The source population occupies a riparian area, which is the only part of its regional range in which the butterfly can overwinter successfully. Every spring, emigrants found numerous smaller colonies on outlying patches of the host plant, sometimes at considerable distances from the source population. However, these colonies persist for about five generations, at most, before becoming extinct at the onset of the following winter. Similarly, a population of *Euphydryas editha wrightii* in Southern California was observed to undergo an explosive increase in numbers, following a series of especially favourable years. A number of peripheral colonies appeared on patches of marginal-quality habitat and subsequently disappeared (Murphy & White, 1984).

Peripheral or sink areas may be occupied only infrequently, while the source areas are always occupied, as in the examples above. From such situations, a continuum extends to metapopulations in which peripheral areas are occupied most of the time, but populations retract to core areas during adverse conditions. Emigrants from these refuge habitats then recolonize the extinction-prone habitats when favourable conditions return. An example is the Amargosa vole, a microtine subspecies endemic to an isolated desert marsh. Vole populations are widespread throughout the marsh in most years, but during occasional flood

years the vole survives only as disjunct populations on isolated hilltops (Freas & Murphy unpublished). Similarly, Strong *et al.*, 1990) found that populations of a leafhopper and its parasitoid in a coastal marsh survived a rare winter freeze under scattered piles of beach wrack.

Species coexistence may also be mediated by mainland-island or source-sink dynamics. In some insect predator-prey systems, it appears that the prey species is able to persist, despite the ability of the predator to drive it locally extinct, because of habitat refuges in which it is invulnerable to the predator (Beddington, Free & Lawton, 1978; Murdoch, Chesson & Chesson, 1985). Iwasa & Roughgarden (1986) model coexistence in locally competing intertidal organisms by assuming that for each species there is a source habitat in which it outcompetes the others. Regional sources or refuges constitute a qualitatively different explanation for coexistence than the extinction-colonization dynamics proposed in classical patch models (e.g. Horn & MacArthur, 1972; Slatkin, 1974; Hastings, 1978; Hanski, 1983; Bengtsson, 1991).

Hanski (1983) and Gilpin (1987) have previously noted the unrealism of the assumption that all local populations in a metapopulation are equally subject to extinction and contribute equally to colonization. To the extent that this assumption is violated, metapopulation processes (extinction and colonization) become less crucial to regional persistence. Persistence may depend more upon the local factors, such as large size or favourable habitat, that permit mainland or source populations to resist extinction.

Patchy populations

The kind and degree of connectedness between patches or populations is a critical feature in models of spatially structured populations. The classical metapopulation concept of Andrewartha & Birch (1954), Ehrlich & Birch (1967), and Levins (1969, 1970) portrays sets of relatively independent demes undergoing turnover on a timescale of years to generations. In contrast, models concerned with the effects of spatio-temporal variability on population stability (e.g. Roff, 1974; Chesson, 1981; Crowley, 1981; Roughgarden & Iwasa, 1986), though superficially similar to metapopulation models in that they depict local population units fluctuating independently, differ in that these units are coupled by very high dispersal (see also Taylor, 1988). In the extreme, complete mixing of progeny among patches is assumed. Here the designation 'patchy population' is used for such demographically united systems of patches. High interpatch dispersal means that the differentiation between local and regional timescales, a principal attribute of metapopulations, is diminished, and so is the potential for local extinction.

In practice, of course, it is impossible to draw a sharp distinction between metapopulations with true local extinction, and patchy populations in which extinction is absent or unimportant. However, if the average individual inhabits more than one patch in its lifetime, the patches clearly do not support separate populations. The fauna of patchy and ephemeral habitats, such as the insects that specialize on fallen fruit, rotting logs or water-filled treeholes, are often regarded as forming metapopulations. But such species are typically highly mobile; each patch usually supports only one generation of the insect, and adults oviposit on numerous patches (Kitching, 1971; Hanski, 1987). Similarly,

butterfly species which specialize on weedy host plants typically show high vagility compared with species using more permanent habitats (Scott, 1975; Blau, 1980). Gerrid water bugs (Kaitala, 1987) move frequently among the ephemeral ponds which they inhabit. In general, high interpatch dispersal may be said to be common trait in species of unstable, transient, and/or patchy habitats (see Hanski, 1987 for a review).

A considerable number of other 'metapopulations' in the literature appear to lie toward the high dispersal end of the continuum. A case in point is the classic study in which den Boer (1970, 1981) found asynchronous fluctuations in the numbers of carabid beetles trapped at various sampling points within a continuous habitat, on the scale of tens to hundreds of metres apart. Den Boer (1970, 1981) theorized that the beetle population is stabilized by the movement of individuals over distances greater than the scale of localized environmental fluctuations. Within-habitat dispersal also appears to enhance the persistence of populations of *Euphydryas editha*. Larval survival varies among different slope exposures, because the suitability of host plants is affected by an interaction between topography and yearly weather patterns. Both larvae and ovipositing adult butterflies disperse among slopes within continuous habitat (Weiss, Murphy & White, 1988). Many sessile marine organisms appear to spread their propagules widely in comparison to the scale of the patches on which recruitment and growth occur (Strathmann, 1974). Random dispersal may be a very general means of population persistence in spatiotemporally varying environments (Goodman, 1987).

Local differences in the abundance of predators or competitors are another source of spatiotemporal variation in population dynamics. High dispersal by a prey species or an inferior competitor may allow it to coexist with a predator or superior competitor. However, since the dynamics of predators and prey are coupled, the relationship of prey dispersal rates to coexistence may be complex; see Taylor (1988, 1991) for recent reviews of theory.

Thus, patchy population dynamics arise when dispersal takes place on a spatial scale greater than that of the local events causing population fluctuations. This may be expected to be the case in many species of patchy, transient or otherwise risky habitats; or such species may 'escape in time' through dormancy. High dispersal means that patches or sub-populations are united into a relatively persistent population in which there is little potential for local extinction. Local 'turnover' on patches, in such systems, is more the product of the movements of individuals than of mortality.

Non-equilibrium metapopulations

A great number of local extinctions take place, not in the context of a regional colonization-extinction equilibrium, but in the context of the regionwide decline of a species. Recolonizations may occur infrequently or not at all. This usually occurs as the species' habitat is undergoing long-term fragmentation, reduction or deterioration. Habitat fragmentation leaves local populations more prone to extinction, because they are isolated from 'rescue' by immigration, and also to limit or prevent recolonization. One natural example is the series of extinctions of mountain mammal populations, caused by the reduction and isolation of mountaintop habitats during post-Pleistocene warming (Brown, 1971; Taylor,

1991). Much more abundant, however, are cases of regional declines caused by human impacts on natural habitats. Wilcove, McLellan & Dobson (1986) and Rolstad (1991) provide reviews of habitat fragmentation and local extinction in temperate birds and mammals. Arnold (1983), Thomas (1984) and Cappucino & Kareiva (1985) provide similar examples from butterflies.

Conservation of species in fragmented habitats is an important area for the application of metapopulation models. This issue is discussed by Gilpin (1987) and Hanski (1989, 1991), and only a few additional points are raised here. First, fragmentation may very often result in mainland-island situations in which a single remnant population is of overwhelming importance (e.g. the grizzly bear in the United States, Gilpin, 1987). Second, fragmentation may be fine-grained in relation to the range of movement of individuals; this appears to be true in many cases involving birds in forest fragments (Rolstad, 1991). Fine-grained fragmentation is perhaps better thought of as altering habitat quality than as leading to the isolation and extinction of local populations.

Third, unstable regional extinction-colonization dynamics may be induced by anthropogenic habitat changes other than outright fragmentation. For example, species dependent on disturbance-generated habitats are sensitive not only to reduction in the amount of the habitat matrix, but also to changes in the disturbance regime. This is the situation for a number of endangered butterflies in Britain and the United States. In Britain, several species requiring sunny openings in woodlands are declining not only due to deforestation, but also to the cessation of traditional forest coppicing, which generates forest clearings (Warren, Thomas & Thomas, 1984; Warren, 1985). Another British species is declining because of the demise of peat-cutting, which opens up patches in heathlands (Thomas, 1985). In the U.S., the combination of fire suppression and habitat loss to urbanization threaten the Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) which depends on a host plant characteristic of post-fire succession (Cryan & Dirig, 1978; Fried, 1987; Thomas, 1983).

Because of reduced disturbance, new habitats are generated for these butterflies at insufficient rates. When new habitats do appear, they are increasingly unlikely to become colonized by the butterflies (Thomas, 1984). These cases are similar to the disturbance-driven population dynamics which have been frequently studied in intertidal communities (e.g. Paine & Levin, 1981; Caswell & Cohen, 1991), with the important difference that the butterflies' rates of dispersal between disturbed patches are low, quite possibly too low to prevent eventual regional extinction. An interesting application for metapopulation models would be to predict the minimum size of the disturbance mosaic (Pickett & White, 1985) required to support these species. This has been attempted for the Karner blue butterfly by Givnish *et al.* (1988).

Classical metapopulations and intermediate cases

Waterflies (*Daphnia* spp.) in rockpools (Bengtsson, 1988, 1989, 1991) and pool frogs (*Rana lessonae* Camerano) in successional ponds (Sjögren, 1988, 1991) form metapopulations in which there is neither extreme variation in population sizes or other determinants of persistence, nor extremely high rates of movement among patches. These appear to represent close approximations to Levins

metapopulations, sets of discrete local populations which are subject to local extinction and persist regionally because of (re-)colonization.

Of course, the distinction between these and the other types of metapopulations is largely a function of the timescale being considered. There is sufficient variation in persistence among pool frog populations that this metapopulation could probably persist for decades without recolonization, despite numerous extinctions (Sjögren, personal communication). Similarly, Pajunen (1986) has suggested that certain *Daphnia* pools support mainland populations considerably more persistent than those in other pools. But metapopulations such as these, with moderate levels of variation in population size and moderate dispersal among patches, may provide the majority of real-world cases in which local extinction both occurs and has regional significance.

Other intermediate cases may arise from the spatial arrangement of patches. There is widespread evidence in island biogeographic studies for rescue effects (Brown & Kodric-Brown, 1977; see review in Ebenhard, 1988), in which a patch is more likely to be occupied the nearer it is to other occupied patches (see also Ray *et al.*, 1991). This suggests the possibility of a metapopulation (Fig. 1E) combining features of the mainland-island and patchy population structures: dispersal unites central patches into a single population, but is low enough to allow local extinctions on peripheral patches. A possible example of this is the metapopulation of hyraxes on kopjes (rockpiles) studied by Hoeck (1982, 1989). Another intermediate case, one which combines mainland-island and classical metapopulation structure, is exemplified by the archipelago vole populations studied by Ebenhard (1988). With increasing distance from the mainland, insular populations are influenced less by the mainland population and more by among-island dynamics.

SUMMARY

A critical examination of the metapopulation literature reveals that local extinction does not have the same role or degree of importance in all situations. Local extinction may not occur at all, if interpatch dispersal is always high, or it may only affect populations in small patches or poor habitats. Local extinctions may be a manifestation of a species' regional decline. Only in a subset of metapopulations in the empirical literature does the analogy of a 'population of populations', existing in a balance between birth (colonization) and death (extinction), seem to apply well.

The birth-death analogy arose from a simple model which did not include such refinements as variation in population persistence, explicit spatial structure of patches and temporal correlation in extinction. When such real-world features are considered, a general result may be to shift importance away from regional process (extinction and colonization) and more toward local factors, such as large population size, habitat heterogeneity and within-population dispersal, in determining persistence.

Of course, the empirical evidence is far too limited for secure generalizations to be made. There is undoubtedly a research bias toward systems with rapid local turnover, and too little evidence on the extinction and colonization dynamics of long-lived organisms. However, there may also be real biological reasons for the seeming scarcity of cases of classical metapopulations. It is reasonable to expect

that most organisms are adapted to escape, in space or time, from the environmental risks they normally face, and a side effect of such adaptations will be to make the extinction of local populations less likely to be a routine part of population dynamics.

If these empirical considerations suggest a diminished role for local extinction in metapopulations, they are not intended to downplay the significance of metapopulation dynamics broadly defined. The interplay between local and regional processes can promote the regional persistence of locally unstable species, and the regional coexistence of locally incompatible combinations of species, with or without the complete extirpation and refounding of separate local populations.

ACKNOWLEDGEMENTS

I thank J. Quinn and P. Ward for help and advice during the preparation of this paper; J. Bengtsson, D. Debinski, T. Ebenhard, M. Gilpin, I. Hanski, P. Kareiva, O. Jarvinen, W. Murdoch, G. Nachman, T. Schoener, P. Sjögren and S. Vail for comments on the manuscript; and the participants in the NCE course on metapopulations for useful discussions.

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