

# Single-species metapopulation dynamics: concepts, models and observations

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This paper outlines a conceptual and theoretical framework for single-species metapopulation dynamics based on the Levins model and its variants. The significance of the following factors to metapopulation dynamics are explored: evolutionary changes in colonization ability; habitat patch size and isolation; compensatory effects between colonization and extinction rates; the effect of immigration on local dynamics (the rescue effect); and heterogeneity among habitat patches. The rescue effect may lead to alternative stable equilibria in metapopulation dynamics. Heterogeneity among habitat patches may give rise to a bimodal equilibrium distribution of the fraction of patches occupied in an assemblage of species (the core-satellite distribution). A new model of incidence functions is described, which allows one to estimate species' colonization and extinction rates on islands colonized from mainland. Four distinct kinds of stochasticity affecting metapopulation dynamics are discussed with examples. The concluding section describes four possible scenarios of metapopulation extinction.

**KEY WORDS:**—Extinction – colonization – incidence function – heterogeneous environment – core and satellite species – stochasticity – alternative equilibria – structured model.

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## INTRODUCTION

The ecological literature provides two perspectives from which to view the dynamics of metapopulations. One tradition emphasizes how “a natural population occupying any considerable area will be made up of a number of . . . local populations” (Andrewartha & Birch, 1954), how “the risk of wide fluctuation in animal numbers is spread unequally over a number of

subpopulations”, and how “the consequences of this spreading of the risk in space will be a relative reduction in the amplitude of fluctuations of animal numbers in the entire population” (den Boer, 1968). The point Andrewartha & Birch (1954) and den Boer (1968) are making is the varying conditions experienced by individuals living in different local populations. The second line of thinking is not focused so much on local populations but on the dispersal between them, and on the evolutionary pressures modifying the rate of dispersal; Gadgil’s (1971) work is a fine early example. These two research traditions, emphasizing asynchronous dynamics of local populations and dispersal among them, respectively, cover two of the three elements that are required for metapopulation persistence in the face of unstable local dynamics. The third requirement is some density dependence at the level of local populations (Taylor, 1988; Murdoch & Walde, 1989; Hanski, 1990).

This paper commences with a description of Levins’s (1969, 1970) phenomenological metapopulation model, which has provided a conceptual framework for empirical studies and has served as the starting point of many theoretical analyses during the past 20 years. Even this simplest model of metapopulation dynamics makes testable predictions about how habitat patch size and isolation affect metapopulation persistence. I outline how data on island or habitat patch occupancy may be used to draw inferences about the processes on which metapopulation persistence hinges, the rates of extinction and colonization. I then describe some variants of the Levins model, motivated by empirical data, and indicate the need for structured metapopulation models, in which the distribution of local population sizes is considered (reviewed by Hastings, 1991). Current models, both simple and structured, assume that all habitat patches are of the same size. This is seldom true in nature (Harrison, 1991), and I examine some consequences of relaxing this assumption. I then describe four kinds of stochasticity with distinct consequences to metapopulation persistence. Finally, I draw the previous results together into a summary of four scenarios of metapopulation extinction.

#### THE LEVINS MODEL

Let us imagine a species living in an environment consisting of many similar habitat patches. The size of local populations occupying these patches is assumed to be either 0 (extinct) or  $K$  (local carrying capacity). Local dynamics are thus ignored, apart from the extinction and colonization events. Movements from an occupied patch are assumed to be equally likely to all other patches, in other words the spatial arrangement of patches is ignored or is assumed to have no consequence. The rate of colonization is assumed to be proportional to  $p$ , the fraction of occupied patches (sources of colonists), and to  $1-p$ , the fraction of unoccupied patches (targets for colonization). All local populations have the same, constant extinction probability. With these assumptions, changes in  $p$  in continuous time are given by,

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

where  $m$  and  $e$  are the colonization and extinction parameters, respectively. The equilibrium value of  $p$  is

$$\hat{p} = 1 - e/m. \quad (2)$$

$\beta$  is positive if  $m$  is greater than  $e$ , otherwise  $\beta = 0$ . Equation (1) is the Levins model, and equation (2) summarizes its main predictions. Note that the Levins model incorporates the three elements that are required for population regulation at the metapopulation level (Introduction): asynchronous dynamics in local populations (uncorrelated colonization and extinction events), dispersal among patches and density-dependent local dynamics (constant carrying capacity).

In spite of its simplicity and obvious limitations, equation (2) is fundamentally important in highlighting a key aspect of metapopulation dynamics: metapopulation persistence requires that, for a given extinction rate, the colonization rate exceeds a threshold value; and that for a given colonization rate the extinction rate is smaller than a threshold value. Numerous empirical studies have demonstrated how the extinction rate decreases with increasing area of habitat patches, and how the colonization rate decreases with increasing isolation, in small mammals (Smith, 1974, 1980; Pokki, 1981; Hanski, 1986), birds (van Dorp & Opham, 1987), *Daphnia* waterfleas (Pajunen, 1986; Bengtsson, 1988, 1989), spiders (Toft & Schoener, 1983; Schoener & Spiller, 1987), freshwater snails (Brönmark, 1985), aphids (Addicott, 1978) and many other taxa. These observations allow us to relate metapopulation persistence to the structure of the environment: for a given average isolation between habitat patches, metapopulation persistence requires that the average patch area is greater than a threshold value; and for a given average area of patches, their average degree of isolation must be smaller than a threshold value.

The Levins model thus predicts that a species may be missing from systems of small habitat patches, and from systems in which the average degree of isolation is great, even if the patches may offer temporary support to local populations. Carter & Prince (1981) suggest that the geographical distribution limit of many plant species may be explained by metapopulation dynamics along a gradient of decreasing habitat patch density, rather than, for example, by species' climatic tolerances. Prince & Carter (1985) present (indirect) supporting evidence for one species, the prickly lettuce *Lactuca serriola*. Sjögren (1991) develops a similar argument for the pool frog *Rana lessonae* studied on its northern distribution limit. Another example of the effect of habitat patch isolation on metapopulation persistence is the frequent absence of *Daphnia* waterfleas from islands with only few and isolated rock pools (Hanski & Ranta, 1983; Bergtsson, 1991).

#### *Evolutionary considerations*

The extinction and colonization parameters in equation (1) are assumed to be constants. One component of the colonization parameter is dispersal rate, which varies greatly between species, and is clearly the result of natural selection (Roff, 1974; Hamilton & May, 1977; Comins, Hamilton & May, 1980, and others). It has been appreciated for a long time that frequent extinctions of local populations, which create vacant patches suitable for colonization, should select for increased rate of dispersal (Brown, 1951; Southwood, 1962). In this evolutionary perspective, the rate of dispersal is expected to evolve to compensate for extinctions, and to keep  $\beta$  positive. Though a seemingly reassuring consideration for conservation biologists, one should remember that dispersal rates are likely to change so slowly that metapopulations living in

habitats fragmented by man are unlikely to be rescued by this factor (den Boer, 1977).

It is also worth emphasizing that the 'optimal' rate of dispersal, the rate which natural selection is expected to produce, depends on the optimization criterion, for example whether individual fitness (the fitness of the disperser) or genetic fitness (the fitness of a gene controlling dispersal) is used (Comins *et al.*, 1980). The difference between these two criteria increases with increasing variance in gene frequency between habitat patches, which is likely to mean that the genetic fitness criterion predicts more dispersal than the individual fitness criterion in metapopulations consisting of small local populations. Both the individually and genetically optimal rates of dispersal may be different from the 'species optimum', the rate of dispersal which would give the highest value of  $\hat{p}$  (Comins *et al.*, 1980). This is an especially important consideration for environments with much regional stochasticity, which decreases the advantage of dispersal to individuals (Gadgil, 1971; see also pp. 30–34).

#### *Compensatory effects*

It is important to realize that there are threshold values of habitat patch area and isolation for metapopulation persistence, but it should also be noted that metapopulation persistence depends simultaneously on the area and isolation of patches. Therefore, small average area may be compensated by little isolation, and great average isolation may be compensated by large areas. This point may be made with the Levins model, by making  $m$  and  $e$  explicit functions of isolation and area, respectively. In both cases, negative exponential functions provide a plausible description:

$$m = m_0 e^{-aD} \quad (3a)$$

$$e = e_0 e^{-bA}. \quad (3b)$$

$D$  and  $A$  are the average isolation and area of habitat patches, and  $m_0$ ,  $a$ ,  $e_0$  and  $b$  are four parameters (the equation for  $e$  is valid only for  $A$  greater than some minimum value, below which extinction is immediate). Equation (2) now becomes

$$\hat{p} = 1 - (e_0/m_0) e^{-bA+aD}, \quad (4)$$

illustrating the compensatory effect between  $A$  and  $D$ . Figure 1 gives one example, in which both the area and the isolation of islands in a lake has a significant effect on the occurrence of the shrew *Sorex araneus*. Such compensatory effects between area and isolation have been analysed and discussed in the context of island biogeography of mammals by Lomolino (1986), Lomolino, Brown & Davis (1989) and Hanski (1986).

One more complication should be mentioned. Although the average area and isolation of habitat patches in some large region may be such that persistence of a species is not expected by equation (4), or by some more sophisticated model, the species may nonetheless persist within a subset of patches with greater than average area and/or smaller than average degree of isolation (DeAngelis, Travis & Post, 1979).

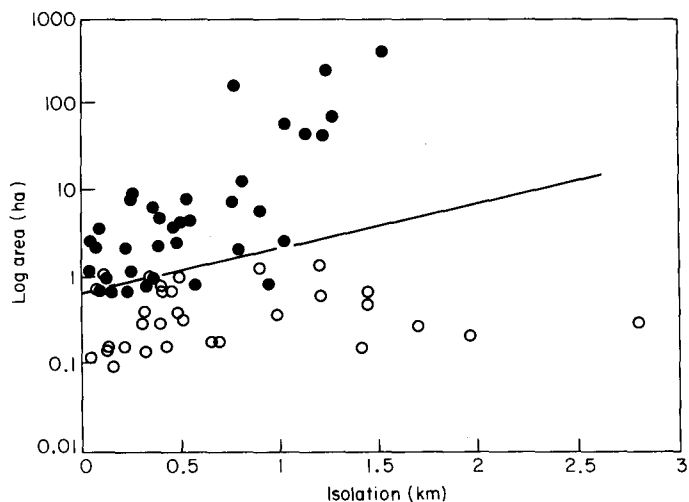


Figure 1. Presence (black dot) and absence (open circle) of the shrew *Sorex araneus* on islands in two lakes in Finland. The horizontal axis gives the isolation of the island, and the vertical axis gives the logarithm of island area. The line gives the best separation of occupied and unoccupied islands with respect to size and isolation (multiple regression as described by Lomolino *et al.*, 1989). Island area has a clearly significant effect, but the effect of isolation is also significant (the regression slope,  $t = 3.00$ ,  $P < 0.004$ ), indicating a compensatory effect between isolation and area (from Peltonen & Hanski, 1991).

#### INCIDENCE FUNCTIONS

Diamond (1975) devised a simple way of depicting how the probability of occurrence of a species on islands (or habitat patches) depends on island area or some other comparable attribute. In the case of area, islands are sorted into size classes, and a histogram is prepared giving the proportion of islands in each class on which the species was found—the species' incidence function (B. Taylor, 1991, describes a more sophisticated method of fitting incidence functions to empirical data). Figure 2 gives an example for three species of shrew.

Incidence functions have been used in island biogeographic studies, which assume a mainland from which dispersing individuals to islands originate. The appropriate model is a single-species version of the MacArthur-Wilson (1967) model,

$$dp/dt = m(1-p) - ep, \quad (5)$$

with  $\hat{p} = m/(m+e)$ . As the colonization and extinction rates are typically measured as events per year, I shall replace  $m$  and  $e$  by  $M$  and  $E$ , the per year colonization and extinction probabilities. For simplicity, I assume that  $M$  is constant, and that only  $E$  depends on island area. Following earlier suggestions by Diamond (1979), Diamond & May (1981) and Gilpin & Diamond (1976, 1981), I assume that  $E = e'/A^x$ . Thus the incidence function  $\mathcal{J}$  is given by

$$\mathcal{J}(A) = 1/[1 + (e'/M)A^{-x}], \quad (6)$$

where  $e'$  and  $x$  are two extinction parameters. Parameter  $x$  describes how fast the extinction probability decreases with increasing  $A$  and, assuming constant

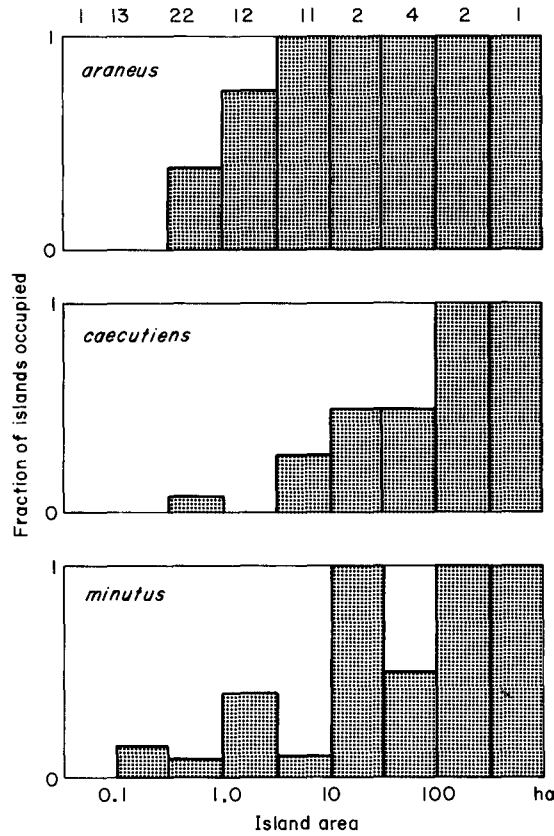


Figure 2. Incidence functions for three species of shrew (*Sorex araneus*, *S. caecutiens* and *S. minutus*) on islands in lakes Koitere and Sysmä in eastern Finland (68 islands; from Peltonen & Hanski, 1991). Islands have been grouped in logarithmic size classes (horizontal axis). The vertical axis gives the fraction of occupied islands in each size class. The number of islands is given by the small figures above the histograms.

population density, with increasing population size. (The Levins model would yield another incidence function, which has not been used in the literature.)

Equation (6) may be fitted to empirical data to yield estimates of  $x$  and  $e'/M$ . As the extinction probability  $E$  cannot exceed unity, there must be a value of  $A$ ,

TABLE 1. Parameter estimates of the incidence functions of the three species of shrew in Fig. 2 (average and standard error).  $A^*$  is the island size at which  $J = 0.5$ . This table gives also the predicted and observed colonization ( $M$ ) and extinction probabilities ( $E$ ) per year in the three species. While calculating the predicted values,  $A_0$  was assumed to be 0.5 ha, and  $E$  was calculated for  $A = 1.6$  ha, the average size of islands from which the empirical results were collected. The observed values are based on a 5-year survey of 17 islands (Peltonen & Hanski, 1991)

Species	$x$	SE	$e'/M$	SE	$A^*$	Predicted		Observed	
						$M$	$E$	$M$	$E$
<i>araneus</i>	2.30	0.68	0.79	0.22	0.9	0.26	0.07	0.20	0.04
<i>caecutiens</i>	0.91	0.24	17.67	11.36	23.5	0.03	0.35	0.05	0.33
<i>minutus</i>	0.46	0.16	4.09	1.51	21.4	0.18	0.59	0.13	0.46

say  $A_0$ , for which  $A_0^x = e'$ . If  $A_0$  is known, or a good guess can be made, one may estimate the value of  $e'$  and thus obtain an estimate of  $M$ .  $E$  may then be calculated for any required value of  $A$ .

Table 1 gives the estimated values of  $x$  and  $e'/M$  for the three species of shrew with incidence functions shown in Fig. 2. The extinction parameter  $x$  is greater than 1 for the largest species *araneus*, indicating exponentially increasing persistence time with increasing population size, and hence suggesting that demographic stochasticity is the main cause of extinctions in this species. In contrast, the exponent is only about 0.5 in the smallest species *minutus*, showing that persistence time increases roughly logarithmically with population size, which suggests an important role for environmental stochasticity. This difference makes biological sense, because the smaller species of shrew have exceptionally small body energy reserves and short starvation times, and are hence particularly sensitive to temporal variation in food availability (Hanski, 1984, 1985a).

Table 1 gives also the predicted and observed values of  $M$  and  $E$  (the observed values are from Peltonen & Hanski, 1991). The predicted and observed colonization and extinction rates agree remarkably well, which strongly supports the previous conclusion (Hanski, 1986) that island occupancy of these shrews is determined by recurrent colonizations and extinctions. The close match between the predicted and observed rates in Table 1 also suggests that the above procedure may be used to draw useful inferences about the colonization and extinction rates in other species. The slope of the incidence function equals  $x/(4A^*)$  at  $J = 0.5$ , where  $A^*$  is the corresponding island area. The model thus supports the intuitive notion (Schoener, 1986) that species which are much affected by environmental stochasticity have shallow incidence functions.

#### INCORPORATING LOCAL DYNAMICS INTO METAPOPULATION MODELS

Let us return to the Levins model. It makes two important simplifying assumptions: (1) there is no spatial correlation in the state (occupied or not) of habitat patches (the 'zero-correlation' assumption), and (2) there are only two states, presence and absence (the 'discrete-state' assumption with two states). In reality, spatial correlations in occupancy may arise for two reasons, because dispersal to a nearby patch is more likely than dispersal to a far-away patch ('stepping-stone' dispersal), and because extinctions due to some common environmental cause may be spatially correlated. Possible correlation due to dispersal does not seem to be always critical, however, as several studies comparing the consequences of 'island' (assumed in equation (1)) and stepping-stone dispersal have reached broadly similar results (Gurney & Nisbet, 1978; Comins *et al.*, 1980; Vance, 1984). In Nachman's (1991) simulations, increasing the fraction of island dispersal and decreasing the fraction of stepping-stone dispersal had roughly the same effect as increasing the overall rate of dispersal. The discrepancies that arise due to the two types of dispersal are largest when  $p$  is small (Gurney & Nisbet, 1978). When quantitative predictions are needed it may be necessary to assume the more realistic stepping-stone dispersal and to resort to simulation studies (for an example see Soulé & Gilpin, unpublished). Violation of the zero-correlation assumption due to correlated extinction events will be discussed later.

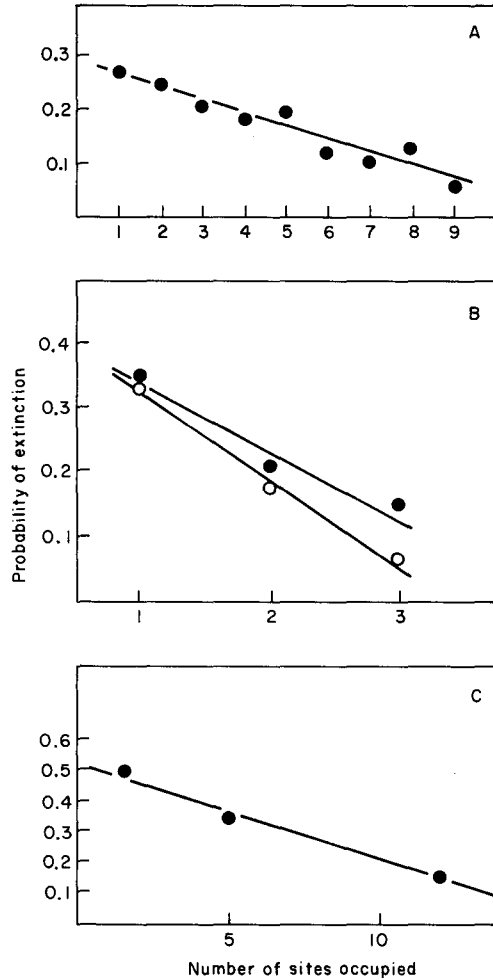


Figure 3. Relationship between the probability of local extinction and  $p$  in A, mangrove island insects (Simberloff, 1976), B, leafhoppers (Kontkanen, 1950) and C, fresh-water molluscs living in small ponds (Boycott, 1930).

The second simplifying assumption of the Levins model, the discrete-state assumption with two states, implies that all local populations have equal extinction probabilities. Figure 3 gives three examples which suggest that the extinction probability decreases with increasing  $p$ , the fraction of occupied patches. In fact, one has a good reason to expect that this is a general trend. The reason is the nearly universally observed increase in average population size with increasing  $p$  (Hanski, 1982a; Brown, 1984; Gaston & Lawton, 1990), and the even more ubiquitous increase in extinction probability with decreasing population size (Williamson, 1981; Diamond, 1984; Schoener & Spiller, 1987). These two relationships, when combined, produce a negative relationship between extinction probability and  $p$ , such as is shown in Fig. 3 for three sets of closely related species.



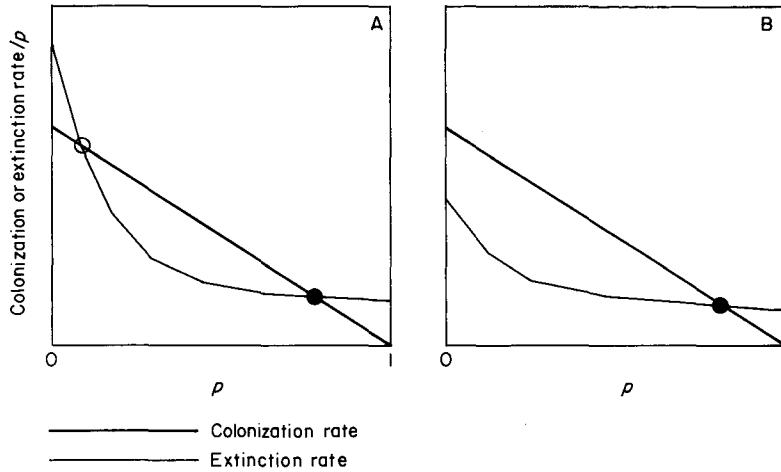


Figure 4. Alternative stable equilibria in a modified Levins model, equation (7), which takes into account the empirically observed (Fig. 3) negative relationship between extinction probability and  $p$ . The thick and thin lines give the colonization and extinction rates divided by  $p$ . In B the two functions have only one intersection point, which is stable, but in A there are two intersection points, a stable one (black dot) and an unstable one (open circle). In this case the trivial equilibrium ( $p = 0$ ) is also stable.

The positive relationship between average population size  $N$  and the fraction of occupied patches  $p$  has been given three explanations. First, this relationship may be a sampling artefact: locally rare species are more difficult to detect than common species, and hence appear to occur at fewer sites (Gaston & Lawton, 1990). This explanation is most likely to apply at small spatial scales, and especially when several samples are taken from one local population (in this case  $p$  is the fraction of samples in which the species was found). Second, Brown (1984) suggested that the positive correlation between  $N$  and  $p$  is due to ecological differences among species, which affect both their average abundance and distribution. And third, the positive relationship between average abundance and distribution may be due to metapopulation dynamics, as I will demonstrate below. Though the second and third hypotheses are quite different, they both highlight another complication in metapopulation dynamics, alternative stable equilibria.

Let us take first Brown's (1984) position but assuming that the correlation between  $N$  and  $p$  applies to single-species dynamics as well as to interspecific comparisons. Decreasing  $p$  is associated with decreasing  $N$ , and this is reflected in increased extinction rate. To take this into account, I modify the Levins model as follows:

$$dp/dt = mp(1-p) - e_0 e^{-ap} p, \quad (7)$$

where  $e_0$  and  $a$  are two extinction parameters. If  $e_0$  is greater than  $m$ , this model may have two alternative stable equilibria, separated by an unstable equilibrium, a threshold value for metapopulation persistence (Fig. 4).

#### *A simple model of N and p*

To develop the metapopulation explanation of the positive relationship between  $N$  and  $p$  in detail would require a structured metapopulation model, of

the type pioneered by Hastings & Wolin (1989) and Hastings (1991). I shall present here a simpler model by assuming that the time scale of local dynamics is much faster than the time scale of metapopulation dynamics (this model may also be justified as a limiting case of a structured model; Gyllenberg & Hanski, unpublished). All local populations are hence assumed to be of equal size  $\hat{N}$ , but unlike in the Levins model, the equilibrium population size is affected by dispersal as well as by local dynamics. Let us denote by  $I$  the number of dispersers per habitat patch. The following three ordinary differential equations give the rates of change in  $p$ ,  $N$  and  $I$ :

$$dp/dt = \alpha\beta I(1-p) - ep \quad (8a)$$

$$dN/dt = -mN + \alpha I + rN(1-N) \quad (8b)$$

$$dI/dt = mpN - vI - \alpha I. \quad (8c)$$

In this model, the colonization rate is assumed to be proportional to the numbers of dispersers and the fraction of empty habitat patches. The numbers of dispersers increase due to emigration from occupied patches, and they decrease due to mortality and immigration to presently occupied and empty patches. Most dispersers to empty patches are assumed to perish without giving rise to a new local population, hence the colonization rate is given as a product of two parameters, the immigration parameter  $\alpha$  and the probability of successful colonization,  $\beta$ . Local population size decreases due to emigration, which is assumed to be density-independent, and it increases due to immigration and local population growth, the latter modelled by the logistic equation (for simplicity, carrying capacity is set to unity). Several empirical studies have reported that immigration significantly increases the growth rate of small populations (Smith, 1974; Holliday, 1977; Gottfried, 1979; Rey, 1981; Rey & Strong, 1983; Conner, Faeth & Simberloff, 1983; Fahrig & Merriam, 1985).

At equilibrium, equations (8) give two relationships between  $N$  and  $p$ :

$$\hat{N} = (1-a) + ab\beta, \quad (9)$$

where  $a = m/r$  and  $b = \alpha/(\alpha+v)$ , and

$$\hat{N} = (c/b)/(1-\beta). \quad (10)$$

where  $c = e/\beta m$ . The intersection points of equations (9) and (10) give the equilibria of the system. There is one stable equilibrium if  $c/b < (1-a)$ . There is no positive equilibrium if  $c$  is substantially greater than  $(1-a)b$ , while in the intermediate cases there are two alternative stable equilibria. Note that alternative equilibria are not possible if  $\alpha = 0$ , in other words when immigration makes no contribution to local dynamics. This conclusion also emerges from a structurally different metapopulation model (Hanski, 1985b; Hastings, 1991; see also Roughgarden & Iwasa, 1986).

Varying the parameter values in equations (8) within reasonable limits and calculating the corresponding positive stable equilibrium, if any exists, tends to yield a cloud of points with a positive relationship between  $N$  and  $p$  (Hanski, unpublished). This is most apparent if only  $e/\beta$  is varied, because then all equilibria lie on the straight line given by equation (9). This model thus demonstrates that metapopulation dynamics may explain the empirically observed positive relationship between  $N$  and  $p$ .

In the present model, the fraction of occupied patches depends primarily on the extinction and colonization rates ( $e/\beta$ ), while average population size is mostly affected by emigration rate in relation to population growth rate ( $m/r$ ) and by the rate of mortality of dispersers ( $v$ ). Gadgil (1971) suggested in a pioneering study that average population size decreases with increasing isolation of habitat patches due to increasing mortality during dispersal. Similarly, Fahrig & Paloheimo (1988) found in a simulation study that average population size was strongly affected by dispersal processes. Huffaker's (1958) well-known experiment with mites feeding on oranges and the study by Fahrig & Merriam (1985) on *Peromyscus leucopus* inhabiting more or less isolated woodlots are two examples demonstrating how isolation may influence average population size in the laboratory and in the field, respectively.

### *Three kinds of rare species*

One may distinguish between four kinds of species with respect to their average local abundance  $N$  and the fraction of occupied patches  $p$ : species with large  $N$  and  $p$  (core species), species with small  $N$  and  $p$  (satellite species), species with small  $N$  but large  $p$  (rural species) and species with large  $N$  but small  $p$  (urban species; the first two terms are from Hanski, 1982a, and the latter two are from Söderström, 1989). There are thus three kinds of rare species, with either  $N$  or  $p$ , or both, small. What does the model say about the characteristics of the different kinds of rare species? (The reader is warned that the well-known classification of rare species by Rabinowitz, Cairns & Dillon, 1986, is based on different criteria than are used here.)

In the present model, rural species are characterized by low growth rate (small  $r/m$ ) and low ratio of extinction to colonization rates (small  $e/\beta$ ), while the opposite attributes are typical for urban species. Increasing mortality of dispersers ( $v$ ) may turn a core species into a satellite species (assuming that  $1 - a$  is close to  $c/b$ ). A study by Söderström (1989) gives an opportunity to test some of these predictions. He surveyed the occurrence of epixylic bryophyte species in stands of late successional spruce forest in northern Sweden. Local abundance was estimated as percentage cover on available logs in occupied forest stands. Söderström (1989) identified three urban species in his material, all of which regularly produced gemmae (asexual reproduction) but none of which were recorded to reproduce sexually. In other words, these species probably have high local growth rate but low dispersal rate (large  $r/m$ ), as predicted for urban species. The seven core species had both asexual and sexual reproduction, while the seven satellite species had only sexual reproduction, and thus probably lower  $r$  than the core species, which is consistent with the present model. The only species classified as rural showed intermediate rates of sexual and asexual reproduction.

### METAPOPOPULATION DYNAMICS IN HETEROGENEOUS ENVIRONMENTS

Current metapopulation models assume that all habitat patches are similar in size and quality. Variation in local population size in the existing structured metapopulation models (Hastings & Wolin, 1989; Gyllenberg & Hanski, unpublished) is due to the history of local populations, not to differences in the

environment. This is a severe shortcoming of the models, because the dominant metapopulation structure in nature is one or more large and practically invulnerable local populations in large and/or favourable habitat patches, surrounded by relatively unstable populations in smaller habitat patches (Harrison, 1991). Such 'mainland-island' metapopulation structure has been examined theoretically in the context of group selection by Boorman & Levitt (1973). The shrew example described above belongs to this category, and other well documented examples include *Daphnia* in rock pools on some islands (Pajunen, 1986), the heath fritillary butterfly *Mellicta athalia* (Warren, Thomas & Thomas, 1984), and the bay checkerspot butterfly *Euphydryas editha bayensis* (Harrison, Murphy & Ehrlich, 1988).

There is an urgent need to develop metapopulation models that include variation in habitat patch size and quality. Meanwhile, one consequence of environmental differences between patches may be captured with another version of the Levins model. Let us take as our starting point equation (7), which takes into account the rescue effect, decreasing extinction rate with increasing fraction of occupied patches. If there are differences among the habitat patches that affect the extinction probability, it is clear that when more of the patches are occupied the average extinction rate is higher than when a species is present only in few patches, which tend to be the most favourable ones for the species. Habitat heterogeneity and the rescue effect thus have opposite effects on average extinction rate, which is likely to be highest when  $p$  has an intermediate value. To take habitat heterogeneity into account, let us multiply the extinction rate in equation (7) by  $p^\tau$ :

$$dp/dt = mp(1-p) - e_0 e^{-ap} p^{1+\tau}. \quad (11)$$

Small but positive values of  $\tau$  correspond to situations in which there are large differences among habitat patches, and only a few of them are large and occupied by local populations with a low extinction probability (equation 11 gives unrealistically low extinction rates for metapopulations with very low  $p$ , but this does not affect the result about the distribution of  $p$  values, described below).

This model may have up to three positive equilibria, and hence there is a possibility for alternative positive, stable equilibria (compare with equation 7). For a small value of  $\tau$  and for a range of values of the other parameters,  $m$ ,  $e_0$  and  $a$ , the distribution of  $p$  values tends to be bimodal, most values being very large or very small. This is a commonly observed pattern in nature (Fig. 5; see also Hanski, 1982a, b; Gotelli & Simberloff, 1987; Collins & Glenn, 1990; for a possible counter-example see Gaston & Lawton, 1989). Bimodal distribution of  $p$  values is also predicted by the core-satellite species model (Hanski, 1982a), which is a simple stochastic metapopulation model. However, the original core-satellite model has two problems: rare species are likely to become rapidly extinct from the entire system of patches, and the predicted switches of species between the core (large  $p$ ) and the satellite (small  $p$ ) status are not commonly observed in nature (Solbreck, 1990, gives an example). Equation (11) does not have these problems, because it predicts a bimodal distribution of  $p$  values as a stable equilibrium distribution. There has been substantial discussion in the literature on the validity of the core-satellite species hypothesis (Hanski, 1982b; Gotelli & Simberloff, 1987; Gaston & Lawton, 1989; Collins & Glenn, 1990).

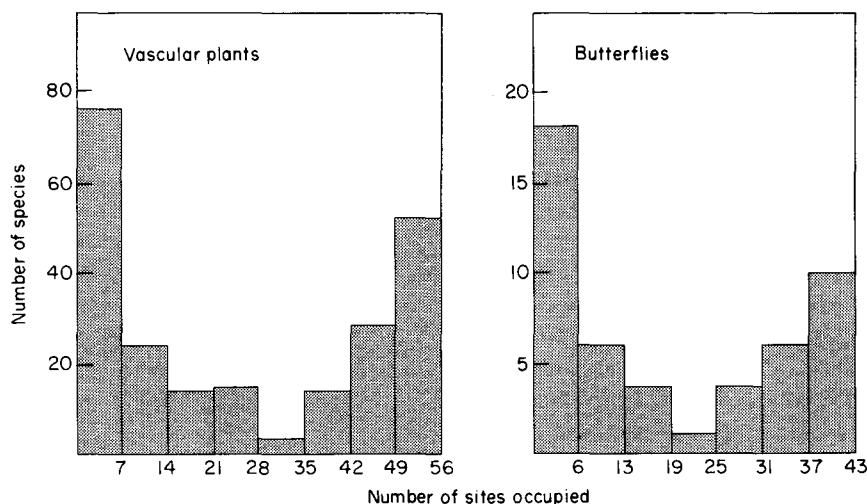


Figure 5. Two examples of bimodal distributions of  $\beta$  values in assemblages of species with similar ecology. A, Anthropochorous plants surveyed in villages surrounded by forest (data from Linkola, 1916; for a full analysis see Hanski, 1982b). B, Butterflies in Britain (data from Pollard *et al.*, 1986).

Equation (11) demonstrates that a bimodal distribution of  $\beta$  values can be expected also in species assemblages for which the original stochastic model is an unrealistic description.

#### FOUR KINDS OF STOCHASTICITY

May (1973) made an important distinction between two forms of stochasticity affecting population growth. Demographic stochasticity refers to the chance events of death and birth that are uncorrelated between individuals, while environmental stochasticity alludes to correlated birth and death events, due to some common environmental factor, for example poor breeding success in cold and rainy spring or increased death rate due to exceptional frost. The distinction between the two kinds of stochasticity may occasionally be difficult to make in practice, but this does not detract from the value of the concepts.

Analogous types of stochasticity may be defined for metapopulations by substituting 'local population' for 'individual' in the above definitions. To avoid confusion, it would be convenient to have distinct terms for the metapopulation-level stochasticities. I suggest the terms immigration-extinction stochasticity and

TABLE 2. Definitions of the four kinds of stochasticity operating in metapopulations

Type of stochasticity	Unit affected	Correlation between units
Demographic	Individual	No
Immigration-extinction	Population	No
Environmental	Individual	Yes
Regional	Population	Yes

regional stochasticity for the metapopulation-level equivalents of demographic and environmental stochasticity, respectively (Table 2).

#### *Immigration-extinction stochasticity*

Real metapopulations consist of a finite number of local populations. When that number is small, and when the extinction probability of local populations is not negligible, it is possible that a metapopulation which is expected to persist by equation (1), or by some analogous deterministic model, nonetheless becomes extinct simply because all local populations happen to become extinct at the same time. In the case of demographic stochasticity, 20 breeding females has been cited as the 'magic' number below which extinction due to demographic stochasticity is a real threat (Soulé, 1986). We may expect that a qualitatively similar result holds for metapopulations.

Nisbet & Gurney (1982) give the following approximation for  $T_M$ , the mean lifetime of a metapopulation:

$$T_M = T_L \exp[\hat{P}^2/(2(H-\hat{P}))], \quad (12)$$

where  $T_L$  is the mean lifetime of a local population,  $H$  is the number of habitat patches, and  $\hat{P}$  is the equilibrium number of local populations;  $\hat{P} = H(1 - 1/mT_L)$ , where  $m$  is the colonization parameter. Equation (12) may be rewritten as

$$T_M = T_L \exp[H(mT_L + 1/mT_L - 2)/2], \quad (13)$$

showing that the metapopulation persistence time increases exponentially with  $H$  and hence with  $\hat{P}$ . As a numerical example, if  $H = 20$  and  $\hat{P} = 10$ , then  $T_M$  is 150 times greater than  $T_L$ . Nisbet & Gurney (1982) find that a metapopulation will persist for a long period of time if the average proportion of occupied patches exceeds  $3H^{-0.5}$ . For example, if half of the patches are occupied on average,  $H$  should exceed 36 for the metapopulation to persist for a long time, but if only 10% are occupied,  $H$  should exceed 900. The absence of *Daphnia* waterfleas from islands with few rock pools (Hanski & Ranta, 1983) is a likely example of immigration-extinction stochasticity. Both demographic and immigration-extinction stochasticities pose a real threat to forest raptors in Java, as they are confined to a small number of relatively small forest reserves (Rolstad, 1991).

It is important to make a clear distinction between the effects of demographic and immigration-extinction stochasticities on metapopulation persistence time. If demographic stochasticity is the only cause of local extinctions, metapopulation persistence time decreases with increasing fragmentation, which decreases the size of local populations to the limit where demographic stochasticity is important (Burkey, 1989). However, this assumes that there are many populations. If there are not, immigration-extinction stochasticity will counteract the effect of demographic stochasticity, and it remains unclear how metapopulation persistence time is affected by fragmentation.

#### *Regional stochasticity*

There are many ways to talk about regional stochasticity. Levins (1969, 1970) analysed the effect of temporal variance in extinction rate (of local populations);

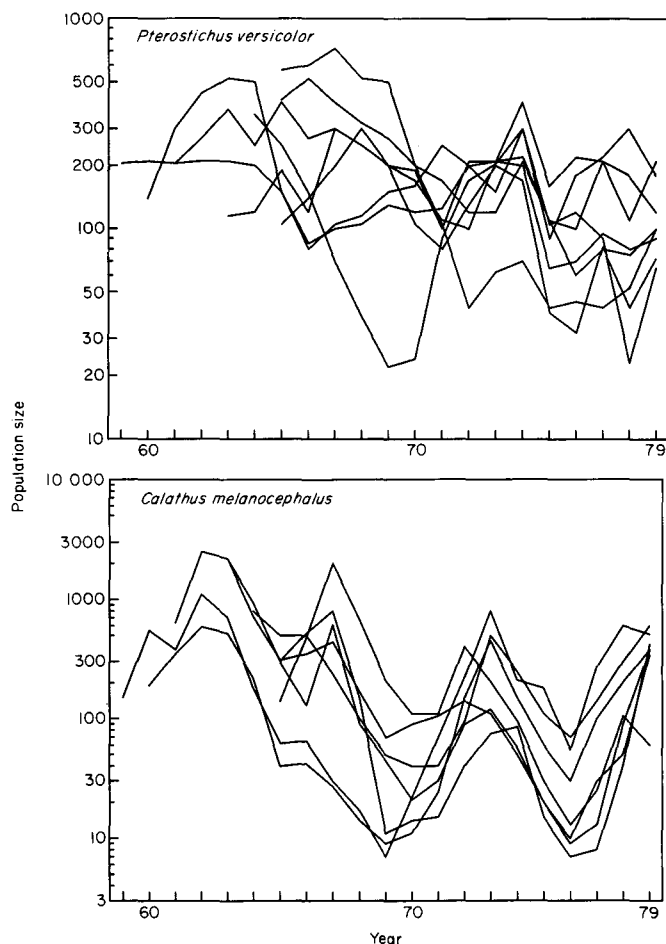


Figure 6. Temporal changes in several local populations of two carabid beetles, *Pterostichus versicolor* and *Calathus melanocephalus*, sampled in a Dutch heath. The former species shows less regional stochasticity than the latter (see also Fig. 7) (from den Boer, 1981).

den Boer (1968) stressed the importance of “spreading of risk” among many local populations; and, most recently, Gilpin (1990) and Harrison & Quinn (1990) emphasized the significance of correlated extinction events in metapopulation dynamics. All of them were concerned with regional stochasticity. Figure 6 gives an example from den Boer’s (1981) 20-year study of two carabid beetles living in a Dutch heath. Assuming that the population fluctuations shown in this figure are due to stochasticity, and not to the intrinsic dynamics of the species, *Pterostichus versicolor* has experienced less regional stochasticity than *Calathus melanocephalus* (see also Fig. 7).

Environmental stochasticity decreases metapopulation persistence time by increasing  $e$  in equation (1), but metapopulation persistence time is additionally decreased by increasing regional stochasticity, in an exactly analogous manner as the expected lifetime of a local population is decreased by environmental stochasticity. If there is no regional stochasticity, a metapopulation of many populations, provided they are not so small that demographic stochasticity

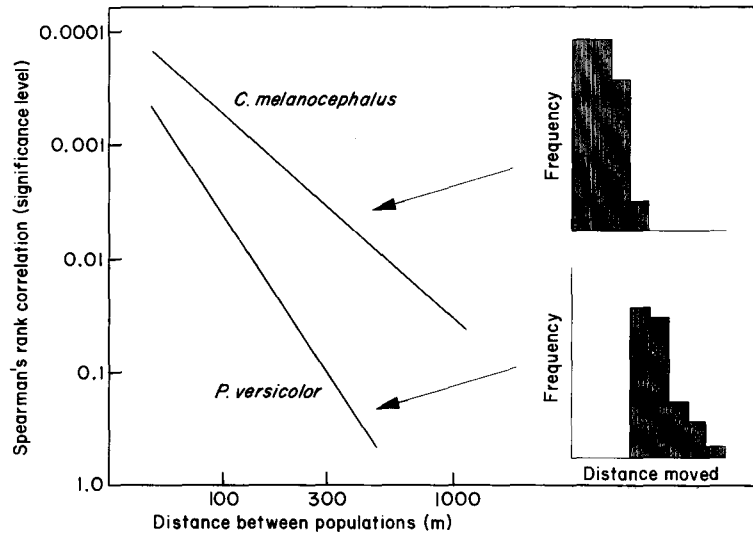


Figure 7. Correlation in the dynamics of pairs of local populations of *Pterostichus versicolor* and *Calathus melanocephalus* (Fig. 6) as a function of the distance between the populations. The vertical axis gives the significance of the Spearman's rank correlation test (from Baars & van Dijk, 1984). On the right are illustrated simulated movements of the two species in one season (based on an empirical study of beetles' movement behaviour). Note that *P. versicolor* has a higher rate of dispersal than *C. melanocephalus* (from Baars, 1979).

becomes important, may have a longer persistence time than one undivided, large population (Quinn & Hastings, 1987). However, if regional stochasticity is important, this conclusion becomes doubtful (Goodman, 1987; Gilpin, 1988, 1990). On the other hand, regional stochasticity makes little difference if the extinction rate is very low, or if variation in extinction rate is low (Hanski, 1989; Harrison & Quinn, 1990).

Table 3 summarizes how the significance of different kinds of stochasticity depends on habitat patch size and number. Demographic and immigration-extinction stochasticities are important in systems consisting of small and few habitat patches, respectively, while environmental and regional stochasticities may occur in any environment, regardless of habitat patch size and number. Regional stochasticity is more likely to occur when the degree of isolation is small (cf. Fig. 7). Of the four simple combinations of stochasticities in Table 3, the

TABLE 3. The environmental factors which affect most the different types of stochasticity. The last four columns indicate four simple combinations of the different kinds of stochasticity (more complex combinations are of course possible). For discussion see the text

Type of stochasticity	Type of environment	Combinations			
		1	2	3	4
Demographic	Small patches	+	+	—	—
Immigration-extinction	Few patches	—	+	+	—
Environmental	Any patches	—	—	+	+
Regional	Little isolated	—	—	—	+



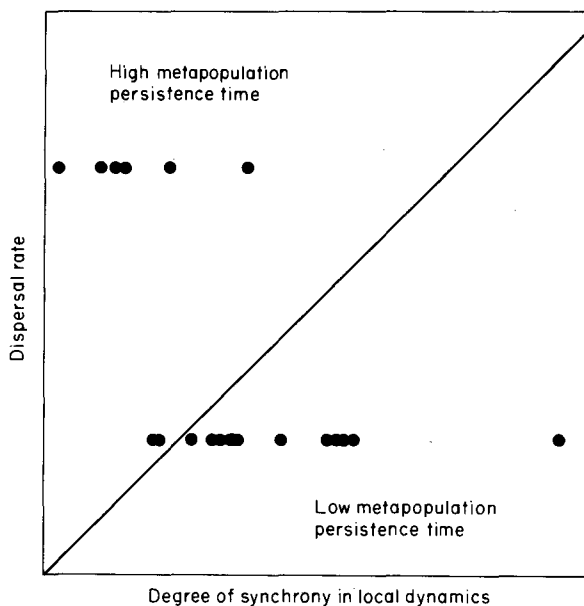


Figure 8. Metapopulation persistence time is expected to increase with increasing dispersal rate among habitat patches but to decrease with increasing regional stochasticity, which increases the degree of synchrony in local dynamics. In many species, dispersal rate among patches and regional stochasticity change with spatial scale, parallel to the diagonal in the figure, with perhaps a relatively small net effect on metapopulation persistence time. Metapopulations in the upper-left corner are expected to have long persistence times, while metapopulations in the lower-right corner are expected to have short persistence times (according to Hanski, 1989). The data points are for 19 common carabid beetles sampled in a Dutch heath by den Boer (1977; sites N, Z and AG). Six of the species have long wings and high dispersal rates (B species in den Boer, 1977), while the remaining species are short-winged and have low dispersal rate (A and C species). Regional stochasticity was measured by the average of the three pair-wise temporal correlations ( $n$  is 6 or 7 years; the horizontal axis extends from  $-0.2$  to  $1.0$ ). Species with low dispersal rate had significantly more correlated dynamics at the three sites than species with high dispersal rate ( $F = 8.48$ ,  $P < 0.001$ ).

effects of combinations 1 and 3 to metapopulation persistence time have been examined by Burkey (1989) and Quinn & Hastings (1987), respectively. Under combination 1 increasing fragmentation decreases metapopulation persistence time, while under combination 3 metapopulation persistence time increases with fragmentation (but see Gilpin, 1988, for complications, including regional stochasticity).

Increasing isolation is expected to decrease regional stochasticity (Table 3), and hence to facilitate metapopulation persistence. Figure 7 demonstrates that increasing the distance between a pair of populations decreases regional stochasticity in the two carabid beetles, *Pterostichus versicolor* and *Calathus melanocephalus* (see also Fig. 6). But as far as metapopulation persistence time is concerned, this is clearly not the full story, because increasing isolation tends to decrease colonization rate. For many species, the two opposing effects of isolation on metapopulation persistence time may cancel each other. Species which are located away from the diagonal in Fig. 8 are in a different situation. Species with high dispersal rate but little regional stochasticity are expected to have long metapopulation persistence times, while species with low dispersal rate but much

regional stochasticity have short metapopulation persistence times (see also Roff, 1974). The contrast between the carabids *Pterostichus versicolor* and *Calathus melanocephalus* is a case in point. *Pterostichus versicolor* shows lower regional stochasticity but substantially higher dispersal rate than *C. melanocephalus* (Fig 6, 7). A comparison between short-winged (low dispersal rate) and long-winged (high dispersal rate) carabid beetles gave the same result, the species with lower rate of dispersal apparently experiencing more regional stochasticity (Fig. 8).

Gadgil (1971) was perhaps the first to clearly point out that dispersal is most advantageous to an individual if there is little regional stochasticity, and least advantageous when regional stochasticity is high. The results in Fig. 8 are in agreement with this reasoning, and they suggest that synchronous dynamics are due to regional stochasticity and not to dispersal, because in the latter case we would expect the reverse association, more synchronous dynamics (more 'regional stochasticity') in species with higher dispersal rate. Species living in highly correlated environments may have other means of surviving hard times than dispersal, for example different forms of dormancy (for a review see Hanski, 1988). Another interesting question is whether such species have less persistent metapopulations than species with high dispersal rate. The answer is not known.

#### CONCLUSION: FOUR CAUSES OF METAPOPOPULATION EXTINCTION

Much of the early interest in metapopulation dynamics stemmed from the idea that metapopulations tend to be, for one reason or another, more stable and less likely to become extinct than single local populations, even if the latter were the size of all local populations in a metapopulation put together. Today the incentive for examining metapopulations is different. With most environments becoming increasingly fragmented, metapopulations abound, but many occur in environments where their long-term persistence is by no means guaranteed. Metapopulation ideas are increasingly scrutinized by conservation biologists (Clark *et al.*, 1987; Quinn & Hastings, 1987; Gilpin, 1988; Opdam, 1988; Hanski, 1989). It seems appropriate to conclude this paper by summarizing the possible scenarios of metapopulation extinction (Table 4), which also allows me to draw together many of the results reviewed in the earlier sections of this paper.

1. *No positive equilibrium point.* Levins's (1969) simple model (equation 1) highlights the most fundamental cause of metapopulation extinction: the rate of establishment of new local populations is lower than the rate of local extinctions when  $p$  is small. Conservation biologists are interested in this result because

TABLE 4. The environmental factors which are most important in four scenarios of metapopulation extinction

Cause of extinction	Habitat patches			
	Size	Number	Isolation	History
1. No positive equilibrium	Yes	—	Yes	—
2. Alternative equilibria	—	—	—	Yes
3. Immigration-extinction stochasticity	—	Yes	—	—
4. Regional stochasticity	—	—	Yes	—

environmental changes brought about by human activities may increase the extinction rate or decrease the colonization rate so much that metapopulation extinction becomes inevitable.

2. *Alternative equilibria*. If there are two stable equilibria, one of which corresponds to metapopulation extinction, a small metapopulation becomes deterministically extinct, and a large one may become extinct if it happens to become smaller than a threshold size due to some form of stochasticity. Alternative stable equilibria are an important consideration when a when immigration makes a substantial contribution to local population growth. Alternative stable equilibria are also an important consideration when a metapopulation is being established by introducing the species to one or more sites within a system of habitat patches. If alternative equilibria exist, the introduction should consist of a large enough propagule to push the metapopulation beyond the threshold value, and possible multiple sites of introduction should be located close to each other to facilitate dispersal between them and to minimize mortality during dispersal. One example where these considerations are potentially important is the establishment of the critically endangered black-footed ferret *Mustela nigripes* in North America (Clark *et al.*, 1987; Brussaard & Gilpin, 1989).

3. *Immigration-extinction stochasticity*. Immigration-extinction stochasticity is a potential cause of metapopulation extinction when the number of local populations is small, for example because the number of habitat patches is small. As with demographic stochasticity in local population dynamics, immigration-extinction stochasticity may often be the proximate cause of metapopulation extinction, even if the ultimate cause (for a small number of populations) is different.

4. *Regional stochasticity*. How great a threat regional stochasticity poses to endangered species is still an open question. The spatial scales over which population dynamics are synchronized by different kinds of regional stochasticity remain largely unexplored. The dual role of isolation in determining metapopulation persistence time via its effects on colonization rate and regional stochasticity (Table 4) may show much variation between taxa, but we do not know where most real populations are located in Fig. 8. Are rare and endangered species over-represented in the lower-right corner? The recent interest in regional stochasticity in metapopulation dynamics and in conservation biology is well justified by these questions.

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