Metapopulation dynamics

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Metapopulation biology is concerned with the dynamic consequences of migration among local populations and the conditions of regional persistence of species with unstable local populations. Well established effects of habitat patch area and isolation on migration, colonization and population extinction have now become integrated with classic metapopulation dynamics. This has led to models that can be used to predict the movement patterns of individuals, the dynamics of species, and the distributional patterns in multispecies communities in real fragmented landscapes.

Spatial structure of populations was a key element in some early concepts and models of population ecology[1,2], genetics[3,4] and adaptive evolution[4]. In the past decade, the implications of spatial structure and dynamics have become widely recognized across population biology. The attention of ecologists has now been captivated by models[5–7] demonstrating the profound influence of spatial locations of individuals, populations and communities on their dynamics: the essence of spatial ecology is that the spatial structure of ecological interactions affects populations as much as do average birth and death rates, competition and predation. The rapid destruction of natural habitats has highlighted the importance of spatially explicit ecological models.

I distinguish between three approaches to large-scale spatial ecology (Fig. 1). Theoretical ecologists have investigated a range of models depicting individuals with localized interactions and restricted movement range in uniform space[6–8], demonstrating how population dynamic processes can generate complex dynamics and spatial patterns without any environmental heterogeneity. By contrast, landscape ecologists have been occupied by descriptions of the generally very complex physical structure of real environments and the movement of individuals and resources in them[9,10]. Symptomatically, the line of research pursued by theoretical ecologists is short of testable model predictions, whereas landscape ecology lacks a convincing theoretical framework. The third approach, metapopulation ecology, attempts to strike a compromise: here landscapes are viewed as networks of idealized habitat patches (fragments) in which species occur as discrete local populations connected by migration. Many species live in such well delimited habitat patches (ponds, woodlands in agricultural landscapes, and so on) that the 'patch network' assumption (Fig. 1) is really no simplification at all; for other species, it is a useful approximation; whereas for others, it is unhelpful because these species have a more continuous popula-

tion structure in space.

The kind of metapopulation approach depicted in Fig. 1 does not include everything that is commonly assigned to metapopulation ecology. Other approaches have been reviewed, for instance theoretical work based on lattice models[6,7,11–13] and conservation-oriented empirical studies[14–16]. The term 'metapopulation' is often used for any spatially structured population, and 'metapopulation dynamics' then covers all spatial dynamics. My agenda here is more restricted: I aim to highlight the ways in which the patch network assumption (Fig. 1) has facilitated the concurrent development of models and empirical research and so provided insight into the dynamics of real metapopulations in highly fragmented landscapes.

The foundation of the current metapopulation concept is in Levins's[17] vision of a metapopulation as a 'population' of unstable local populations, inhabiting discrete habitat patches such as those shown in Fig. 1. A classic metapopulation persists, like an ordinary population of mortal individuals, in a balance between 'deaths' (local extinctions) and 'births' (establishment of new populations at unoccupied sites). In this respect, metapopulation ecology shares similar conceptual underpinnings with epidemiology[18,19]: susceptible and infected individuals represent empty and occupied 'patches' for parasites. Some key results are essentially the same, for instance the critical community size for stochastic persistence of infectious diseases[20] can be compared with both patch-area-dependent extinction of local populations and patch-number-dependent extinction of metapopulations of free-living organisms, as discussed below.

Metapopulation dynamics in a broad sense are not restricted to systems with population turnover, extinctions and colonizations, but the concept developed here is based on Levins's classic metapopulation idea with extinction-prone populations in discrete habitat patches. I first discuss the new perspective that metapopula-
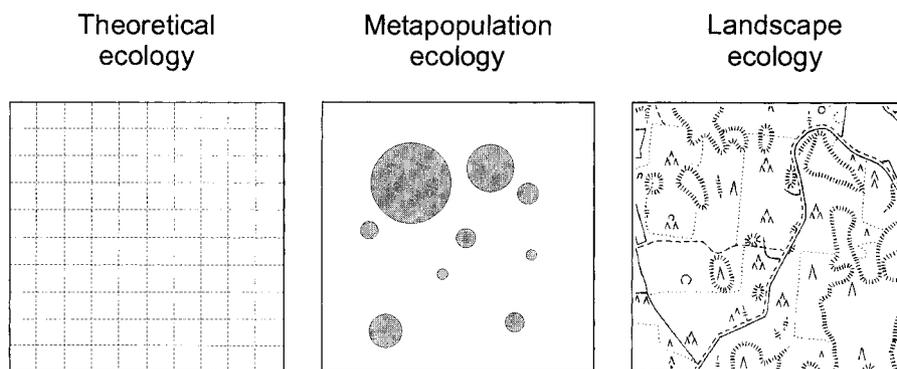

Figure 1 Three approaches to spatial ecology. Theoretical ecologists typically assume homogeneous continuous or discrete (lattice) space. Landscape ecologists tend to analyse the structure of complex real landscapes, with less emphasis on modelling population dynamics. Metapopulation ecology, in the middle, makes the simplifying assumption that suitable habitat for the focal species occurs as a network of idealized habitat patches, varying in area, degree of isolation and quality (the latter is not shown or discussed here, but see ref. 77), and submerged in the midst of uniformly unsuitable habitat.

Table 1 Processes influencing extinction in metapopulations

Scale of extinction	Scale of process	Extinction due to stochasticity	Extinction due to extrinsic causes
	Local processes	**Demographic**[*]	**Habitat loss**
		Environmental	Generalist enemies and competitors
Local extinction		**Genetic**[*]	**Persecution by humans** etc.
	Metapopulation processes	**Migration in small populations**	**Specialist enemies** and competitors
Metapopulation extinction		**Extinction–colonization**	**Habitat loss and fragmentation,**
		Regional	**extinction typically delayed**

The processes that operate in the well studied Glanville fritillary butterfly metapopulation[21] are printed in bold.
[*] Demographic and genetic stochasticity assume an increased significance in metapopulations with many small local populations.

tion ecology provides for population extinction, previously considered largely in the context of isolated populations. The general implications of extinction–colonization dynamics are then outlined. The basic model is augmented by assuming the kind of spatially realistic network structure shown in the middle panel in Fig. 1, with spatial variation in patch areas and degrees of isolation. The subsequent discussion is focused around the key question for ecology and conservation, the conditions under which metapopulations persist when habitat area is lost and the remaining habitat becomes ever more fragmented.

Extinction in metapopulations

In metapopulations, population extinction is a recurrent rather than a unique event, which adds to the range of extinction processes that have significance in nature and forces us to construct an increasingly mechanistic and biologically enriched view of extinctions. Table 1 summarizes the processes of extinction operating in metapopulations, some of which will be discussed below. Most of these processes have been documented in a large metapopulation of a well studied species, the Glanville fritillary butterfly, *Melitaea cinxia*[21], underscoring the point that many processes typically contribute to extinctions in metapopulations.

The two familiar forms of stochasticity affecting local populations, demographic and environmental stochasticity, have exact counterparts at the metapopulation level in extinction–colonization and regional stochasticities[22]. To appreciate the significance of extinction–colonization stochasticity, let us first attend to the following necessary condition for long-term metapopulation persistence: the expected number of new populations generated by one existing population during its lifetime in an otherwise empty patch network must be greater than one[23]. An analogous replacement condition naturally applies to individuals in local populations and is well developed in the epidemiological theory[18]. The replacement condition is necessary but not sufficient for long-term persistence. In a small metapopulation, all local populations may happen to go extinct at the same time owing to extinction–colonization stochasticity, even if the replacement condition is met, just as all individuals in a small population whose finite rate of population increase is greater than unity may happen to die without leaving any surviving progeny. In real patch networks, there is additionally the complication that not all patches are equally connected, hence whether the replacement condition is met or not may depend on the focal patch[24].

Studies on the Glanville fritillary butterfly have produced results that illustrate the operation of extinction–colonization stochasticity in metapopulations. In a comprehensive survey of 127 relatively independent patch networks, only a third of networks with less than 15 patches were occupied, whereas practically all larger networks were occupied[25], in agreement with theoretical predictions about extinction–colonization stochasticity[26]. Not all absences from small patch networks are necessarily due to extinction–colonization stochasticity only, because some of the metapopulations may not satisfy the replacement condition and are hence expected to go extinct any way. Nonetheless, an important conclusion is that, whether the replacement condition is met or not, a metapopulation

of extinction-prone local populations in a small patch network is necessarily more threatened than are metapopulations in large and well connected networks.

Regional stochasticity[22] influences the dynamics of many populations simultaneously and leads to spatially correlated population dynamics. Large-scale spatial synchrony may also be generated by other processes such as migration and predation[7], but regional stochasticity in the form of spatially correlated weather conditions is probably the dominant synchronizing mechanism. Regional stochasticity reduces the number of effectively independent local populations[27] and, if strong enough, can make metapopulation-level persistence of classic metapopulations less likely.

Apart from the local processes, local extinction in metapopulations is influenced by processes that are best addressed at the metapopulation level. Emigration may reduce population growth rate and, in combination with demographic and environmental stochasticity, lead to increased risk of extinction. This is particularly likely to happen in small habitat patches with a frequently increased per capita emigration rate (ref. 28, and I.H., J. Alho and A. Moilanen, manuscript in preparation). Conversely, immigration from nearby large populations may reduce extinction risk in small populations[21].

Metapopulation structure gives extra scope for demographic and genetic stochasticities to operate, because classic metapopulations
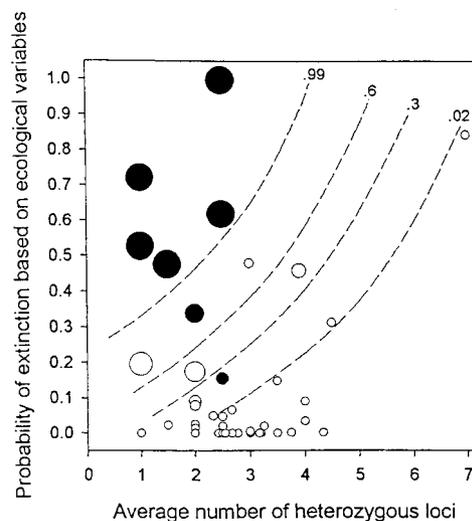

Figure 2 The probability of extinction in the Glanville fritillary butterfly is influenced both by ecological factors and by heterozygosity, which is here used as a measure of the level of inbreeding[29]. The vertical axis gives the probability of extinction for 42 populations as predicted by a model including several ecological factors[29]. The horizontal axis gives the average number of heterozygous loci per individual in a sample of eight polymorphic enzyme and microsatellite loci. The size of the symbol is proportional to the probability of extinction predicted by a model including both the ecological factors and heterozygosity (the isoclines of equal extinction risk were drawn by eye). Of the 42 populations studied, seven populations (black) went extinct in one year[29].

typically include many small populations in which these forms of stochasticity may have a great impact. A recent study[29] on the Glanville fritillary butterfly demonstrated a significant increase in extinction risk with increasing level of inbreeding (Fig. 2). This finding appears to be contrary to the common wisdom that populations with a history of bottlenecks should not suffer from inbreeding, because such populations have supposedly become purged of deleterious recessive alleles, or have gone extinct[30]. The Glanville fritillary metapopulation has not only gone through bottlenecks—the metapopulation literally exists in bottlenecks, because most individuals reside in very small local populations[21]. Theory and intuition developed to explain the effect of genetic stochasticity in isolated populations are inadequate for highly structured metapopulations. For instance, weakly deleterious alleles may accumulate in small populations because of genetic drift. In a metapopulation, different local populations will by chance carry different deleterious alleles, which become transferred between populations by migration. Present theory is inadequate to predict the ultimate outcome of these processes, and there is an urgent need to construct a more comprehensive theory of genetic stochasticity for highly fragmented metapopulations and to develop field projects to increase our empirical knowledge.

One of the greatest virtues of the metapopulation approach to population extinction is the opportunity to contribute to a mechanistic understanding of the biological consequences of habitat loss and fragmentation, the greatest threat to biodiversity worldwide. This will be addressed below, following a brief review of the general implications of extinction–colonization dynamics.

Extinction–colonization dynamics

Metapopulations consisting of small extinction-prone local populations can only persist regionally, in a balance between local extinctions and colonizations[17,25]. Long-term persistence of classic metapopulations is essentially due to asynchrony in the dynamics of local populations, which reduces the variance in the intrinsic rate of metapopulation increase and hence reduces the risk of metapopulation extinction (applying theory developed for single populations[31,32]). This type of persistence is very different from the one traditionally studied by population ecologists using life table and key factor analyses, where the ecologist's task is to uncover the density-dependent processes that lead to the regulation of individual populations[33,34]. Nonetheless, the conclusion should not be drawn that metapopulation dynamics allow long-term persistence without any local density dependence, as has been repeatedly but mistakenly assumed for the past 40 years[35]. Some density dependence operating in local populations is necessary for long-term persistence, even if metapopulation persistence is compatible with infrequent local density dependence in species with ephemeral local populations[21].

Extensive theoretical literature has explored the population dynamic, genetic and evolutionary consequences of extinction–colonization dynamics[6–8,21,25,36–41]. For ecology and conservation, a key consideration is whether the expected growth rate of a metapopulation in an almost empty network is positive, in other words whether the replacement condition referred to above is satisfied. The expected growth rate of a small metapopulation depends both on the intrinsic attributes of the species (local dynamics and migration behaviour) and on the spatial configuration of the habitat. For comparative purposes, fragmented landscapes can be characterized by measures of 'colonization potential' (Box 1), but a quantitatively valid estimate of metapopulation growth rate requires a spatially realistic metapopulation model.

The frequency with which species persist as metapopulations in extinction–colonization balance, as opposed to persisting as a result of stable large populations, is still debated among ecologists[14,25]. Given that a large fraction of species on Earth are highly specific in their habitat requirements and are generally uncommon, it is

reasonable to guess that metapopulation dynamics represent a valuable and even necessary approach to a satisfactory understanding of the dynamics of a large number of species in many regions[21,42]. However, there are so few comprehensive studies on particular species that it remains possible to argue both ways. For parasites

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Box 1 Calculations

Parameter estimation and simulation of the incidence function model (IFM). In the examples in Fig. 3, the IFM was parameterized with one snap-shot of patch occupancy data, as displayed in Fig. 3a, using maximum likelihood regression, assuming independent patch dynamics (Fig. 3b), and making an informed guess about the value of the minimum patch area for which the probability of extinction in unit time equals one[48,49]. Parameter estimation for the three species is discussed in depth elsewhere (the Glanville fritillary[48,50,69], the American pika[51], and the European nuthatch[49]). For parameter estimation based on a Monte Carlo method and incorporating all spatial and temporal autocorrelations in patch occupancy, see ref. 50.

Having estimated the model parameters, one may numerically simulate extinction–colonization dynamics in any patch network, by assigning area-dependent extinctions and isolation-dependent colonizations independently for each patch in each generation using the probabilities given by the model[21,48]. Regional stochasticity (spatially correlated environmental stochasticity) can be included by multiplying all patch areas in each time step with the same lognormally distributed random variable with mean 1 and standard deviation σ, which will translate into correlated temporal changes in extinction and colonization rates in metapopulation dynamics[26,51].

Deterministic equilibrium of the IFM. Apart from calculating the incidences (long-term probabilities of patch occupancy) by simulation, one may calculate the respective deterministic values by iterating the equation

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) p_j A_j$$

where $p_j = \dfrac{C_j}{C_j + (1 - C_j)\dfrac{e}{A_j^x}}$ and $C_i = \dfrac{S_i^2}{S_i^2 + y^2}$

until convergence[21,66]. p_j is the probability of patch j being occupied, d_{ij} is the distance between patches i and j, A_j is the area of patch j, S_i and C_i are the connectivity (Box 2) and the probability of colonization of patch i, respectively, and α, e, x and y are model parameters. To check for alternative equilibria, the iteration was started with either all p values equal to 1, or all except one equal to 0 (repeated for each i and averaged to obtain the initial values of S_i).

Colonization potential of a patch network. Whether a species is able to persist in a patch network or not depends on the amount of habitat in and the spatial configuration of the network as well as on the attributes of the species. For comparative purposes, networks can be characterized by their 'colonization potential', which is here calculated as $M = \bar{S}$, where S is the measure of connectivity in Box 2, now calculated on the assumption that all patches are occupied (because M reflects the potential, not the realized, rate of colonization). Note that of the attributes of the species, M includes only the migration range ($1/\alpha$), and is hence only an approximation. In the application in Fig. 4, the empirically observed scaling $N_j = A_j^{0.5}$ was used[26], and M was square-root transformed to spread out the data points more evenly along the horizontal axis.

Calculating the time delay in metapopulation response to habitat destruction. The following calculation gives a practical measure of the length of the delay. Calculate first the deterministic incidences before habitat destruction, say J_1, as explained above. Next calculate the expected number of occupied patches following habitat destruction, say P_2, as the sum of the respective deterministic incidences. Then start a simulation in the reduced network but initializing patch occupancy with probabilities J_1, and calculate the time until the number of occupied patches drops at or below P_2. Repeat the simulation 100 times and use the median value as a measure of the delay.

living in 'networks' of host individuals, extinction–colonization dynamics are self-evident owing to the limited lifespan of host individuals.

Although this review is concerned with ecological dynamics, it is appropriate to mention that metapopulation dynamics have profound implications for the genetic structure and dynamics of species, potentially also for the adaptive evolution of species, even if Sewall Wright's[4] 'shifting balance process' is no longer considered to be of wide importance in evolution[39,43]. A key genetic question is the degree to which extinction–colonization dynamics decrease the effective genetic population size[39,40]. Convincing empirical evidence is lacking on whether there is reduced genetic variability in species with a classic metapopulation structure.

If the rates of population extinction or colonization are influenced by genetically determined traits of populations, natural selection may operate at the level of local populations (group selection), either reinforcing or opposing selection at the level of individuals. As an example, the Glanville fritillary butterfly has two host plants in Finland, with a geographic variation in genetically determined oviposition preference (host plant choice), corresponding to a geographic trend in host plant abundances (M. Kuussaari, M. Singer and I.H., manuscript in preparation). Recent results indicate that the oviposition preference influences the probability of colonization of habitat patches with different mixtures of the two host plants (I.H. and M. Singer, unpublished results), such that butterflies from *Veronica*-preferring populations have a smaller probability of colonizing a *Plantago*-dominated habitat patch than have butterflies originating from *Plantago*-preferring populations. A model shows that, depending on the spatial structure and plant species composition of a patch network, group selection (biased colonizations) may either increase or decrease preference for a particular host plant in a metapopulation. The model-predicted shift in oviposition preference in particular metapopulations explained a large amount of the observed variation in host plant use, suggesting that group selection has influenced the oviposition preference in the Glanville fritillary metapopulations (I.H. and M. Singer, unpublished results).

Of the life history traits that are thought to be influenced by metapopulation-level selection[41], the evolution of migration rate has a special significance because it directly influences metapopulation dynamics. Evolutionary ecologists have investigated whether species are likely to evolve an elevated migration rate in response to habitat destruction[41], which might help species survive in increasingly fragmented landscapes. This may happen[44], but, given the current rate of environmental change, it seems more likely that species will go extinct before significant evolutionary changes have had time to occur.

The patch area and isolation paradigm

Real metapopulations do not consist of identical and equally connected populations as is assumed in the basic models[14]. Recognizing differences among local populations is important, but this does not mean that the original concept of metapopulation as a 'population of populations'[17] would become obsolete. On the contrary, a new synthesis is taking shape in which the classic metapopulation concept is enriched with general effects of patch area and isolation on movements of individuals, extinction of populations and the establishment of new populations at empty sites (Box 2).

Individuals born to a metapopulation may stay all their life in the natal habitat patch or they may move one or more times to a new patch during their lifetime. To estimate the probabilities of survival and migration per unit time with mark-recapture data, a model of individuals' capture histories may be constructed based on the effects of patch area on migration and isolation on mortality during migration (I.H., J. Alho and A. Moilanen, manuscript in preparation). Because it is reasonable to assume that mortality within

habitat patches does not depend on isolation, unlike mortality during migration, one can tease apart, at least in principle, the two kinds of mortality. This is of interest to ecologists, because mortality during migration is an important cost of migration and has been hard to measure for most species. In a case study on the butterfly *Melitaea diamina*[45], the model was applied to a metapopulation consisting of 14 local populations within an area of $4\,km^2$, using data on 557 marked individuals with 1,301 recaptures. Immigration and emigration scaled as patch area to power 0.2, roughly half of the daily losses of individuals from large habitat patches (~ 1 ha) were due to emigration, only <1% of daily migration distances were

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Box 2 Incorporating habitat patch areas and isolations into metapopulation models

Real fragmented landscapes typically show much spatial variation in patch areas and isolations. Individual and population processes and community patterns are generally influenced by patch area and isolation, and it is desirable to include these effects into metapopulation models, especially because such models can often be parameterized with data that are readily available from field studies (ref. 48, and I.H., J. Alho and A. Moilanen, manuscript in preparation). Adding the patch area and isolation effects into patch occupancy models of metapopulation dynamics has promoted a close link between modelling and field studies[21,66].

The scaling of individual and population processes and community patterns with patch area (A) has been described by the power function: process or pattern $\propto A^\beta$. At the individual level, the process is migration rate (I.H. *et al.*, in preparation), at the population level it is extinction risk[48], and at the community level the pattern is species number[67]. There is no simple connection between the three power functions, but they can each be justified as an approximation based on biologically reasonable assumptions or model predictions (the latter in the case of species number). At the population level, the extinction risk scales asymptotically as a power function of the population ceiling and hence of patch size in a diffusion approximation to an extinction model[31,32].

Isolation of a habitat patch or a local population from existing populations influences the rate of immigration to a patch and hence the probability of colonization of an empty patch. A sensible index of connectivity (inverse of isolation) of patch i is $S_i = \Sigma_{j \neq i} \exp(-\alpha d_{ij})N_j$. Thus connectivity of patch i increases with decreasing distances (d_{ij}) from, and sizes (N_j) of, existing other populations. The species-specific migration range is given by $1/\alpha$. The distance d_{ij} may be the Euclidian distance or some more complex measure taking into account the influence of landscape structure on migration[69]. If knowledge on patch occupancy only is available, N_j values may be crudely estimated by a power function of patch areas, multiplied by one for occupied and by zero for empty patches. To measure connectivity for emigrants, values of N_j are replaced by a power function of patch areas for all patches, whether occupied or not, which assumes that probability of colonization of patch i is proportional to A^β.

The probability of an emigrant from patch i surviving migration and the probability of an empty patch i becoming recolonized are increasing functions of the respective S_i values. In both cases, a reasonable simple choice for the functional form is the sigmoid model (ref. 48, and I.H. *et al.*, in preparation)

$$x_i = \frac{1}{1 + \left(\frac{y}{S_i}\right)^2}$$

where x_i is probability of survival during migration from patch i or the probability of colonization of an empty patch i. y is a parameter.

Specific models of migration (I.H. *et al.*, in preparation), metapopulation dynamics[48] and community pattern[66] can be constructed with the above (or other comparable) assumptions about the patch area and isolation effects.

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greater than 1 km, and 16% of all deaths were estimated to have occurred during migration (I.H., J. Alho and A. Moilanen, manuscript in preparation; for a general discussion of movement patterns in metapopulations, see refs 46, 47).

The incidence function model (IFM)[21,48] is a prime example of the value of incorporating the patch area and isolation effects into a basic metapopulation model. The IFM is built on the well supported assumptions that extinction risk of local populations decreases with increasing habitat patch area (because extinction risk decreases with increasing expected population size, which increases with patch area[21]), and that the colonization probability is a function of patch isolation from existing local populations (Box 2). From these assumptions, a Markov chain model for state transitions in individual habitat patches leads to an expression for the average long-term probability of patch occupancy, called the incidence, as a function of the area and isolation of the patch[48]. The IFM thus relates the pattern of habitat occupancy to the structure of the fragmented landscape as reflected in patch areas and isolations (Fig. 1, middle panel). The IFM has only a few parameters, which facilitates parameter estimation. Of particular interest is that the model allows one to estimate the parameters of the spatial processes, local extinction and recolonization, with spatial data on patch occupancy, although more robust parameter estimates can be obtained if data are also available on population turnover[48–50].

The IFM has been used to model the metapopulation dynamics of plants, insects, small mammals and birds[21]. Figure 3a–c gives three examples, which are used below in a discussion of the consequences of habitat destruction for metapopulation dynamics. The IFM has been tested by comparing the observed population turnover rate with the predicted one[49,51,52] and by testing predicted patterns of patch occupancy in landscapes other than the one from which parameters were estimated[21]. In one case, parameter values estimated for a species of butterfly were used successfully to predict the distribution of a related species in another patch network[45]. This example illustrates the potential predictive power of the IFM to explain the distribution of species in fragmented landscapes.

The IFM can be used to investigate the scaling of extinction risk with habitat patch area, and thereby with population size, using patch occupancy data. This scaling gives an interesting opportunity to relate the parameters of local extinction models[31,32] to the parameters of metapopulation models[21]. The scaling constant was related to body size in small mammals and birds but not in insects, which implies that the strength of environmental stochasticity increases with decreasing body size in vertebrates[21].

Complex spatial dynamics

Theoretical studies have demonstrated that spatial population dynamics may generate complex spatial patterns in species abundances in the absence of any environmental heterogeneity[6,7,38]. Complex spatial patterns in spatially explicit models are due to localized interactions and restricted migration range of individuals, localized interactions amplifying small-scale chance variation and short-range migration 'memorizing' the altered abundances[53]. Complex spatial patterns occur in single-species models but are especially well documented for metapopulation models of interspecific competition[53] and predator–prey dynamics[12,16,38]. Unfortunately, because of formidable logistical problems and the ever-present spatial heterogeneity in real landscapes, the model predictions have remained largely untested (but see refs 54–56). The predictions stem from deterministic models, and the outcome of the deterministic processes interacting with environmental stochasticity remains to be determined.

Another type of complexity that may arise in metapopulation dynamics is alternative stable equilibria[23], of which one corresponds to metapopulation extinction and the other to a state with most of the habitat occupied (Fig. 4a). In finite patch networks, every metapopulation will ultimately go extinct because of extinction–

colonization stochasticity, but meanwhile the metapopulation may settle to a positive quasi-stable equilibrium (Box 1), which for practical purposes is stable in large and well connected networks. Alternative stable equilibria are generated by a positive feedback in metapopulation dynamics (the rescue effect), migration from existing large local populations increasing the sizes of, and thereby decreasing the risk of extinction in, nearby small populations[57]. Propagule size-dependent success of colonization (local Allee effect) may also contribute to alternative equilibria in metapopulations.

An extensive data set on the Glanville fritillary butterfly from many semi-independent patch networks shows a pattern of habitat occupancy that is suggestive of alternative equilibria (Fig. 4b). These results can be modelled with the IFM parameterized for the butterfly (Fig. 3b) to predict the quasi-stable equilibria in particular patch networks (Box 1). The IFM includes the rescue effect and propagule size-dependent colonization success and may hence generate alternative equilibria. The modelling results suggest that 12 of the 66 patch networks have alternative quasi-stable equilibria (Fig. 4c). Simulation of metapopulation dynamics in the 66 networks yields snap-shots of habitat occupancy (Fig. 4d) that are similar to the observed one (Fig. 4b). In these simulations, a small probability of colonization from outside the network was assumed to prevent permanent metapopulation extinction. An especially noteworthy feature of the simulation results is that many networks with colonization potential just below the threshold for a positive equilibrium can nonetheless have a large fraction of the habitat occupied at a given point in time (Fig. 4d), a pattern that is also apparent in the empirical data (Fig. 4b). This result indicates that the dynamic force pushing the metapopulation towards extinction is weak in these networks, a situation with important consequences for the response of metapopulations to habitat destruction, as will be discussed next.

Response to habitat loss and fragmentation

Habitat destruction—involving downright loss of habitat, degrading habitat quality, and fragmentation of the remaining habitat—is by far the most significant cause of population and species extinction. For instance, of the endangered bird species in the world, habitat loss has been singled out as the main threat in 82% of the species[58]. Predicting the consequences of habitat destruction is perhaps the greatest challenge for metapopulation dynamics.

Conservation-oriented ecologists have employed complex simulation models of multiple populations to assess the large-scale and long-term effects of habitat loss and fragmentation[59,60]. Unfortunately, these models tend to have many untested assumptions and a large number of parameters that are difficult to estimate. Given that the practical task is generally to compare alternative scenarios of landscape change, rather than to predict quantitatively the extinction risk of a particular metapopulation, simpler and more robust models such as the IFM or state-transition models[21,61] may be preferable to complex simulation models, especially for highly fragmented landscapes[21]. But for metapopulations including one or more very large populations, these patch occupancy models are inadequate because they ignore local dynamics, and hence some more complex approach is needed.

Studies of landscape connectivity and metapopulation dynamics employing simple strategic models have led to three general conclusions about metapopulation response to habitat destruction. First, landscape ecologists have suggested that the response is nonlinear, because habitat connectivity is lost in a highly nonlinear manner in simple scenarios of habitat destruction[62]. A metapopulation dynamic reason for a nonlinear response to habitat destruction is alternative equilibria—the positive equilibrium may be suddenly lost with increasing habitat loss (consider moving to the left in Fig. 4). Second, metapopulation decline in response to habitat destruction occurs with a time lag[26], dubbed the 'extinction debt'[36]. And

third, simple models suggest that the equilibrium amount of empty habitat in a landscape before habitat destruction equals the extinction threshold, the minimum amount of habitat required for long-term persistence[63], which has been termed the 'Levins rule'[26]. Figure 3d–f examines these conclusions for metapopulations of an insect (the Glanville fritillary), a passerine bird (the European nuthatch) and a small mammal (the American pika), with the help of the IFM. To make examples as realistic as possible, the IFM was parameterized (Fig. 3b) with a snapshot of patch occupancy data (Fig. 3a) for each species. Three forms of habitat loss were used to generate hypothetical landscape scenarios: a contiguous region of the landscape may be lost; habitat fragments may be lost randomly; and individual fragments may lose area. In reality, habitat destruction is likely to involve a combination of these situations.

The Levins rule is applicable when habitat is lost by random elimination of patches. In the examples shown in Fig. 3d, the number of empty patches decreases with decreasing habitat availability in the nuthatch metapopulation, but in the butterfly and mammal metapopulations there is no systematic change, in agreement with the Levins rule, although there is substantial variance for different landscape configurations. When habitat is lost in large blocks, the number of empty patches tends to decrease with decreasing amount of habitat. In contrast, when each individual patch loses area, leading to the same number but smaller patches, the number of empty patches inevitably increases with a reduction in total habitat area (Fig. 3d), as such habitat loss will increase local extinction risk and reduce colonization rate. In conclusion, there is not much practical value in the Levins rule—metapopulation response is too specific to the particulars of habitat loss and to the

original fragmented landscape for the idealized model to be useful.

Metapopulations inevitably go extinct when the colonization potential of the landscape falls below a threshold, but stochasticity may lead to extinction even in landscapes with more and better connected habitat patches than specified by the threshold (Fig. 3e). In the small mammal example, the risk of extinction in 100 years increases rather gradually with decreasing amount of habitat, whereas in the butterfly and bird examples the response is more sudden. Note that in these examples the extinction risk is set chiefly by the amount of habitat remaining, not by the type of habitat destruction (Fig. 3e), which underscores the primary importance of the total area of suitable habitat.

Metapopulations track reduction in habitat area with a delay (Fig. 3f). The delay tends to become longer when the original amount of habitat (before the reduction) is smaller. The delay is especially long when the new equilibrium following habitat loss is metapopulation extinction (Fig. 3f). Long delays in these cases reflect the weak dynamic forces operating in landscapes that have colonization potential just below the threshold for persistence (Fig. 4d). The important message here is that many species may be hanging around for a long time in landscapes that have already lost their capacity to support these species on the long term.

Community patterns

Metapopulation models have been extended to interactive and non-interactive multispecies communities. Models of interacting metapopulations have been used to explain patterns in species succession[64], species richness and composition[36] and food web structure[65] of communities. Metapopulation dynamics may set a
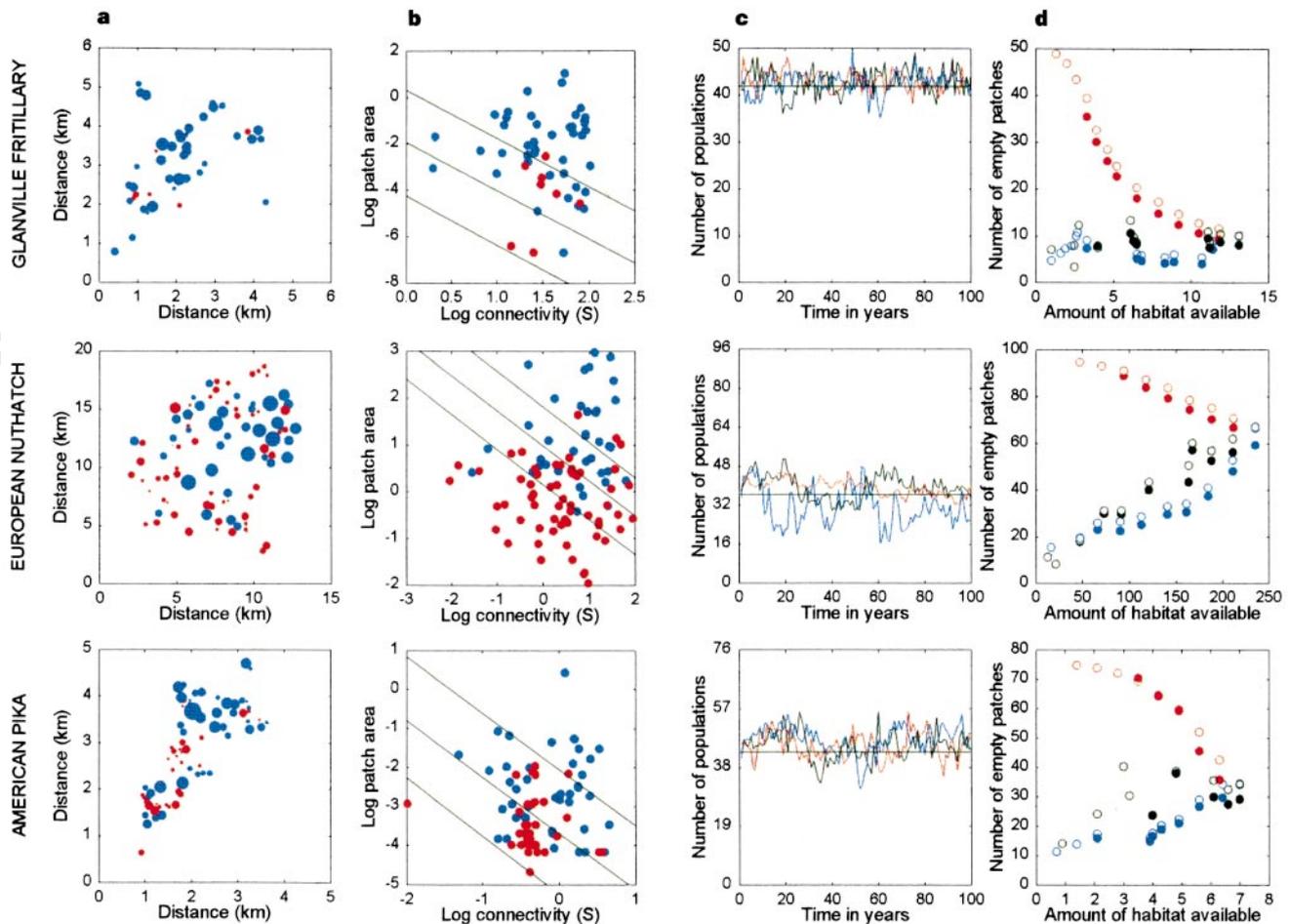
limit to food-chain length in communities of specialist species in fragmented landscapes, as the density of suitable (prey-occupied) habitat patches is necessarily lower for high trophic levels[65]. Predator–prey[12,13,38] and competitive[36,53,63] metapopulation dynamics will not be discussed here.

Community models for non-interactive species are constructed simply by summing up the predicted patterns for individual species. Using this approach, it has been demonstrated[66] that the two most general patterns in the distribution of species, the species–area (SA) curve[67] and the distribution–abundance (DA) relationship[68], which have been studied in complete isolation, can be derived from the same metapopulation model with area-dependent extinction rate and distance-dependent colonization rate (this demonstration by itself does not exclude alternative explanations).

Our model[66] was constructed for a community in which species have different densities, reflecting, for example, interspecific differences in the degree of ecological specialization. Other things being equal, higher density increases colonization rate by increasing the absolute number of immigrants, and decreases extinction rate by boosting population sizes. The metapopulation model leads to an expression for the incidence of species i on island (or habitat patch) j. Summing up the incidences across the species gives the expected number of species on islands, and regressing this number against island area gives the SA curve. Similarly, summing up the incidences across the islands gives the expected distribution of the species; and regressing the distribution against species' density leads to the DA curve. Figure 5 gives examples of model-predicted SA and DA curves and demonstrates how the slopes of these curves depend on a small number of parameters. The predicted slope values are testable

for landscapes and communities for which appropriate data can be collected.

Conservation and landscape management

Species have adapted to their environments and hence, according to the common wisdom in ecology, the distribution of species' abundances in space reflects the match between the environment and the species' ecological requirements, with an appropriate caveat for ecological interactions such as competition and predation and recent perturbations caused by humans. Spatial ecology challenges a strict interpretation of this habitat–organism relation, as species may exhibit complex spatial patterns in uniform environments; species may be absent where environmental conditions are favourable (owing to stochastic extinction of local populations); and species may be present where conditions are not favourable (sink populations). These general conclusions have profound implications for conservation, as do several more specific results stemming from research in metapopulation dynamics.

The total amount of habitat in the fragmented landscape is often a good predictor of long-term metapopulation persistence (Fig. 3e), though it is easy to construct counter-examples[45]. Thus, in spite of all the interest in fragmented populations, the primary aim in conservation should be simply to preserve as much habitat as possible. Spatially realistic metapopulation models may be used[45,51,59,60,69] to generate more refined species-specific and landscape-specific predictions, which replace the infamous rules of reserve design based on the dynamic theory of island biogeography[70]. The emphasis in modelling should be in transient dynamics, to provide insight about the dynamics at the timescale at
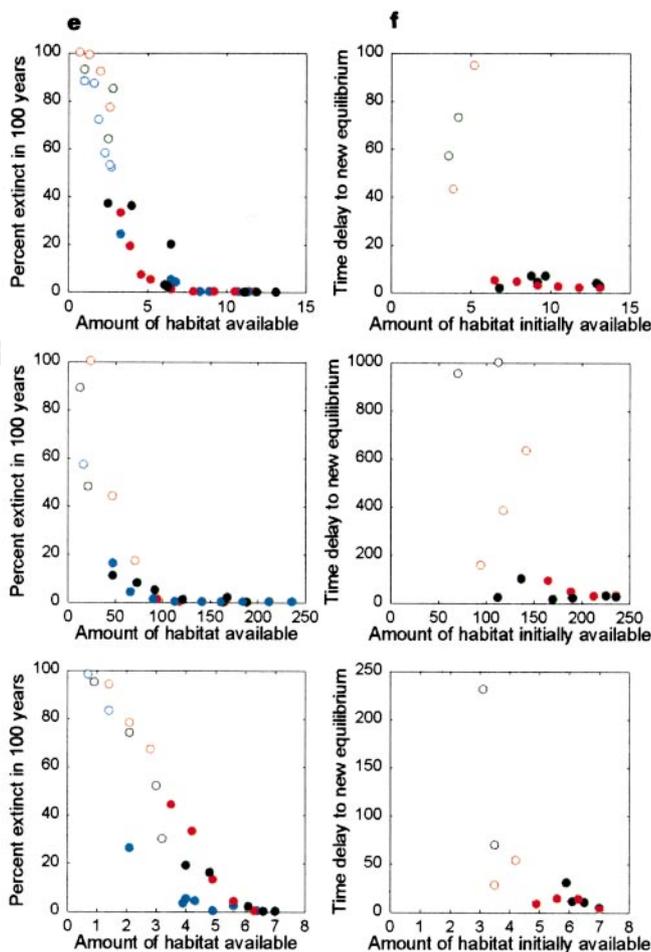

Figure 3 The incidence function model (IFM) is here parameterized for metapopulations of an insect (the Glanville fritillary butterfly, *Melitaea cinxia*), a passerine bird (the European nuthatch, *Sitta europaea*), and a small mammal (the American pika, *Ochotona princeps*), and the parameterized model is used to investigate the consequences of hypothetical scenarios of habitat destruction. For each species (the three rows), the six panels give the following information: **a**, a snap-shot of habitat patch occupancy in a fragmented landscape (blue and red dots represent occupied and empty patches, respectively; dot size proportional to habitat patch area); **b**, an area-isolation plot, showing patch occupancy as a function of patch area and connectivity (*S*, Box 2), with the fitted 10, 50 and 90% lines of incidence; **c**, predicted trajectories of patch occupancy during 100 yrs, with no (red line) and two levels of regional stochasticity ($\sigma = 0.4$, black line, and 0.8, blue line; Box 1), as well as the expected fraction of occupied patches (straight line; Box 1); **d**, number of empty patches as a function of the pooled amount of habitat in the remaining patches (horizontal axis) under three forms of habitat destruction: removal of patches within a continuous area (blue), random removal of patches (black), and removal of area (constant fraction) from each patch (red), with filled symbols giving the expected value (Box 1) and open symbols the realized number in a 100-yr simulation (result calculated for the years 51–100); **e**, fraction of metapopulations going extinct in 100 replicate 100-yr simulations in the previous three scenarios of habitat loss, with regional stochasticity set at $\sigma = 0.8$ for the insect and $\sigma = 0.4$ for the other species. Symbols as in **d**, with filled symbols giving the result for landscapes in which the expected metapopulation size was positive; **f**, the time delay in metapopulation response to habitat destruction calculated as described in Box 1. The horizontal axis gives the amount of habitat before the extra habitat destruction, which amounted to 50% for the butterfly and the pika and 20% for the nuthatch (these calculations were made only for random elimination of entire patches and loss of patch area). Open symbols represent cases where the new equilibrium was metapopulation extinction.
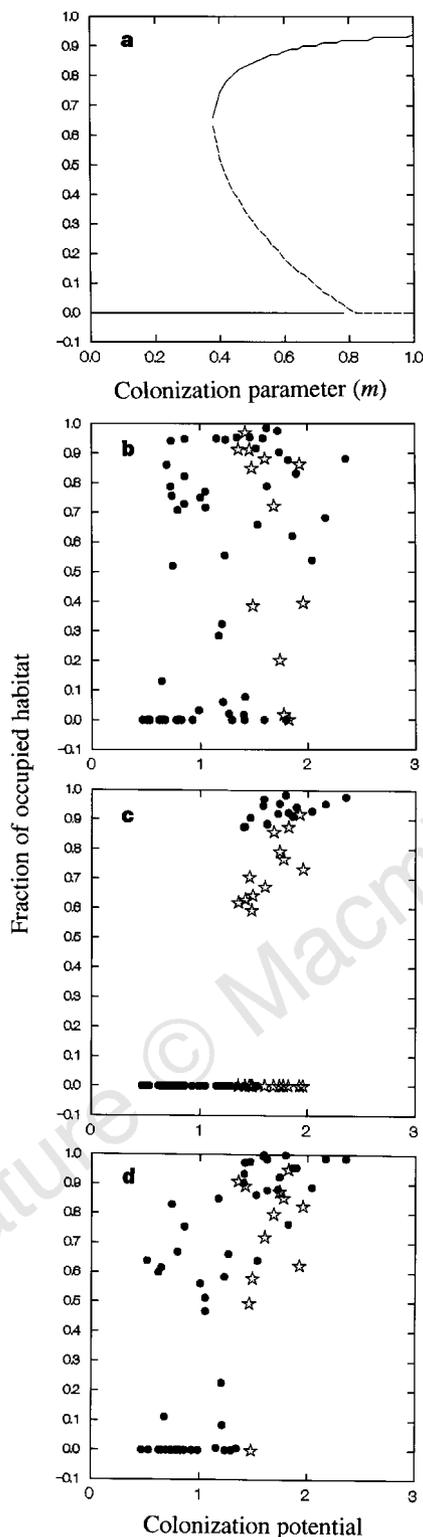
Figure 4 Bifurcation diagrams for the fraction of occupied habitat in metapopulations. **a**, Theoretical result in which the fraction of occupied habitat is plotted against colonization rate parameter in a deterministic structured model[57]. The continuous line represents stable equilibria, the broken line is unstable equilibria. **b**, Empirical result for 66 semi-independent patch networks of the Glanville fritillary butterfly with at least 5 patches[78] and with the fraction of occupied habitat plotted against the colonization potential described in Box 1. Stars indicate patch networks for which the IFM had two alternative equilibria (Box 1). **c**, Expected fraction of occupied habitat as predicted by the IFM parameterized for the butterfly (Fig. 3b). **d**, One snap-shot from stochastic simulations of the IFM. In this case, a small probability of colonization (0.01) from outside the patch network was assumed for each patch to prevent permanent metapopulation extinction.
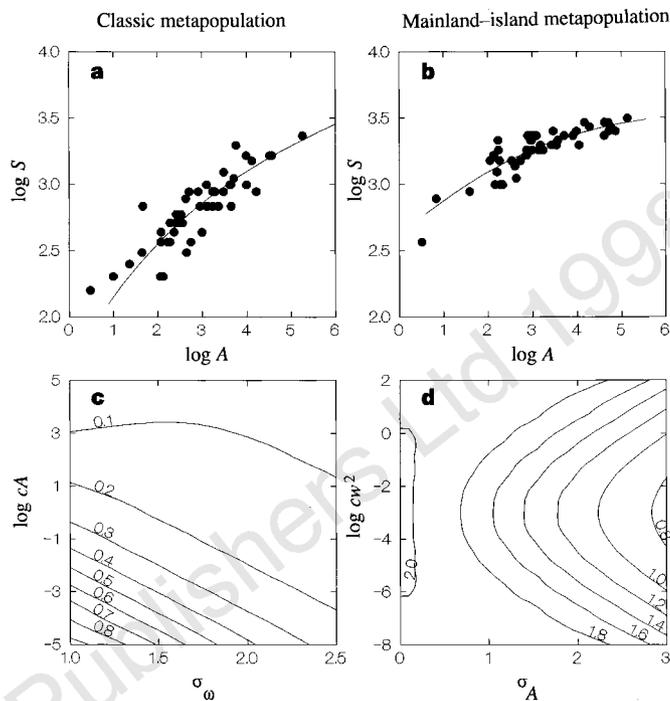

Figure 5 Examples of species–area (SA) curves in classic and mainland-island metapopulations predicted by a metacommunity model of non-interactive species with interspecific differences in population density[66]. **a**, Classic metapopulation; **b**, Mainland–island metapopulation. The lines are the expected relationships, the dots give one stochastic realization, obtained by assigning the presence or absence of species on islands according to the incidences. **c**, **d**, Dependence of the slopes of the SA (**c**) and distribution–abundance (**d**) curves on the isolation of the islands or habitat fragments (increases with decreasing c), average island area (A) and species density (w), and the standard deviations of the respective distributions (σ_A and σ_w) in mainland–island metapopulations. Analogous predictions can be made for classic metapopulations without an external mainland[66].

which managers operate[71]. Further work is needed to extend the single-species metapopulation models to multispecies communities, essentially to merge the spatially explicit and dynamic metapopulation models with non-dynamic site-selection algorithms used in conservation[72] and with models of habitat connectivity used in landscape ecology[73].

If only small fragments of habitat with extinction-prone populations can be preserved, it is desirable to have at least 15–20 fragments located within the migration range of the species, to reduce the probability of metapopulation extinction due to extinction–colonization stochasticity. Managers should absorb the key message of classic metapopulation dynamics: currently unoccupied habitat fragments may be critical for long-term persistence. Optimal spacing of preserved habitat fragments is a compromise between the need to have them located sufficiently close to each other to allow recolonization, but far enough apart to reduce the impact of regional stochasticity. Another means of alleviating regional stochasticity is to include substantial spatial variance in habitat quality among the preserved areas. Habitat quality interacts with stochasticity caused by varying weather conditions, hence a set of dissimilar fragments is unlikely to experience the most unfavourable conditions simultaneously[74,75].

One prediction of metapopulation models with great importance for conservation is the time delay with which species are expected to track changes in the structure of fragmented landscapes. We do not know which fraction of currently endangered populations and species are already committed to metapopulation extinction in

their present environments. A real worry is that such 'living dead' populations and species are numerous, especially because the delay in reaching the new equilibrium is particularly long in just those cases that matter most, where the new equilibrium is metapopulation extinction (Fig. 3f).

Finally, it has to be agreed with the critics[76] who have cautioned against uncritical application of the metapopulation concept and models to conservation. Not all endangered species have the spatial structure of metapopulations, and even if they do, the immediate conservation concern may be elsewhere. Rather than in the conservation of species that are already on the brink of extinction, the metapopulation concept may turn out to be most helpful in the conservation of biodiversity in general in our everyday landscapes. Regionally, many habitats have become so fragmented that isolated populations cannot be expected to last for long, hence long-term persistence can occur only via metapopulation dynamics. □

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1. Nicholson, A. J. The balance of animal populations. *J. Anim. Ecol.* **2,** 132–178 (1933).
2. Andrewartha, H. G. & Birch, L. C. *The Distribution and Abundance of Animals* (University of Chicago Press, Chicago, 1954).
3. Wright, S. Evolution in Mendelian populations. *Genetics* **16,** 97–159 (1931).
4. Wright, S. The roles of mutation, inbreeding, crossbreeding and selection in evolution. *Proc. Sixth Int. Congr. Genet.* **1,** 356–366 (1932).
5. Hanski, I. & Gilpin, M. E. *Metapopulation Biology: Ecology, Genetics, and Evolution* (Academic, San Diego, 1997).
6. Tilman, D. & Kareiva, P. *Spatial Ecology* (Princeton University Press, Princeton, 1997).
7. Bascompte, J. & Solé, R. V. *Modeling Spatiotemporal Dynamics in Ecology* (Springer, New York, 1998).
8. Durrett, R. & Levin, S. A. Stochastic spatial models: a user's guide to ecological applications. *Phil. Trans. R. Soc. Lond. B* **343,** 329–350 (1994).
9. Forman, R. T. T. Some general principles of landscape and regional ecology. *Landscape Ecology* **10,** 133–142 (1995).
10. Wiens, J. A. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 43–68 (Academic, San Diego, 1997).
11. Kareiva, P. & Wennergren, U. Connecting landscape patterns to ecosystem and population processes. *Nature* **373,** 299–302 (1995).
12. Wilson, H. B. *et al.* in *Modeling Spatiotemporal Dynamics in Ecology* (eds Bascompte, J. & Solé, R. V.) 63–82 (Springer, New York, 1998).
13. Nee, S., May, R. M. & Hassell, M. P. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 123–148 (Academic, San Diego, 1997).
14. Harrison, S. in *Large-scale Ecology and Conservation Biology* (eds Edwards, P. J., May, R. M. & Webb, N. R.) 111–128 (Blackwell Scientific, Oxford, 1994).
15. Settele, J. *Species Survival in Fragmented Landscapes* (Kluwer, Dordrecht, 1996).
16. McCullough, D. L. *Metapopulations and Wildlife Conservation* (Island, Washington DC, 1997).
17. Levins, R. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* **15,** 237–240 (1969).
18. Anderson, R. M. & May, R. M. *Infectious Diseases of Humans: Dynamics and Control* (Oxford University Press, Oxford, 1991).
19. Grenfell, B. & Harwood, J. (Meta)population dynamics of infectious diseases. *Trends Ecol. Evol.* **12,** 395–404 (1997).
20. Bartlett, M. S. Measles periodicity and community size. *J. R. Stat. Soc. A* **120,** 48–70 (1957).
21. Hanski, I. *Metapopulation Ecology* (Oxford University Press, Oxford, in the press).
22. Hanski, I. Single-species metapopulation dynamics: concepts, models and observations. *Biol. J. Linn. Soc.* **42,** 17–38 (1991).
23. Gyllenberg, M., Hanski, I. & Hastings, A. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 93–122 (Academic, San Diego, 1997).
24. Hanski, I. Patch-occupancy dynamics in fragmented landscapes. *Trends Ecol. Evol.* **9,** 131–135 (1994).
25. Hanski, I. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 69–92 (Academic, San Diego, 1997).
26. Hanski, I., Moilanen, A. & Gyllenberg, M. Minimum viable metapopulation size. *Am. Nat.* **147,** 527–541 (1996).
27. Chesson, P. in *Modeling Spatiotemporal Dynamics in Ecology* (eds Bascompte, J. & Solé, R. V.) 151–166 (Springer, New York, 1998).
28. Thomas, C. D. & Hanski, I. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 359–386 (Academic, San Diego, 1997).
29. Saccheri, I. J. *et al.* Inbreeding and extinction in a butterfly metapopulation. *Nature* **392,** 491–494 (1998).
30. Lande, R. Genetics and demography in biological conservation. *Science* **241,** 1455–1460 (1988).
31. Lande, R. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* **142,** 911–927 (1993).
32. Foley, P. Predicting extinction times from environmental stochasticity and carrying capacity. *Cons. Biol.* **8,** 124–137 (1994).
33. Royama, T. *Analytical Population Dynamics* (Chapman & Hall, London, 1992).
34. Turchin, P. in *Population Dynamics: New Approaches and Synthesis* (eds Cappuccino, N. & Price, P.) 19–40 (Academic, London, 1995).
35. den Boer, P. J. Seeing the tree for the wood: random walks or bounded fluctuations of population size? *Oecologia* **86,** 484–491 (1991).
36. Tilman, D. *et al.* Habitat destruction and the extinction debt. *Nature* **371,** 65–66 (1994).
37. Hastings, A. & Harrison, S. Metapopulation dynamics and genetics. *Annu. Rev. Ecol. Syst.* **25,** 167–188 (1994).
38. Hassell, M. P., Comins, H. N. & May, R. M. Species coexistence and self-organizing spatial dynamics. *Nature* **370,** 290–292 (1994).
39. Barton, N. H. & Whitlock, M. C. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 183–214 (Academic, San Diego, 1997).
40. Hedrick, P. W. & Gilpin, M. E. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 166–182 (Academic, San Diego, 1997).
41. Olivieri, I. & Gouyon, P.-H. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 293–324 (Academic, San Diego, 1997).
42. Murphy, D. D., Freas, K. S. & Weiss, S. B. An environment-metapopulation approach to the conservation of an endangered invertebrate. *Cons. Biol.* **4,** 41–51 (1990).
43. Coyne, J. A., Barton, N. H. & Turelli, M. A critique of Wright's shifting balance theory of evolution. *Evolution* **51,** 643–671 (1997).
44. Leimar, O. & Nordberg, U. Metapopulation extinction and genetic variation in dispersal-related traits. *Oikos* **80,** 448–458 (1997).
45. Wahlberg, N., Moilanen, A. & Hanski, I. Predicting the occurrence of endangered species in fragmented landscapes. *Science* **273,** 1536–1538 (1996).
46. Ims, R. A. & Yoccoz, N. G. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 247–266 (Academic, San Diego, 1997).
47. Turchin, P. *Quantitative Analysis of Movement: Measuring and Modelling Population Redistribution in Animals and Plants* (Sinauer, Sunderland, MA, 1998).
48. Hanski, I. A practical model of metapopulation dynamics. *J. Anim. Ecol.* **63,** 151–162 (1994).
49. ter Braak, J. F., Hanski, I. A. & Verboom, J. in *Modeling Spatiotemporal Dynamics in Ecology* (eds Bascompte, J. & Solé, R. V.) 167–188 (Springer, New York, 1998).
50. Moilanen, A. Patch occupancy models of metapopulation dynamics: efficient parameter estimation with implicit statistical inference. *Ecology* (in the press).
51. Moilanen, A., Smith, A. T. & Hanski, I. A. Long-term dynamics in a metapopulation of the American pika. *Am. Nat.* **152,** 530–542 (1998).
52. Hanski, I. Inferences from ecological incidence functions. *Am. Nat.* **139,** 657–662 (1992).
53. Pacala, S. W. & Levin, S. A. in *Spatial Ecology* (eds Tilman, D. & Kareiva, P.) 204–232 (Princeton University Press, Princeton, 1997).
54. Cain, M. L. *et al.* Neighbourhood models of clonal growth in the white glover *Trifolium repens. Am. Nat.* **145,** 888–917 (1995).
55. Turchin, P. *et al.* in *Modeling Spatiotemporal Dynamics in Ecology* (eds Bascompte, J. & Solé, R. V.) 199–213 (Springer, New York, 1998).
56. Maron, J. L. & Harrison, S. Spatial pattern formation in an insect host-parasitoid system. *Science* **278,** 1619–1621 (1998).
57. Hanski, I. & Gyllenberg, M. Two general metapopulation models and the core-satellite species hypothesis. *Am. Nat.* **142,** 17–41 (1993).
58. Temple, S. A. The problem of avian extinctions. *Curr. Ornithol.* **3,** 453–485 (1986).
59. Akçakaya, H. R. & Ferson, S. *RAMAS/Space User Manual: Spatially Structured Population Models for Conservation Biology* (Applied Biomathematics, New York, 1992).
60. Possingham, H. P. & Noble, I. R. in *Research Consultancy for the Research Assessment Commission, Forest and Timber Inquiry* (Canberra, 1991).
61. Sjögren-Gulve, P. & Ray, C. in *Metapopulations and Wildlife Conservation* (ed McCullough, D. R.) 111–138 (Island, Washington DC, 1997).
62. Andrén, H. in *Mosaic Landscapes and Ecological Processes* (eds Hansson, L., Fahrig, L. & Merriam, G.) 225–255 (Chapman & Hall, London, 1995).
63. Nee, S. & May, R. M. Dynamics of metapopulations: Habitat destruction and competitive coexistence. *J. Anim. Ecol.* **61,** 37–40 (1992).
64. Caswell, H. & Cohen, J. E. Disturbance, interspecific interaction and diversity in metapopulations. *Biol. J. Linn. Soc.* **42,** 193–218 (1991).
65. Holt, R. D. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 149–165 (Academic, San Diego, 1997).
66. Hanski, I. & Gyllenberg, M. Uniting two general patterns in the distribution of species. *Science* **275,** 397–400 (1997).
67. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography* (Princeton University Press, Princeton, 1967).
68. Lawton, J. H. Range, population abundance and conservation. *Trends Ecol. Evol.* **8,** 409–413 (1993).
69. Moilanen, A. & Hanski, I. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* **79,** 2503–2515 (1998).
70. Hanski, I. & Simberloff, D. in *Metapopulation Biology* (eds Hanski, I. & Gilpin, M. E.) 5–26 (Academic, San Diego, 1997).
71. Thomas, C. D. in *Aspects of the Genesis and Maintenance of Biological Diversity* (eds Hochberg, M. E., Clobert, J. & Barbault, R.) 292–307 (Oxford University Press, Oxford, 1996).
72. Pressey, R. L., Possingham, H. P. & Day, J. R. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. *Biol. Cons.* **80,** 207–219 (1997).
73. With, K. A., Gardner, R. H. & Turner, M. G. Landscape connectivity and population distributions in heterogeneous landscapes. *Oikos* **78,** 151–169 (1997).
74. Weiss, S. J., Murphy, D. D. & White, R. R. Sun, slope and butterflies: topographic determinants of habitat quality in *Euphydryas editha. Ecology* **69,** 1486–1496 (1988).
75. Kindvall, O. The impact of extreme weather on habitat preference and survival in a metapopulation of the bush cricket *Metrioptera bicolor* in Sweden. *Biol. Cons.* **73,** 51–58 (1995).
76. Doak, D. F. & Mills, L. S. A useful role for theory in conservation. *Ecology* **75,** 615–626 (1994).
77. Gyllenberg, M. & Hanski, I. Habitat deterioration, habitat destruction and metapopulation persistence in a heterogeneous landscape. *Theor. Pop. Biol.* **52,** 198–215 (1997).
78. Hanski, I. *et al.* Multiple equilibria in metapopulation dynamics. *Nature* **377,** 618–621 (1995).