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Spatial Scale, Patchiness and Population Dynamics on Land [and Discussion]

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Spatial scale, patchiness and population dynamics on land

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SUMMARY

The most striking difference between land and open sea is the greater structural heterogeneity of terrestrial environments. I make a distinction between two principal kinds of patches at two spatial scales, defined by the relative contributions of behaviour and demography to variation in density. At the scale of resource patches, movements of individuals among the patches influence the frequencies of ecological interaction among the mobile individuals and their offspring. Many studies have demonstrated how independently aggregated spatial distributions generally enhance stability of single-species and many-species dynamics. At the scale of habitat patches, assemblages of local populations connected by migration constitute metapopulations. I outline a range of modelling approaches to metapopulation dynamics, including spatially implicit, explicit and realistic models. I describe a novel spatially realistic approach, based on generalized incidence functions, which can be parameterized with data on the pattern of occupancy in a network of habitat patches. This approach allows one to make quantitative predictions about transient dynamics in particular metapopulations.

1. INTRODUCTION

A most striking difference between land and open sea, and to a lesser extent between land and the bottom of sea, is the greater structural heterogeneity of terrestrial environments, which typically consist of physical 'patches' of different kind at many spatial scales (Steele 1991). Spatial population structures and dynamics of terrestrial species are greatly affected by the physical structure of the environment. This paper is focused on dynamics in physically patchy environments, and I only touch patchiness of populations in spatially continuous environments (this is reviewed in other papers in this volume and elsewhere: Kareiva 1990; Levin 1992, this symposium).

Ecologists have produced a voluminous literature around the themes of spatial scale, hierarchy of scales, patchiness and other related concepts (Steele 1989). Spatial patchiness, in particular, has been a dominant theme in many branches of population biology in recent years, including foraging behaviour (Stephens & Krebs 1986), life history evolution (Stearns 1992), population dynamics (Hassell & May 1985), community organization (Caswell & Cohen 1991) and landscape ecology (Wiens *et al.* 1993; dozens of relevant references could be added). One general approach to questions about spatial scale and patchiness is based on describing patterns. An example from terrestrial population ecology is the variance–mean regression (Taylor 1961), which has been used to characterize population patchiness across spatial scales (Taylor 1986). Lack of significant progress in developing a mechanistic model for, and the small number of interesting and testable predictions stemming from, the variance–mean regression epitomizes problems in pattern-oriented approaches to population dynamics. Such topics as 'hierarchy theory' and 'landscape ecology' have had, so far, less impact in ecology than their subject matters would suggest. An alternative, although admittedly less ambitious approach, adopted in this paper, is to begin with particular ecological processes, which in the terrestrial context typically implies a focus on particular spatial scales.

2. RESOURCE PATCHES, HABITAT PATCHES AND RATES OF MOVEMENT

Keeping the terrestrial perspective, I recognize two principal kinds of environmental patches at two spatial scales, defined by the relative contributions of behaviour and demography, respectively, to variation in density. For most terrestrial species, the environment is patchy because their essential resources occur patchily. I call these patches resource patches. At a higher spatial scale, most terrestrial organisms find appropriate resource patches in only certain kinds of habitats, immersed in the matrix of unsuitable habitat. I call these patches habitat patches. For many organisms, habitat patches are clearly defined, for others they are less distinct, often because their resources occur in many kinds of habitats.

By definition, most individuals visit many resource patches but stay within one habitat patch during their lifetime. Movements between resource patches are

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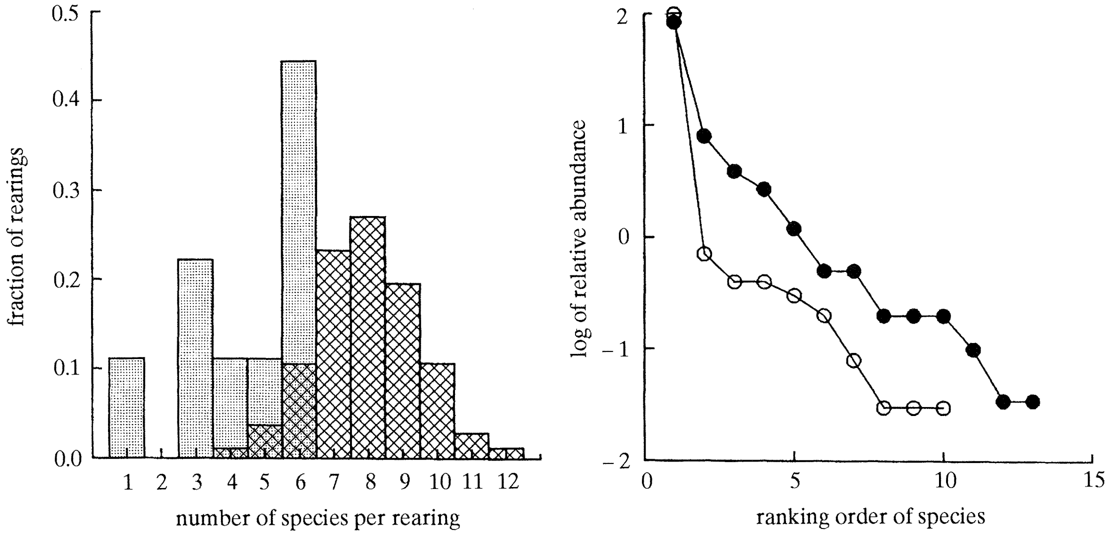

Figure 1. An empirical test of the prediction that intraspecific aggregation facilitates coexistence of competitors. Left panel: fewer species of blowflies emerged from rearings in which four resource patches had been combined after oviposition, and among which maggots could move freely, thereby reducing spatial aggregation (shaded histogram, $n=9$), than from rearings in which the patches were kept isolated (stippled histogram, showing the number of species in all 4845 four-patch permutations of the single-patch control rearings). Right panel: combining the resource patches in sets of four increased the dominance of the superior competitor and decreased the total number of species emerging from 13 to 10 in the pooled material (line with open symbols, resource patches combined in sets of four patches; black symbols, resource patches kept in isolation). (Data from Hanski 1987; J. Kouki & I. Hanski, unpublished data)

often necessary simply because the patches are so small that they are quickly depleted; longer movement distances are expected where the density of resource patches is lower. In the case of resource patches that are used for reproduction, such as larval host plants for herbivorous insects, an important reason for movements between patches is the 'spreading-of-risk' principle (Den Boer 1968). The same principle may explain movements between habitat patches, especially the smaller ones, which approach in extent single resource patches and are often ephemeral. Since the pioneering studies by Brown (1951) and Southwood (1960), ecologists have known that insect species using more temporary resource or habitat patches move more than species using more stable patches. In the case of habitat patches, with locally breeding populations, a major determinant of between-patch movement rate is mortality during migration (Comins *et al.* 1980). Lower density of habitat patches generally increases migration mortality and hence favours reduced movements. In summary, movement rate is expected to increase or decrease with patch density depending on patch sizes.

3. LOCALIZED INTERACTIONS IN RESOURCE PATCHES

Many species of plants and animals are mobile during some stage of their life cycle but much more sedentary during other stages. What are the population dynamic consequences of such behaviour? Research conducted over the past 15 years has attempted to answer this question for single-species dynamics, predator–prey dynamics, and for competing species.

De Jong (1979) originally showed how increasing the variance in the density of competing individuals among resource patches has a generally stabilizing effect on single-species population dynamics (see also Ives & May 1985; Hassell & May 1985). Spatial variance in density may go some way of explaining why complex population dynamics appear infrequent in insects (Hassell *et al.* 1976; Turchin & Taylor 1992), despite their often high intrinsic rates of population increase and strongly nonlinear competition. Current theory about predator–prey dynamics emphasizes the stabilizing effect of variation in the risk of predation among host individuals, most naturally generated by spatial variation in density (Hassell & Pacala 1990). The reason for enhanced stability in this case is increased competition among predators with increasing predator density (Taylor 1988; Kretzschmar & Adler 1993). Spatial aggregation of the prey may have an additional stabilizing effect by bringing more prey individuals into competition amongst themselves. Models of interspecific competition have demonstrated that independent aggregation of competitors among resource patches facilitates coexistence, fundamentally because such spatial aggregation increases the strength of intraspecific competition in relation to the strength of interspecific competition (Hanski 1981; Atkinson & Shorrocks 1981, Ives & May 1985; Ives 1991). Figure 1 reports the results of an experiment demonstrating how intraspecific aggregation facilitates coexistence in an assemblage of several competitors.

Conclusion 1. Stability of single-species, predator–prey and competitive dynamics is generally enhanced by aggregated spatial distributions, provided that, at equilibrium, the level of aggregation (variance-to-mean ratio) increases with mean density (Kretzschmar & Adler 1993), and provided that in the case of two or more species the spatial distributions of different species are not completely correlated. Aggregated spatial distributions of species among resource patches are likely to contribute significantly to the great numbers of insect species in many terrestrial habitats (May, this symposium).

4. METAPOPULATION DYNAMICS

By metapopulations I refer to assemblages of local populations living in discrete habitat patches and connected by some movement of individuals between the patches (Hanski & Gilpin 1991). The metapopulation notion involves an explicit separation between two spatial scales, the local (within habitat patch) and metapopulation scales. Figure 2 describes a range of modelling approaches to metapopulation dynamics. The following discussion is focused on the way the spatial locations of local populations are modelled.

(*a*) *Spatially implicit approaches*

Spatially implicit metapopulation models are based on two ideas, Levins's (1969) notion of a metapopulation as a 'population of populations', and the general idea of metapopulation persistence at a balance between local extinctions and colonizations. In the spatially implicit models, each local population is equally connected to each other (as are individuals in an ideal population), and hence their spatial locations are effectively ignored.

Assuming that the probability of local extinction increases with decreasing population size and hence with decreasing size of habitat patches, and that the probability of colonization increases with increasing strength of between-patch contacts and hence with increasing patch density, the well-known Levins model (1969, 1970) makes the following key prediction (Hanski 1991):

Conclusion 2. Long-term persistence of a metapopulation requires that the habitat patches are sufficiently large and that their isolations are not too great.

Prediction 2 and indeed the underlying theory has close parallels in the epidemiological literature, where it has been found both theoretically and empirically that many disease agents will not persist in low-density host populations (Anderson & May 1991).

The Levins model and other 'patch' models (Hanski 1991) describe only the presence or absence of local populations in habitat patches. This simplification has been relaxed in structured metapopulation models, which incorporate explicitly local dynamics and migration (Hanski 1985; Hastings & Wolin 1989; Hastings 1991; Gyllenberg & Hanski 1992; Hanski & Gyllenberg 1993, Hanski & Zhang 1993). Structured metapopulation models exhibit more complex dynamics than patch models, with the possibility of alternative stable equilibria.

Conclusion 3. Metapopulations in which migration is substantial enough to affect local dynamics may have alternative stable equilibria due to the rescue effect (Hanski 1985, 1991; Hanski & Gyllenberg 1993) and local Allee effects (Gyllenberg & Hanski 1992; Hanski & Zhang 1993).

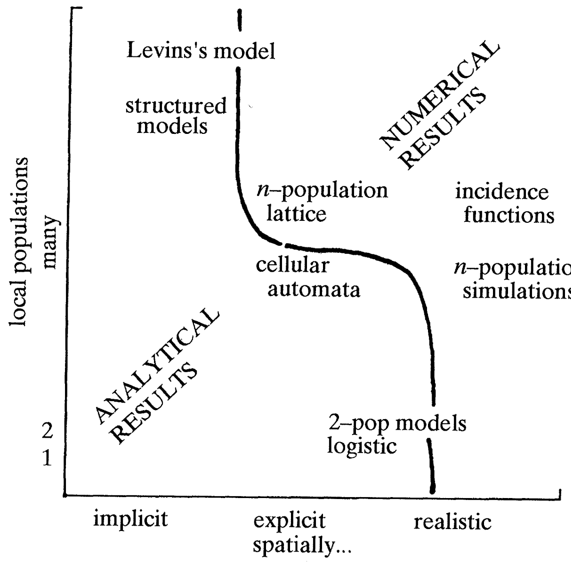

Figure 2. Different approaches to modelling of metapopulation dynamics. For further discussion see Hanski & Gilpin (1991) and Hanski (1994*b*).

(*b*) *Spatially explicit approaches*

The assumption of equal connectance among local populations is unrealistic for most metapopulations: movements are generally distance-dependent. A general modelling approach taking this into account assumes that local populations occupy sites, or cells, on a regular lattice.

Modelling spatial locations explicitly may lead to qualitatively new results. Thus, while Reeve (1988) found that connecting locally unstable predator–prey populations with migration in a spatially implicit island model did not stabilize the metapopulation, Hassell *et al.* (1991) and Comins *et al.* (1992) found such stabilization, on a sufficiently extensive lattice, when migration was restricted. Wilson *et al.* (1993) obtained similar results for an individual-based predator–prey model, in which lattice locations were occupied by single individuals rather than local populations. Hassell *et al.* (1991) reported a range of dynamical behaviours, including 'spatial chaos' (spatio-temporal heterogeneity of abundance in a uniform environment), a moving spiral pattern and a fixed pattern, with constant abundance differences among physically identical lattice sites. It would appear that of these dynamical behaviours 'spatial chaos' would be most robust against changes in model assumptions (e.g. environmental stochasticity, irregular versus regular placement of populations).

Conclusion 4. Distance-dependent migration in a large collection of individuals or local populations may generate spatio-temporal variation in population density in a uniform environment and may stabilize an otherwise unstable interaction.

Spatial variation in density in these models is not due to diffusive movement of individuals only. In a

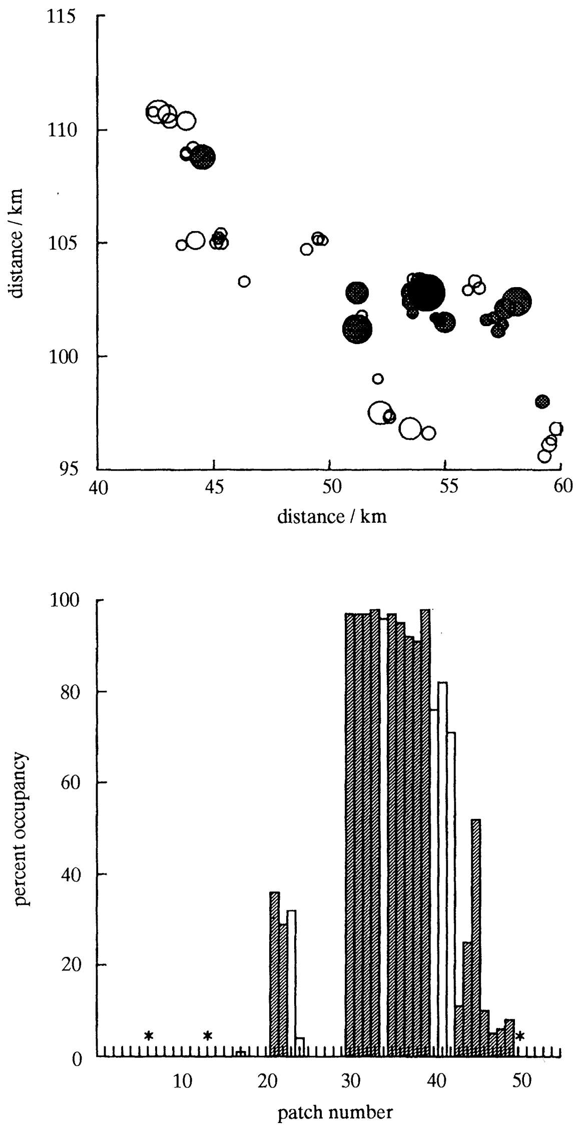

Figure 3. Comparison between the predicted and observed expansion of the butterfly *Hesperia comma* in a network of habitat patches in which the species spread from 3 occupied patches in 1982 (black dots on the map) to 21 occupied patches (shaded) in 1991 (Thomas & Jones 1993). The histogram shows the frequency of predicted occupancy in 1991 in 100 independent simulations of a spatially realistic metapopulation model (Hanski & Thomas 1994). Shaded columns and the asterisks indicate the patches which were occupied in reality. In the histogram, the patches have been arranged roughly in the order of their occurrence from the top-left to the bottom-right corner on the map.

deterministic Lotka-Volterra model, diffusive migration does not generate spatial heterogeneity (Okubo 1980) and the neutrally stable Lotka-Volterra interaction is not stabilized. In the models of Hassell *et al.* (1991) and Wilson *et al.* (1993), metapopulation stabilization is due to local oscillations and stochasticity in a discrete space, breaking up the metapopulation into quasi-independent subpopulations. In classical 'diffusive instability' (Okubo 1980; Kareiva 1990, and references therein), diffusion generates spatial heterogeneity in a system in which there is a stable attractor in the absence of diffusion.

(*c*) *Spatially realistic approaches*

(i) *Simulation models*

For the purposes of predicting transient and equilibrium dynamics in particular metapopulations we need spatially realistic models, in which the areas, exact spatial locations and possibly other characteristics of habitat patches and local populations can be incorporated. This can be achieved in simulation models of n connected local populations (McKelvey *et al.* 1993; Lodge 1993; Hanski *et al.* 1994; Hanski & Thomas 1994).

As an example, I refer to an eight-parameter simulation model which has been parameterized for several butterfly metapopulations (Hanski & Thomas 1994; Hanski *et al.* 1994). In the case of the silver-spotted skipper, *Hesperia comma*, Hanski & Thomas (1994) estimated the parameter values from one metapopulation in the U.K. and used these values to predict the transient dynamics in an independent network of habitat patches, in which *H. comma* has been expanding (Thomas & Jones 1993). The match between the predicted and observed expansion is good (figure 3), suggesting that a model of this type can be used to make quantitative predictions for management purposes (Hanski & Thomas 1994).

Simulation models can also be used to explore more general questions, even if one is restricted to specific examples. Figure 4 gives two examples of metapopulation dynamics in declining networks of habitat patches. For the sake of realism and concreteness, the examples are based on a real butterfly metapopulation (Hanski *et al.* 1994) and the calculations were accomplished with the model referred to in the previous paragraph. In one case, the fraction of occupied patches remained high and the metapopulation survived, in each replicate simulation, for 100 generations. In the second simulation, with the risk of patch disappearance being independent of patch size, the fraction of occupied patches started to decline when less than 30 patches were left, and by generation 60 some of the replicate metapopulations had gone extinct (figure 4). Some replicate metapopulations persisted until generation 100, but only just, and it is clear that all of them were doomed to extinction.

Conclusion 5. Many metapopulations may presently occur in networks of habitat patches which are not adequate for long-term persistence. In the absence of any positive management actions, these metapopulations are slowly declining to extinction.

(ii) *Incidence function models*

The general incidence function model is a linear, first-order Markov chain with two states, the presence or absence of a species in patch i. It is assumed that if patch i is currently empty, it has a constant probability C_i of becoming colonized in unit time, and if patch i is currently occupied, it has another constant probability E_i of becoming empty. The incidence of the species in patch i, defined as the stationary probability of occupying patch i, is then given by

$$J_i = C_i/(C_i + E_i). \qquad (1)$$

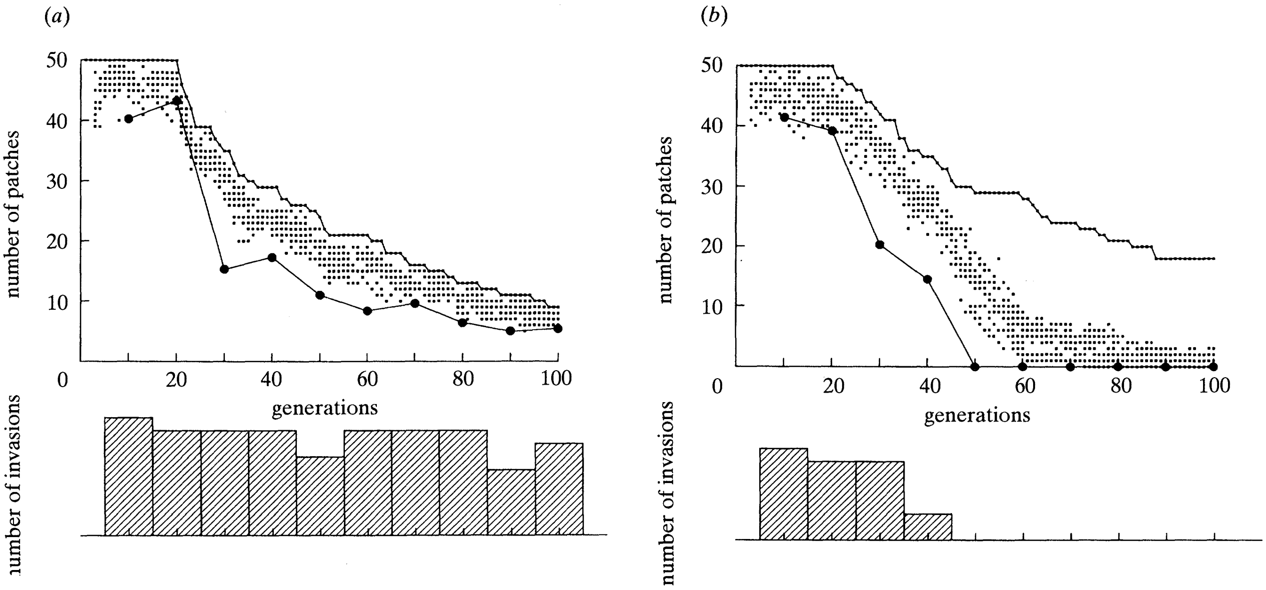

Figure 4. Metapopulation dynamics in declining networks of habitat patches. Results are based on the spatially realistic simulation model described in § 4*c*i, which was applied to the real 50-patch network occupied by the butterfly *Melitaea cinxia* (Hanski *et al.* 1994). In two sets of simulations, I assumed that starting in generation 21, all but one of the habitat patches had a constant probability of disappearance, which was either the same constant for all the patches (*b*) or greater for smaller patches (*a*). The upper lines give the decline in the number of patches in existence, and the dots show the numbers of occupied patches in ten replicate simulations. The lower line shows the mean number of occupied patches after 100 generations in successful establishments of the metapopulation following introduction to one large patch (population A in Hanski *et al.* 1994). The histogram gives the fraction of ten independent attempts to establish the metapopulation from this large patch that were successful.

To construct a quantitative model, we need to make specific assumptions about how various patch attributes affect the probabilities C_i and E_i. Table 1 summarizes some possible simple assumptions, appropriate for different kinds of situations: forms A and B for mainland–island metapopulations, in which all migrants come from a permanent 'mainland' population (as in the island biogeographic theory of MacArthur & Wilson (1967)); C and D for metapopulations without a mainland, and without (C) or with (D) 'rescue effect' (which decreases the effective extinction rate due to immigration; Brown & Kodric-Brown 1977; Hanski 1991; Hanski & Gyllenberg 1993). The models which these assumptions lead to (table 1) may be fitted to empirical presence–absence data using nonlinear regression with maximum likelihood estimation. In some cases (B and C), all model parameters may be estimated independently using presence–absence data only; in other cases (A and D), some extra information is needed because some parameters occur as a combination in the incidence function (table 1). For more details see Hanski (1994*a*).

Having estimated the parameter values of the extinction and colonization probabilities in equation (1), we may iterate numerically the transient and equilibrium dynamics of the species in the original or modified network of habitat patches, or in some entirely different set of habitat patches, to answer very practical questions about metapopulation dynamics. I have obtained encouraging results with this approach for a range of metapopulation structures as reported elsewhere (Hanski 1992, 1993, 1994*a*).

Conclusion 6. Generalized incidence functions may be fitted to readily available data on patch occupancy to estimate the parameters of the extinction and recolonization rates. Using these parameter values, one may

Table 1. *Specific assumptions about extinction* (E$_i$) *and colonization probabilities* (C$_i$) in equation (1) and the consequent incidence function model

($M_i = \gamma \Sigma p_j A_j \mathrm{e}^{-\beta d_{ij}} = \gamma S_i$; $y' = y/\gamma$.

Type of metapopulation: (A) mainland–island, islands equally isolated from the mainland; (B) mainland–island, islands vary in isolation from the mainland; (C) 'Levins metapopulation', with variation in patch sizes and isolations; (D) as (C) but with 'rescue effect'.)

	E_i	C_i	incidence function	reference
(A)	μ/A_i^x	C	$[1 + \mu/CA_i^x]^{-1}$	Hanski (1992)
(B)	μ/A_i^x	$\mathrm{e}^{-\beta Di}$	$[1 + \mu \mathrm{e}^{\beta D_i}/A_i^x]^{-1}$	Hanski (1993)
(C)	μ/A_i^x	$M_i^2/(M_i^2 + y^2)$	$[1 + (1 + (y'/S_i)^2)\mu/A_i^x]^{-1}$	Hanski (1994*a*)
(D)	$(1 - C_i)\mu/A_i^x$	$M_i^2/(M_i^2 + y^2)$	$[1 + y'^2\mu/S_i^2A_i^x]^{-1}$	Hanski (1994*a*)

predict transient and equilibrium metapopulation dynamics in any network of habitat patches.

5. CONCLUSIONS

In the previous sections, I formulated six conclusions about population dynamics in patchy terrestrial environments. Here I emphasize two more general facets of these results.

At the scale of local populations, spatial variance in the density of interacting individuals in resource patches has a generally stabilizing influence on single-species and many-species dynamics. At this scale, spatial variation in density is often largely due to the behaviour of the most mobile stage in the species' life cycle. Optimal foraging models (Stephens & Krebs 1986) do not generally predict strongly aggregated spatial distributions of individuals (or their offspring) in relation to variation in resource availability, because individuals in the crowded patches would generally benefit by moving to the less crowded ones. Thus behaviour that leads to strongly aggregated spatial distributions and thereby, indirectly, to enhanced population dynamic stability is unlikely to have been selected for that reason. More probably, the aggregated spatial distributions reflect a constraint: dispersing individuals are unable to distribute themselves (or their offspring) more evenly, because of general limitations of time and information. An important element in the maintenance of species diversity may thus be constrained (suboptimal) movement behaviour of individuals in patchy environments.

Kareiva (1990) has deplored the 'disappointingly primitive' empirical investigations of population dynamics in spatially heterogeneous environments, which he contrasts with the achievements of the more mathematically minded ecologists working in this area. The contrast may not be as great as Kareiva suggests, but if and when a gap between theory and experiments exists, one culprit must be the general scarcity of biologically significant and realistically testable model predictions. There are exceptions, of which Andow *et al.*'s (1990) analysis of range expansion is a fine example. Metapopulation models are currently making recommendations about what should be measured in the field to test model predictions. These recommendations and predictions can be made more sophisticated without making them too complicated, using for instance the incidence function approach. The dual challenge in this field, as indeed in any field in ecology, is to maintain the momentum in the direction of making and testing interesting predictions, and at the same time to strengthen the links between the more general theory and the models generating particular predictions.

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Discussion

R. J. H. Beverton (*Emeritus Professor of Fisheries Ecology in the University of Wales College of Cardiff, U.K.*). Defining the minimum viable habitat size necessary to conserve the essential features of various kinds of ecosystems is a frequent challenge to the conservation ecologist. Do Professor Hanski's studies offer a new way of tackling this problem?

I. Hanski. Yes, but only to the limited extent of answering Professor Beverton's question for individual species. The spatially realistic incidence function models can be used to assess the risk of metapopulation extinction of particular species living in particular networks of discrete habitat patches, assuming, of course, that the dynamics of these species adequately conform to the model assumptions. The most important assumption is that the metapopulation which is used for parameter estimation occurs at a stochastic colonization–extinction steady-state. With parameter estimates derived from one metapopulation, one may assess transient and steady-state dynamics of the species in arbitrary networks of habitat patches, for instance to answer questions about the minimum viable size of habitat networks necessary to conserve a metapopulation.