Population Dynamics in Spatially Complex Environments: Theory and Data [and Discussion]

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Population dynamics in spatially complex environments: theory and data

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SUMMARY

Population dynamics and species interactions are spread out in space. This might seem like a trivial observation, but it has potentially important consequences. In particular, mathematical models show that the dynamics of populations can be altered fundamentally simply because organisms interact and disperse rather than being confined to one position for their entire lives.

Models that deal with dispersal and spatially distributed populations are extraordinarily varied, partly because they employ three distinct characterizations of space: as 'islands' (or 'metapopulations'), as 'stepping-stones', or as a continuum. Moreover, there are several different ways of representing dispersal in spatially structured environments, as well as several possibilities for allowing environmental variation to come into play. In spite of this variety, a few common themes emerge from spatial models. First, island and stepping-stone models emphasize that little can be concluded from simply recording patterns of occupancy, instead a metapopulation's fate will be determined by the balance between local extinction and recolonization and how that balance interacts with random catastrophes. Island and stepping-stone models also make it clear that the spatial dimension, in particular spatial subdivision, can alter the stability of species interactions and opportunities for coexistence in both predator–prey and competitive systems. Continuum models, which usually take the form of reaction-diffusion equations, address slightly different questions. Reaction-diffusion theory suggests that in uniform environments, certain combinations of local dynamics and dispersal can produce persistent irregularities in the dispersion of species. These striking spatial patterns, which are called diffusive instabilities, can arise from predator–prey interactions, Lotka–Volterra competitive interactions, and from density-dependent population growth in an age-structured population. Moreover, although they differ fundamentally in their structure, the three major classes of spatial models share the common generalization that spatial effects should be expected only for: (i) selected spatial scales; (ii) specific dispersal rates, and (iii) particular patterns of environmental variation relative to the frequency and range of dispersal. The theoretical possibilities are thus contingent on spatial scale and dispersal rates.

Although explicit experimental tests of spatial models are non-existent, a handful of studies report general changes in species interactions associated with manipulations of habitat subdivision. Observational studies with adequate data concerning dispersal and scale are also scarce; but those few observational studies with the appropriate supporting information consistently show profound spatial effects, especially effects due to habitat subdivision.

The challenge for empiricists is to investigate more rigorously the roles of spatial subdivision and dispersal in natural communities. The challenge for theoreticians is to make the empiricist's job easier; this can best be done by delineating when spatial effects are most likely to be influential, and by offering guidance on how to design appropriate experiments. Simply saying that the spatial environment is important is to mouth a platitude: what we need to know is whether this presumed importance amounts to much in natural systems.

INTRODUCTION

Spatial heterogeneity is one of the most obvious features of the natural world. It may also be one of the most important factors influencing population dynamics. Yet until recently, the spatial dimension of species interactions has been neglected or glossed over in both experimental and theoretical investigations. Fortunately, within the past two decades mathematical ecologists have had great success in showing how specific aspects of the spatial environment can alter population and community dynamics. Meanwhile, in stark contrast, experimental ecology has offered only half-hearted and disappointingly primitive investigations into the effects of heterogeneous environments on population dynamics (Doak *et al.* 1991).

The mismatch between theory and experiment in the area of spatial effects may be because of the fact that spatial models have become so numerous, diverse and complex, that it is difficult to identify which theoretical results (if any) are pertinent to particular systems. The goal of this paper is to narrow the gap between theory and experiments regarding the implications of the spatial dimension for population

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Table 1. *A categorization of spatial models according to the manner in which the spatial dimension is represented. The table selects only the most recent models whenever there are multiple publications dealing with essentially similar formulations*

Island models

Andreasen & Christiansen (1989). The effect of population subdivision on the spread of a disease is examined.

Burkey (1989). A stimulation model is used to predict how the degree of habitat fragmentation and rate of migration interact to determine a specie's probability of extinction.

Chesson (1981). Stochastic versus deterministic models for spatially distributed single species models are contrasted.

Chesson (1985). The effect of environmental variability on the coexistence of competitors that occupy patchy environments is examined.

Chewning (1975). Conditions under which migration can stabilize predator–prey interactions are specified.

Comins & Noble (1985). Coexistence of competitors is shown to be promoted by random environmental variability spread over a spatially distributed system, as long as there is a modest rate of dispersal.

Diekmann, Metz & Sabelis (1988*a*). A detailed analysis of how within-patch dynamics and between-patch dispersal processes interact to determine the stability of a predator–prey–plant interaction.

Diekmann, Metz & Sabelis (1988*b*). The above detailed model is reduced to three ordinary differential equations that are meant to capture the key ingredients of the system without requiring any reference to spatial details.

Gurney & Nisbet (1978). Fluctuations in a predator–prey system are predicted on the basis of migration and extinction, total number of patches, and patterns of environmental variability.

Hanski (1983). Coexistence of competitors is analysed by using a metapopulation model, with special attention to the importance of the relative timescales of within-patch versus regional processes.

Harrison & Quinn (1989). The effect of correlated environments and the persistence of metapopulations is examined via stochastic simulations.

Hastings (1977). The stability of a predator–prey interaction in a subdivided environment is analysed with respect to dispersal rates and the timecourse of local within-patch dynamics.

Hastings (1978). The stability of one predator-two prey interaction in a subdivided environment is examined.

Hastings & Wolin (1989). A metapopulation model is analysed in which subpopulations face random disasters as a function of local population size (and hence patch 'age').

Hilborn (1975). A simulation is used to investigate how dispersal between 'cells' influences the stability of predator–prey interactions, modelled after Huffaker's laboratory system.

Kuno (1981). The effect of dispersal on rate of population growth in a temporally and spatially varying environment is examined.

Levin (1974). The effect of subdivision on pairwise predator–prey or competitive interactions is analysed.

Nakano (1981). The importance of dispersal for population regulation is assessed using connected systems of ordinary differential equations.

Pulliam (1989). The consequences for population regulation of consistence differences in habitat suitability ('sources' versus 'sinks') plus density-dependent dispersal are examined.

Quinn & Hastings (1987). Models that predict the effects of spatial subdivision on single-species dynamics are reviewed.

Reeve (1988). The effect of environmental variability and dispersal on the stability of subdivided host–parasitoid systems is examined.

Reddingius (1970). An age-structured simulation model for the dynamics of a subdivided population subject to random catastrophes suggests that subdivision enhances the stability of the population.

Sabelis & Laane (1986). A detailed simulation of a predator mite–prey mite interaction exhibits stable limit cycle behaviour on a regional scale (averaged over all patches), although locally all subpopulations are doomed to extinction.

Shorrocks, Atkinson & Charlesworth (1979). The effect of transient heterogeneous habitat patches on coexistence in a competitive system are examined.

Slatkin (1974). Competition in a subdivided environment with extinction and recolonization is analysed.

Takafuji, Tsuda & Miki (1983). Simulations are used to explore the role of migration in stabilizing a predator mite–prey mite–plant interaction that consists of numerous patches (plants), each of which can be overexploited by the prey mites.

Vance (1984). The contribution of dispersal to the stability of a metapopulation is analysed.

Stepping-stone models

Crowley (1977). The effects of spatial correlation in environmental disturbances are analysed with respect to how organisms are themselves distributed among different patches.

Crowley (1985). The effect of dispersal rates and the arrangement of patches (or cells) on predator–prey stability is examined.

Doak (1989). The effect of various degrees of habitat clustering on spotted owl persistence is examined.

Fujita (1983). The interplay of migration rates, number of patches, and within-patch dynamics in determining the persistence of a predator–prey–plant interaction is explored.

Nachman (1987*a*, *b*). A stochastic simulation is used to study the effects of patch number and dispersal rates on the temporal fluctuations exhibited by an acarine predator–prey system.

Ziegler (1977). By stimulating a predator–prey interaction with emigration from patches occurring only during specific stages in a patch's cycle of occupancy, the effect of predator and prey dispersal rates on the regional persistence is analysed.

Continuum models

Andow, Kareiva, Levin & Okubu (1991). A simple population growth and diffusion model is applied to three well-documented case studies of ecological invasions.

Table 1. (*cont.*)

Comins & Blatt (1978). The ability of a heterogeneous environment to stabilize predator–prey interactions is analysed, and interpreted in terms of a 'refuge'.

Diekmann (1978). Integral equations are used to model the spatial spread of epidemics.

Hardin, Smith & Namba (1990). The impact of different patterns of dispersal on population persistence and extinction is analysed by using integrodifference equations.

Hastings (1982). The stabilizing influence of diffusion in a spatially varying environment is analysed for single species models of density-dependent population growth.

Hastings (1991). Analysis establishes the possibility of diffusive instability for single-species age-structured population dynamics.

Kishimoto (1982). Lotka-Volterra models of three species systems (3 competitors, 2 predators and 1 prey, or 1 predator and 2 prey) are analysed for the conditions that lead to diffusive instabilities.

Ludwig, Aronson & Weinberger (1979). Reaction-diffusion models are used to ask what is the critical size of a forest patch required to support a spruce budworm outbreak, and how wide a barrier is needed to contain a budworm outbreak.

McMurtrie (1978). A wide variety of reaction–diffusion models are analysed for critical patch size phenomena, diffusive instabilities, and potential stabilizing effects of patchiness. In addition to simple diffusion various forms of density-dependent and biased movement are considered.

Mimura (1984). Diffusive instabilities in three and four-species competitive interactions are analysed.

Mimura & Kawasaki (1980). Spatial segregation for two competing species is established assuming the presence of a cross-diffusion term, which means that individuals of one species 'repel' individuals of the other species.

Mimura & Murray (1978). The conditions that lead to diffusive instabilities in pairwise predator–prey or plant–herbivore interactions are identified.

Murray, Stanley & Brown (1986). The rate at which 'waves' of rabies will spread through fox populations is analysed by using a simple epidemiological model plus diffusion.

Namba (1980). The implications of density-dependent dispersal for the stationary spatial distribution of populations is explored.

Namba (1989). Reaction–diffusion models of competitive interactions are analysed, with special attention to repulsive movement (cross-diffusion and density-dependent diffusion) in a spatially heterogeneous environment.

Namba & Mimura (1980). Reaction–diffusion models are used to examine competition between two species in a spatially heterogeneous environment.

Okubo, Murray & Williamson (1989). A reaction–diffusion model is used to describe the invasion of grey squirrels into England, and their 'wavelike' displacement of red squirrels.

Shigesada, Kawasaki & Teramoto (1987). The speed with which an invading species expands its range in a heterogeneous environment is calculated.

Skellam (1951). A pioneering analysis of waves of invasion, critical habitat size, and competition in heterogeneous environments by using reaction–diffusion equations.

Turchin (1989). The implications of aggregative movement for plant-herbivore interactions are explored by using reaction–diffusion models.

van den Bosch, Zadoks & Metz (1989). The waves of invasion for a wide variety of age-structured populations are analysed by using integral equations.

Yachi, Kawasaki, Shigesada & Teramoto (1989). A reaction–diffusion model of rabies epidemics in which all classes of hosts (susceptible, infected, infectious) are allowed to disperse, creating irregular oscillating travelling waves of infection.

dynamics. I will first review the theory, emphasizing the structure and assumptions of models, as well as major recurring predictions. This leads naturally to a discussion of data, and the extent to which 'spatial theory' has been vindicated by field observations or experiments. To show the difficulties in designing experiments to test spatial models, I will highlight two investigations from my own laboratory. Finally, I will end with an agenda for future research, both empirical and theoretical.

AN OVERVIEW OF MATHEMATICAL MODELS CONCERNING ECOLOGICAL INTERACTIONS IN PATCHY ENVIRONMENTS

The burgeoning literature concerning metapopulation models, patch dynamics, and spatially distributed species interactions has spawned several superb reviews (Levin 1976; Taylor 1988, 1990; Hastings 1990; Reeve 1990; Harrison 1991). To avoid duplicating those earlier reviews, I will gloss over mathematical details and emphasize instead what I feel are the major messages of importance for experimentalists.

(*a*) *How do models represent spatially complex environments?*

The most fundamental distinction between different models of heterogeneous environments is the manner in which the spatial dimension is represented (table 1). The most common approach is to imagine the world subdivided into a large collection of patches, each of which include internal dynamics and are collectively coupled together through one common pool of dispersers. Such models do not have an explicit spatial dimension because there is no specification of the relative distances between patches, instead, all patches are equally accessible to one another. Movement occurs when individuals leave patches at some rate, enter a 'bath' of dispersers, and are then redistributed among patches (usually randomly). The key feature of these '*island models*' is population subdivision. By contrasting population fluctuations is an ensemble of islands as opposed to a single island, it is possible to learn how spatial subdivision alters a system's behaviour. One can also use island models to investigate the effect of between-patch dispersal on ensemble dynamics. However, it is important to remember that because island models have no explicit spatial dimension, dispersal rates refer to the fraction of individuals that move, not to the distances that individuals move.

A second way of representing the spatial environment involves '*stepping-stone models*', in which the world is again divided into patches, but the patches now have fixed spatial coordinates. Stepping-stone models are thus effectively island models with an explicit spatial dimension. Because patches are assigned actual positions in stepping-stone models, these models can be used to contrast the consequences of long-range versus short-range dispersal. The presence of a spatial coordinate system also enables one to introduce environmental variability with spatial structure (i.e. spatial autocorrelation).

The final way of treating the spatial dimension is to represent space with a continuous coordinate system along which populations interact and disperse. These so-called 'continuum models' typically take the form of partial differential equations, or more specifically reaction-diffusion models. Here, 'reaction' refers to the mathematical description of local population growth, and 'diffusion' refers to the mathematical description of dispersal. In most reaction-diffusion models the environment is assumed to be homogeneous, and the questions of interest concern what types of spatio-temporal patterns in population density emerge as a result of combining dispersal with local dynamics. To address this issue, reaction-diffusion models have typically used standard continuous-time Lotka-Volterra representations of local dynamics, with diffusion occurring at a constant rate (which corresponds to an assumption of random motion). However, several recent models have relaxed the assumption of purely diffusive dispersal and examined the consequences of movement that varies with population densities (see, for example, Turchin (1988); Shigesada *et al.* (1979)) or habitat quality (see, for example, Shigesada *et al.* (1987)). Continuum spatial models have also been developed for organisms that reproduce at discrete intervals (Kot & Schaffer 1986; van den Bosch *et al.* 1989).

Each of the above three representations of space has its own advantages and disadvantages: island models lend themselves to analytic solutions, stepping-stone models are probably most easily applied to field data, reaction-diffusion models provide a particularly powerful and compact notation. In some cases different approaches can be formally related to one another; for example, reaction-diffusion models can arise as limiting cases of stepping-stone models (Okubo 1980, 1986). A major gap in the theoretical literature is the absence of comparisons between the different approaches when they are applied to identical ecological processes (exceptions are Chesson (1985); Comins & Noble (1985); Fujita (1983)).

Although the language surrounding spatial models emphasizes 'patchiness' and 'heterogeneity', most models assume that all patches in an ensemble are the same; similarly, most reaction-diffusion models assume the environment is uniform in space. Population densities may vary from position to position, or from patch to patch, but such variation typically results from external perturbations that are equally likely everywhere, but happen to occur by chance in only a few locations at any one time. In other words, the vast theoretical literature on ecological interactions in 'patchy' environments generally does not treat habitats with consistent differences. The heterogeneity in these models results from the interplay of spatial subdivision and transient perturbations, not from permanent spatial heterogeneities. It would be more accurate if we described these models as analyses of 'subdivided' or 'spatially extensive' environments, rather than of 'patchy' or 'heterogeneous' environments (exceptions include Comins & Blatt (1978); Namba (1989); Namba & Mimura (1980); Shigesada *et al.* (1987); Pulliam (1989)).

(*b*) ***Incorporating biological detail and environmental variability into spatial models***

After the mathematical portrayal of space has been selected, there still remain several fundamental decisions regarding model structure. A particularly key decision concerns the detail with which species or populations are described, ranging from recording presence or absence (Levins 1970; Slatkin 1974; Hanski 1983; Horn & MacArthur 1972), through keeping track of population densities (Hastings & Wolin 1989; Reeve 1988; Vance 1984), to a complete age-structured representation of populations (De Blasio & Lamberti 1979; Hastings 1990). Another crucial distinction between spatial models is whether environmental variation is introduced. Although the earlier models tended to be deterministic (Levin 1974), recent variants include chance extinctions and disturbances (Hastings & Wolin 1989), or allow parameters such as reproductive rates to vary randomly from patch to patch (Reeve 1988). Moreover, if environmental variation is featured in the model, the subsequent results are often determined by the degree to which the variation among patches is independent (as opposed to correlated) from patch-to-patch (Crowley 1977; Harrison & Quinn 1989). Since dispersal is the process that connects different patches (or different positions in a continuum), mathematical representations of the dispersal process play a central role in the development of spatial models. The major distinctions are whether dispersal depends on density, and whether the direction of movement is influenced by the quality of habitats.

The different ways of representing space, keeping track of populations, dealing with environmental variability, describing dispersal, and portraying dynamics within patches, together combine to yield an assortment of models that is overwhelming in its variety.

(*c*) *Some general results from island and stepping-stone models*

Many patch models are concerned with the dynamics and persistence of single-species populations that are subdivided to varying degrees. These models, often referred to as 'metapopulation theory', have been applied to longstanding debates about density-dependence and population regulation (den Boer 1970; Reddinguis & den Boer 1970; Kuno 1981), and have been consulted for guidance on matters of conservation in fragmented habitats (Burkey 1989; Doak 1989; Gilpin 1988; Quinn & Hastings 1987). When populations are subdivided, the risk of extinction is the result of two opposing forces: (i) because fragmentation creates smaller populations within each patch, demographic stochasticity and loss of genetic variability enhance extinction risks; (ii) because fragmentation may create statistically separate subpopulations, ensembles of subpopulations could enjoy a lower collective risk of total disaster (since it is unlikely that all fragments would suffer catastrophes simultaneously). The net effect of subdivision will depend on the magnitude of dispersal relative to environmental variation, the life history traits that determine the force of demographic stochasticity, and the likelihood of inbreeding depression. Given these contingencies, it is obvious that one cannot make blanket statements about the effects of fragmentation on a population's persistence. However, metapopulation models do make the generally useful point that we can expect to find vacant patches even if habitat is in short supply. Unfortunately, this idea has not always been appreciated by resource managers (USDA Forest Service 1988), who too often neglect the implications of a dynamic turnover in patches because of extinction and recolonization (Doak 1989).

Community ecologists have used island and stepping-stone models to explore possible contributions of the spatial dimension to competitive coexistence. If competitive interactions are subdivided into different patches and disturbances (or extinctions) are imposed randomly, a species that is an inferior competitor when confined to a single patch can gain an advantage if it is an especially good colonist of newly vacant patches (Horn & MacArthur 1972; Slatkin 1974; Hanski 1983). In general, the appropriate mix of subdivision (or patchiness) plus disturbance and dispersal can promote coexistence in competitive systems.

Patch models also have a long tradition of being applied to predator–prey interactions. Here, the central question is whether 'patchiness' can stabilize predator–prey systems that would otherwise fluctuate wildly. The original impetus for this theoretical inquiry were laboratory experiments, especially Carl Huffaker's (1958) investigation of predator–prey dynamics in a patchy laboratory microcosm. Huffaker found that a predator mite and its prey mite persisted longer in spatially complex than in simple environments. Although his experiment has found its way into most ecology textbooks, Huffaker's results are actually much weaker than is often realized: they were unreplicated, the persistence observed was for only three oscillations, and only one female mite made it through each trough in the oscillations. More convincing evidence of spatial effects was reported by Pimental *et al.* (1963) using an interaction between flies and parasites in which the number of small 'fly boxes' and their degree of connection were manipulated. Several other laboratory studies of predator–prey systems have documented the importance of physical refugia for prey persistence, a situation that may be interpreted as a special kind of 'patchiness' (see, for example, Gause (1934); Flanders & Badgley (1963)).

Although the experimental data may be ambiguous, models that these experiments have inspired make it unequivocally clear that spatial subdivision can stabilize predator–prey interactions (Chewning 1975; Comins & Blatt 1974; Hilborn 1975; Zielger 1977; Nachman 1987*b*). However, models also have made it clear that there are circumstances under which spatial subdivision has no effect on stability, or even reduces stability (Allen 1975; Crowley 1981; Reeve 1988). Fortunately, it is possible to sort out the different theoretical results attributed to spatial subdivision by considering exactly how the different subpopulations of predators and prey are connected. In particular, the key requirements for spatial subdivision to stabilize predator–prey systems are: (i) population densities must fluctuate asynchronously in different patches; (ii) predator and prey dispersal rates must be above some minimal rate (otherwise patches suffering on extinction would not be recolonized), and (iii) predators must not disperse so effectively that they inevitably find prey as soon as the prey colonize vacant patches (Reeve 1990; Taylor 1988). When these criteria are met, spatial subdivision promotes stability because it provides prey with a refuge from attack.

(*d*) *Key results from reaction–diffusion theory*

Reaction-diffusion equations have a rich tradition in mathematical biology (Murray 1989), but are not widely appreciated by field ecologists. This is unfortunate because these models can be used to generate baseline predictions of what to expect when populations interact and disperse without any complications (such as patchiness or subdivision) in the spatial dimension. In other words, reaction-diffusion equations represent a sort of null model for spatially distributed population dynamics; they inform us of the spatial patterns that develop because of random motion and population growth alone. Moreover, if we relax the assumption of constant diffusion and spatial homogeneity, reaction–diffusion models become tools for investigating heterogeneity in any form, not just as 'stepping stones' or 'islands' (see Banks *et al.* 1985, 1987).

One of the most intriguing predictions from reaction–diffusion theory is that species interactions in homogeneous environments can generate permanent spatial patterning. This patterning, or 'diffusive instability', arises when there is some sort of local activation due to one component of the system, and a longer range inhibition due to another component (Meinhardt 1982). The key idea is that an interaction

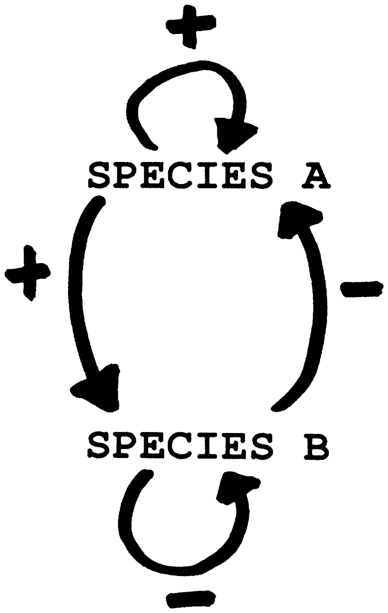

Figure 1. A graphical depiction of what is meant by an activator–inhibitor system. Each arrow shows how a change in the population at the tail of the arrow will alter the rate of population growth at the point of the arrow, all evaluated at equilibrium ((+) represents an increase in the rate of population growth and (−) represents reduction in the rate of population growth). In more technical jargon, the signs on the arrows correspond to the signs of terms in the jacobian matrix for the system.

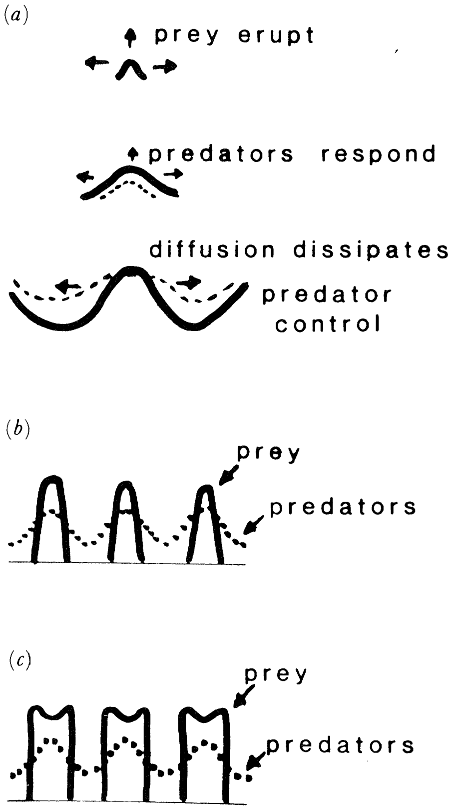

Figure 2. (*a*) How a diffusive instability gets initiated following a small perturbation for a predator–prey system. (*b*) One example of the sort of final stable spatial patterning that is possible for predator–prey diffusive instability. (*c*) Another example of spatial patterning due to diffusive instability in predator–prey systems. The only difference between figures (*b*) and (*c*) is that in (*c*) the prey are 0.01 times as mobile as in (*b*). For many geometries of habitat and ratios of dispersal rates, the patterning could involve much sharper peaks.

which is stable in the absence of dispersal can produce regular or bizarre spatial variations in densities when dispersal occurs. For pairwise species interactions, there is a simple rule of thumb for deciding whether diffusive instability is plausible, the interaction must be an activator–inhibitor system (see figure 1), and the inhibitor must diffuse substantially faster than the activator. To understand how diffusive instability generates spatial patterning, it is useful to consider a concrete example, such as predator–prey interactions in which the prey represents an activator, and the predator an inhibitor. First of all, note that to satisfy the 'activator–inhibitor criterion' (figure 1), increases in prey density above the equilibrium must promote further production of prey and predator; whereas any increases in predator density above the equilibrium must reduce further production of predators and of prey. (We should expect this criterion to be naturally met by many predator–prey systems.) In the absence of dispersal, the positive feedback from the prey (i.e. activation) and the negative feedback from the predators (i.e. inhibition) counteract one another to produce a stable equilibrium. However, when dispersal (diffusion) is added to the system, and the predators wander away from localized prey eruptions, the system can be destabilized. In particular, as prey densities increase and predators respond, some of the predator's inhibition is dissipated because the predators diffuse away from prey eruptions; the key to this 'dissipation' is sufficiently more rapid predator than prey diffusion (see figure 2*a*). It is important to emphasize that for such patterns to arise predator movement need not be purely random or diffusive (although this is usually the assumption pursued in the models); spatial patterns can erupt even if predators tend to move in a biased fashion toward peaks in prey density, as long as there is still some diffusive leakage of predators away from regions of high prey density (Kareiva & Odell 1987). The net result can be fixed spatial predator–prey patterns as shown in figures 2*b* and 2*c*.

The convenient notion of an activator–inhibitor system breaks down for communities of species that cannot be summarized by a simple diagram such as figure 1 (Evans 1980). None the less, when we try to understand the diffusive instabilities that arise in multispecies interactions, we can usually identify some sort of 'inhibition' that is dissipated away from perturbations by dispersal (Mimura 1984; Mimura & Kawasaki 1980; Kishimoto 1982). For example, diffusive instabilities arise in competitive systems when there are two species that cannot coexist unless a third species is also present; that third species is the 'inhibitor' that reduces the other two species to sufficiently low densities that they can coexist, and it is the inhibition of this third species that is dissipated by diffusion (Mimura 1984). In the absence of dispersal, these particular three-species competitive systems attain a stable equilibrium, but with dispersal and a perturbation complex spatial patterns can be generated. Similarly, the diffusive instability that arises in single population models with age-structure involves the dissipation of a stabilizing influence because a particular age class is especially mobile (Hastings 1991). Although this discussion is abstract, the possibility of diffusive instabilities can be shown for a wide variety of ecological systems, ranging from age-structured density-dependent population growth, to predator–prey interactions, to competitive systems that involve three or more species (two-species competitive interactions cannot produce diffusive instabilities unless they include age-structure). I suspect the possibility of diffusive instabilities can also be established for plant–herbivore and host–pathogen interactions. What makes diffusive instability so interesting is that it provides a mechanism for creating persistent spatial variation in population densities without any underlying environmental variation. Indeed, the opportunities for diffusive instability are widespread in nature; the interesting question is, to what extent does this mechanism for pattern formation contribute to the clumped patterns of population dispersion we observe in natural populations? Perhaps much of the patterning attributed to underlying environmental mosaics could be more parsimoniously explained by diffusive instabilities. Or more realistically, perhaps environmentally driven spatial variation in population density is amplified by the mechanism of diffusive instability.

A second phenomenon of interest in reaction–diffusion models is the existence of travelling waves of population densities, or trains of travelling waves. Travelling waves occur when organisms invade a new habitat and then reproduce and disperse (Andow *et al.* 1991; Murray 1988; Okubo *et al.* 1989), or when a disease epidemic is initiated from a single point in space and spreads outward (Murray 1986; Murray *et al.* 1988; Yachi *et al.* 1989). It is often possible to express the speed at which a travelling wave of an invading population should spread as a function of basic life history traits; this calculation may thus usefully summarize the invasiveness of a species in terms of measurable parameters (Andow *et al.* 1991). Predator–prey interactions with diffusion can also produce what look like waves of predators chasing prey, even though both predators and prey move randomly (Dunbar 1983; Murray 1989). Especially complex propagating waves appear when reaction–diffusion models include what is called 'cross-diffusion', or diffusion at a rate that depends on the product of species densities (Murray 1989); cross-diffusion can be used to model predators that actively pursue prey and prey that attempt to evade predators.

A final feature of reaction–diffusion systems is that they generally predict spatial gradients in population densities as a function of habitat geometry. For instance, if a population is confined to a small habitat with diffusive losses across the boundaries of the habitat, there will be a critical patch size below which the population cannot sustain itself (Kierstead & Slobodkin 1954; Skellam 1951; McMurtrie 1978). Moreover, for larger habitats, population densities will attain spatially heterogeneous profiles that are functions of the shape of habitats, the size of habitats, and movement behaviour at habitat boundaries (Turchin 1988; Okubo 1980). The initiation and final patterning due to diffusive instabilities will also be strongly influenced by the size and geometry of habitats. For instance, if we imagine species interacting in a habitat whose boundaries are relatively impermeable (i.e. no-flux boundary conditions), then it is possible for habitats to be too small to allow for the development of spatial patterning through diffusive instability (Murray 1989). In sufficiently large habitats with complex geometries, diffusive instability is likely to produce remarkably intricate chequerboards of peak and trough densities, ranging from 'spots' to 'bands' to 'paisley' mosaics (Murray 1989).

(*e*) '*Pseudospatial*' *models*: *aggregation and species interactions*

Several models deal with heterogeneity by assuming a particular pattern of spatial covariation in species densities, and then attempting to deduce consequences for temporal dynamics. Usually these models have focused on the consequences of aggregation for competitive (Atkinson & Shorrocks 1981; Ives 1988, 1991*a*; Shorrocks *et al.* 1979) or host–parasitoid interactions (Pacala *et al.* 1990; Hassell & Pacala, this symposium; Murdoch & Oaten 1989; Ives 1991*b*). I do not view these aggregation models in the same spirit as the theory discussed above because they assume one panmictic population. Instead of analysing spatially distributed population dynamics, aggregation models examine the temporal consequences of a behaviour that happens to be expressed in the spatial dimension. There is no parameter that reflects a dispersal rate in aggregation models, and there is no sense in which population dynamics are subdivided or spread out over space. Thus when considering this class of models, it is important to realize that 'heterogeneity' refers to the experience of individuals in the interacting populations, but not to well-defined subpopulations. None the less, the approaches used to uncover the effects of aggregative behaviour may suggest ways in which explicit spatial models can be collapsed into more tractable difference equation and ordinary differential equation models.

(*f*) *The recurring theme of critical rates, critical scales and critical geometries*

Mathematical models make it clear that simply by adding a spatial dimension and dispersal to population processes (while holding all other aspects of the ecology the same), population dynamics can be altered fundamentally. Unstable interactions can be made stable (Reeve 1990), competitive exclusion can be thwarted (Hanski 1983), stable interactions can be made unstable (Allen 1975; Crowley 1981; Reeve 1988), and spatially homogeneous systems can be turned into highly patterned or spatially heterogeneous systems (Hastings 1991; Murray 1989). These different possibilities depend on the details of dispersal rates and the spatial scale over which population dynamics are considered. For example, if patchiness is to have any effect on predator–prey dynamics there must be sufficiently many patches that are far enough apart that their dynamics are somehow asynchronized; on the other hand the patches cannot be so widely separated that dispersal is inadequate to recolonize empty patches. Similarly, for patchiness to alter the outcome of competitive interactions, inferior competitors must be sufficiently more mobile than superior competitors, and disturbances must interrupt local within-patch dynamics sufficiently frequently relative to the speed of the exclusion process (Hanski 1983). Finally, for the spatial dimension to produce spatial patterning, the relative diffusion rates of interacting species must exceed some critical ratio (Murray 1989). One clear message of this theory is that although experimentalists can expect important changes in population dynamics due to spatial subdivision or the spatial dimension, such effects will be attained only at certain spatial scales and only for certain dispersal rates.

AN OVERVIEW OF EMPIRICAL EXAMINATIONS OF SPATIAL THEORY

Theoreticians are not the only ones interested in habitat subdivision. Indeed, field biologists often attribute key features of natural populations to the influences of spatially heterogenous environments. For example, in a review of field studies that focused on arthropods and were published between 1975 and 1989, Doak *et al.* (1991) found 62 'data papers' concerning the impact of patchiness on species interactions. Unfortunately, the data in these papers do not offer much insight regarding the applicability of island and stepping-stone models. One problem is that over half of the reviewed studies failed to report the number of patches, the size of patches and the distance between patches; since theory predicts that the effects of patchiness depend on its spatial scale, this lack of information concerning the scale of the investigations hinders our ability to interpret the data that were collected (Addicott *et al.* 1987). A more forgivable shortcoming of patch studies is the absence of between-patch dispersal rates; since collecting these data is a major undertaking it is not surprising that researchers rarely assess dispersal. None the less, without quantitative measurements of dispersal we can never know whether so-called patches reflect genuinely subdivided populations.

Field evaluations of reaction–diffusion models are almost unheard of, probably because the theory itself remains esoteric. The best that has been done with reaction–diffusion theory is to estimate parameters in simple invasion models, and ask whether the models effectively predict observed rates of spread for invading populations of red squirrels (Okubo *et al.* 1989), or cabbage butterflies and muskrats (Andow *et al.* 1991). The problems with these analyses include large gaps in the data such that some critical parameter must be guessed (Okubo *et al.* 1989), matches between model and reality that are often ambiguous (Andow *et al.* 1991), and an assumption of a uniform environment that cannot possibly hold at the scale relevant to most ecological invasions (Andow *et al.* 1991). Ironically, reaction–diffusion models receive much more empirical attention in developmental biology (see, for example, Meinhardt (1982)) than in ecology, even though there is no consensus about what chemical 'species' should be measured when studying developmental processes. In contrast, applying reaction–diffusion models to predator–prey interactions should be comparatively straightforward, since it is obvious that the densities, 'reaction kinetics' (birth, death, consumption, etc.) and diffusion rates of the predator and prey are what need to be evaluated.

Ecologists are proud of the fact their science has become experimental. However, when it comes to even the best-known theory of species interactions in subdivided environments, the number of field experiments can be counted on one hand. This is unfortunate, because varying the spatial arrangement of habitats in some controlled manner is the only way to determine whether subdivision fundamentally alters the dynamics of populations. The few field studies that include such manipulations have generally found an 'effect of subdivision'. For example, when Hanski (1987) divided a fixed amount of liver into either 1, 2, 4, 8, or 16 patches, he found that coexistence occurred more frequently among competing carrion flies in the highly subdivided treatment than when the liver was undivided. Quinn & Robinson (1987) subdivided annual grassland into 2, 8 or 32 subunits and observed higher diversity of flowering plants in the subdivided grasslands (summed over all patches) compared to the single large patches (although total area remained the same). Kareiva (1987) found that aphids attained localized outbreaks far more frequently in subdivided than in continuous strips of habitat. The only experimental investigation that has failed to detect an effect of subdivision was a study of a subtidal snail whose population dynamics were unaltered by the degree to which artificial habitat plates were fragmented (Quinn *et al.* 1989).

In addition to controlled experiments, there are several observational studies that have taken advantage of naturally occurring variation in habitat mosaics to assess the significance of habitat division and geometry (Pokki 1981; Fahrig & Merriam 1985; Jennersten 1988; Franklin & Forman 1987; Quinn & Harrison 1988; Sousa 1979; Solbreck & Sillen-Tullberg 1990). In all but one of these studies (Solbreck & Sillen-Tullberg 1990), the authors conclude that the degree to which habitats are subdivided or isolated from one another, significantly alters the density, dynamics or diversity of residents. Further support for the importance of spatial structure comes from a handful of quantitative investigations that have documented a pattern of within-patch extinctions and between-patch dispersal events that could only be captured by an island or metapopulation model (Addicott 1978; Hanski & Ranta 1983; Bengtsson 1989).

I believe that the above collection of field experiperiments and observational analyses make a strong case for the importance of spatial subdivision in population and community dynamics. However, none of the evidence is compelling vindication of any particular model or theoretical prediction. Simply documenting an effect of patchiness is a long way from testing models that predict particular shifts in dynamical behaviour as a result of changes in dispersal rates, or in the geometry of a spatial mosaic. Before one could convincingly test any of the existing island or stepping-stone models, one would need to know a good deal about dispersal rates, within-patch dynamics, frequencies and dispersion of catastrophes, and the spatial structure of environmental variability. Moreover, when we turn our attention to real systems, rarely will one model cover the full range of processes that are likely to interact with habitat subdivision; instead we are likely to find ingredients at work that are the focus of many different spatial models (e.g. stabilization due to asynchronous fluctuations, bizarre inhomogeneities due to diffusive instability, altered vulnerability to extinction because of demographic stochasticity, and so forth). To make concrete the problems that arise when one attempts to apply 'spatial models' to field studies, we now examine in some detail two experiments involving manipulations of habitat subdivision.

TWO CASE STUDIES THAT HIGHLIGHT THE DIFFICULTIES TO BE EXPECTED WHEN 'TESTING' PATCH MODELS

(*a*) *Manipulating habitat subdivision in an insect predator–prey interaction*

From 1982 to 1985 I manipulated the degree of habitat subdivision in a predator–prey interaction by mowing monocultures of goldenrod into either continuous strips of vegetation or fragmented rows of patches (figure 3). The interaction examined was between an aphid that specializes on goldenrod (living its whole life in goldenrod fields) and a ladybird beetle that specializes on aphids, but not necessarily the goldenrod aphid. I initially analysed these experiments with respect to effects on mean aphid density and the likelihood of aphid outbreaks (Kareiva 1987); instead, here I use the data to ask whether habitat subdivision alters the magnitude of temporal fluctuations in aphid density as predicted by predator–prey models. Since the experiment spanned at least eight predator generations and thirty prey generations, the timespan is adequate for quantification of temporal variability. I focus only on aphid densities because ladybird densities are tightly correlated with aphid numbers and yield identical patterns with respect to degrees of fluctuation.

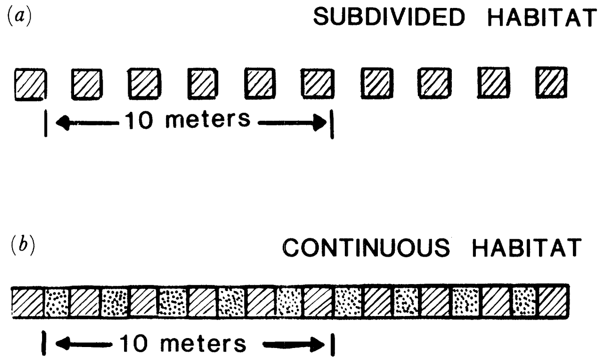

Figure 3. The two treatments used to manipulate habitat subdivision in a ladybird beetle–aphid interaction (from Kareiva 1987): (*a*) is subdivided treatment; (*b*) is undivided treatment. Crosshatched and stipled areas represent monocultures of goldenrod surrounded by mown grass. The distinction between crosshatched and stipled areas is that crosshatched areas were repeatedly censused over a four-year period, whereas the stipled areas are simply part of the treatment background (and were not censused).

My experiment included six ensembles: three ensembles each with ten 'goldenrod islands' (figure 3*a*), and three ensembles each with ten goldenrod quadrats embedded in a continuous goldenrod strip (figure 3*b*). The distance between islands or quadrats was one metre; the difference between the two treatments was the intervening vegetation, the absence of intervening goldenrod in the subdivided treatment hampered the dispersal of both aphids and ladybird beetles compared to their movement in the undivided treatment. By averaging together my censuses from all ten islands or quadrats, I can obtain an ensemble-wide density for aphids and thus a record of population fluctuations at the scale of entire ensembles. The magnitude of fluctuations was identical for subdivided versus undivided treatments (figure 4*a*, paired t-test on coefficients of variation, $p > 0.5$). At first this might seem like a contradiction of theory, since subdivision is generally supposed to be stabilizing. However, when we examine the pattern of fluctuations in individual metre-square islands or quadrats, the absence of any difference in population 'stability' at the ensemble level is no longer paradoxical. In particular, at the level of single patches or single quadrats, we see that in both types of habitat the aphid densities fluctuate asynchronously in space. Such asynchrony is exactly what is needed to promote stability in predator–prey interactions, and thus it appears that even when goldenrod occurs as continuous strips, there is enough asynchrony in dynamics along the strip of goldenrod that stability is promoted. This interpretation is bolstered by the observation that aphid populations do, in fact, appear to fluctuate only modestly at the level of entire ensembles; in particular, the coefficients of variation for ensembles are significantly lower than for patches or quadrats (contrast figure 4*a* with 4*b* and 4*c*; one-way ANOVA, $p < 0.05$). Interestingly, although patches or quadrats within the same field fluctuate out of synchrony, ensembles of patches in different fields fluctuate in remarkable harmony. Thus when aphids are abundant in one field, they are likely to be abundant in a neighbouring field that could be as far as 300 m away; on the other hand, when aphids are abundant in one square metre of goldenrod, that is no indication of likely aphid abundance as close as one metre away. I suspect that the synchronized fluctuations in different ensembles result from the common action of weather on aphid and ladybird demography, whereas the asynchrony among patches in the same fields is driven by the vagaries of aphid colonization,

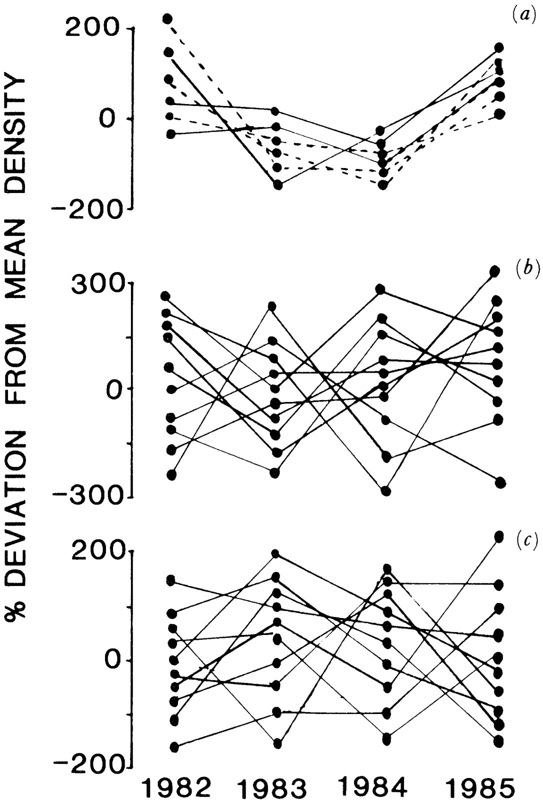

Figure 4. The pattern of temporal variation for aphid populations: (*a*) temporal variation at the level of entire ensembles of goldenrod patches or quadrats; each dashed line represents an ensemble in subdivided habitat, whereas solid lines are for ensembles in continuous habitat; (*b*) temporal variation at the level of single square metre patches of goldenrod from the subdivided habitat treatment; (*c*) temporal variation at the level of single square-meter quadrats of goldenrod from the undivided treatment. These single-patch (i.e. figure 4*b*) or single-quadrat (i.e. figure 4*c*) figures are from only one ensemble; the results from the remaining two ensembles are identical with respect to degree of asynchrony and overall variability as measured by coefficients of variation. To draw these plots only the aphid densities recorded during the week of maximum abundance each summer were used; the pattern is the same if each week's census is included, except a seasonal trend is then embedded in the year-to-year fluctuations.

ladybird searching and heterogeneous goldenrod phenology or chemistry. Clearly scale in terms of the area over which densities are assessed plays a major role in the amount of synchrony detected. Finally, even though subdivision did not appear to alter the severity of fluctuations for ensembles, it did enhance fluctuations at the level of single patches (the coefficient of variation was significantly higher in the thirty patches from subdivided goldenrod than in the thirty patches from undivided goldenrod). The explanation for this effect is that subdividing goldenrod interferes with ladybird searching behaviour, and gives aphids a temporary escape from predation, thereby facilitating localized aphid eruptions (Kareiva 1984, 1986, 1987).

There are several weaknesses in using data from the above experiment to address theories of habitat subdivision. First of all, mowing the goldenrod into patches did more than simply alter the degree of subdivision, it also reduced the total area of goldenrod and changed the competitive circumstances faced by goldenrod plants (which could have changed their quality as aphid food). One option would have been to mow the goldenrod into patches that summed to the same total area as the continuous strips of vegetation; however, pursuing this option would have nearly doubled the spatial dimension spanned by the subdivided goldenrod (i.e. the length of each row of patches). The diameter or span of an experimental unit could alone alter predator–prey dynamics (because span determines the scale over which an environment is sampled as well as opportunities for diffusive instabilities). Finally, the scale at which the experiment contrasts subdivided versus undivided habitats did not produce marked differences in what theoreticians often refer to as ‘the connectedness’ of patches. In other words, from the perspective of dispersal as a process that can synchronize population fluctuations (Taylor 1988), the subdivided and undivided treatments did not differ substantially. (Although, from the perspective of dispersal as a component of foraging behaviour, the subdivided treatment greatly inhibited foraging efficiency.)

One final intriguing feature of this ladybird beetle–aphid interaction is that aphid outbreaks seemed to possess consistently the same ‘wavelength’ or diameter, with a halo of predators aggregated at each aphid peak yet also spilling over to the surrounding vegetation (Kareiva 1984; Kareiva & Odell 1987). It is difficult to determine whether this pattern is stable because aphid populations collapse in late August as goldenrod senesces, making the concept of stability ambiguous. None the less, regular aphid peaks with ladybird halos is exactly what is expected from diffusive instabilities; moreover, the jacobian matrix for the interaction and the ratio of predator–prey diffusion rates are such that diffusive instability is expected (Kareiva 1984). However, because the interaction includes taxis as well as diffusion, a standard analysis does not apply. Numerical simulations verify that one could reproduce the patterns observed in the field with a simple reaction–diffusion–taxis model (Kareiva & Odell 1987), but the results are sensitive to the initial perturbations in aphid density. These data suggest, but do not prove, that diffusive instability occurs in this system.

(*b*) *Resource subdivision in a successional community*

Peter Turchin and I have examined the effects of habitat subdivision at a small scale in an extremely severe environment (Turchin & Kareiva 1989; Kareiva & Turchin, manuscript). In the regions that surround Mount St Helens, we have asked whether dividing fireweed (*Epilobium augustifolium*) into series of isolated stems as opposed to clumps of stems alters the densities of *Aphis varians*, an aphid for which fireweed is the only foodplant in the vicinity of the Mt St Helens blast zone. The question could be framed in terms of the effects of patch size (small versus large) or in terms of divided (many small) versus undivided (one

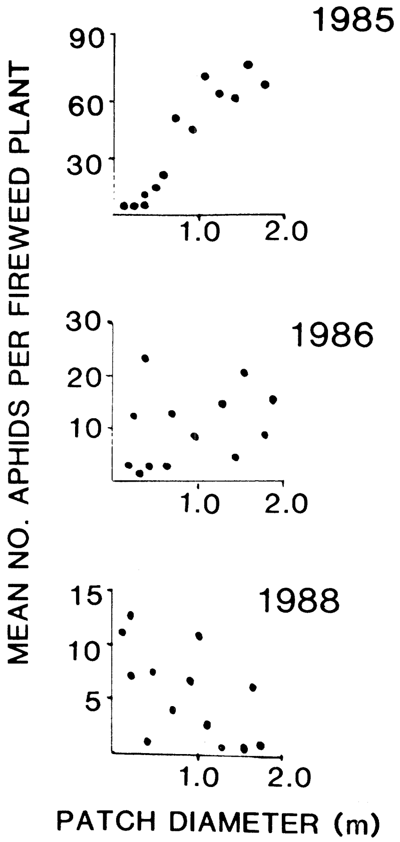

Figure 5. Changes in the relation between aphid density and patch size as succession proceeds at Mount St Helens.

large) habitats. We were initially motivated by reaction–diffusion models that predict strong relations between patch size and the densities of habitat specialists, assuming that the environment surrounding habitat patches is so harsh that individuals wandering out of patches are likely to die (Okubo 1980; McMurtrie 1979). This assumption holds for aphids at Mount St Helens, and preliminary data provided support for the predicted relation between patch size and aphid density (figure 5*a*). This led us to perform experiments in which we manipulated patch size ourselves, as well as continued sampling naturally occurring patches of differing sizes. Our hypothesis that aphids would be more abundant per fireweed stem in large fireweed patches than on isolated fireweed stems was dramatically rejected, but was rejected in a way that is worth examining with respect to tests of spatial theory. First, the pattern we detected by simply sampling fireweed reversed itself between 1985 and 1988 (figure 5*a* versus 5*c*). Secondly, the results of manipulative experiments also changed through time, such that no effect was attributed to patch size in 1986, and a significantly higher aphid density was found on single fireweed stems in 1988 (Kareiva & Turchin, manuscript). We suspect this reversal of patterns is due to the entry of a third species into the fireweed–aphid association. In 1985, colonization of the blast zone was just getting started and ladybird beetles were relatively scarce; however, by 1988 ladybird beetles (mainly *Hippodamia convergens*) were so abundant that they seemed to be the dominant factor regulating *Aphis varians* density (Morris 1990). Thus what was initially a plant–aphid interaction switched to a plant–aphid–predator system. We believe the addition of the third trophic level fundamentally altered the aphid's relation with fireweed patchiness because predation pressure is higher on patches of fireweed than on isolated stems of fireweed (Kareiva & Turchin, manuscript). Of course, to establish rigorously this hypothesis we need to repeat our manipulations in both the presence and absence of predation (an experiment that would require predator removals at a vast spatial scale). None the less, our results suggest that the effects of habitat fragmentation on particular pairwise interactions can disappear or be contradicted when additional species are taken into consideration, a discouraging scenario if we must rely exclusively on experiments to understand the interplay of habitat subdivision and species interactions.

AN AGENDA FOR FUTURE RESEARCH

(*a*) *Empirical challenges*

First, it is worth emphasizing that experimental tests of theory are not tests to see whether theoreticians have done their calculations correctly. They are also not tests of model assumptions, since model assumptions are always 'wrong' to some extent (simplifying assumptions are a key part of model-building). Rather when we test models, we often are asking whether the phenomenon predicted by models emerge as important in natural situations, where numerous other confounding and competing forces act upon the species under study. For instance, a model could be 'mathematically correct', yet offer minimal insight into the workings of real systems simply because the trends it predicted were usually swamped out by factors not included in the model. Thus certain spatial models may fail because they address pairwise species interactions in a world that cannot be described by theory of such a limited scope. Notice that even in failing, models can be instructive (as long as they and their associated experiments are not so silly as to be trivially doomed to failure) – if our existing spatial theory repeatedly fails because its emphasis on pairwise interactions is misplaced, then it is straightforward (albeit cumbersome) to build multispecies and multitrophic level spatial models (see, for example, Mimura 1984; Kishimoto 1982). Good models make it clear in which situations they are most likely to yield insights, or when their predictions will most likely be sharply exhibited. For example, no one conversant with spatial predator–prey theory would expect population subdivision at the level of leaves to have any effect on the stability of coccinellid–aphid interactions; but subdivision at the scale of leaves could have an effect on the microbial predator–prey interactions that take place on plant surfaces. The point is that one does not use experiments to 'keep score' of how many times some model 'wins' or 'loses', a model might repeatedly 'lose' because it was being applied in circumstances where the theory itself predicted ambiguous or weak effects. Rather, one tests a model to gain an appreciation of its range of applications, and to learn directions in which the model ought to be modified.

The key idea in testing a model is to manipulate experimentally some factor identified by the model as important, and to then record responses in terms of the appropriate variables.

The obvious first step is evaluating spatial theory is to manipulate factors that are supposed to alter spatiotemporal dynamics, and to then observe how the manipulation influences patterns of population persistence, of species coexistence, of density fluctuations, or of dispersion. Since all of the existing theory pinpoints dispersal as a process that controls the effects of the spatial environment, manipulations that alter the dispersal rates of species are especially desirable. However, simply performing these manipulations is not enough. The experiments need to be accompanied by measurements of dispersal rates so that it is possible to check whether resulting patterns are in accord with interpretations based on the interplay of local dynamics and dispersal. A particularly clearcut result might be a qualitative shift in the dynamics of a system (e.g. from stable to unstable, or from coexistence to exclusion, and so forth) in the direction predicted by theory upon some manipulation of subdivision. For instance, one's faith in the applicability of spatial models would be greatly enhanced if an unstable predator–prey system could be stabilized by reducing rates of between patch-movement (which in turn converted synchronized fluctuations in subpopulations into asynchronized fluctuations).

Ideally, when we manipulate experimentally habitat subdivision or adjust rates of dispersal, we should impose our manipulations at a hierarchy of scales. Multiple scales are necessary because it will be difficult to know in advance whether one has identified the appropriate scale for detecting a response (Heads & Lawton 1983). Conservationists are already debating the interpretation of habitat fragmentation experiments because of differing opinions about what is the 'right scale' (Murphy 1989). Theory makes it clear that it is not so much a matter of the right scale, as identifying over what scale different spatially mediated processes are likely to be exhibited. For instance, one scale of fragmentation might highlight effects due to changes in predator–prey dynamics, whereas a different scale might reveal changes in extinction due to demographic stochasticity, and yet a different scale would reveal differences in persistence in the face of random catastrophes.

So far, empirical investigations of habitat subdivision have dealt exclusively with single-species dynamics, with pairwise interactions, or with interactions among many species but on one trophic level. Our results concerning fireweed aphids dramatize the problem with such a narrow scope. It may be impossible to extend the understanding we gain from studies of simple interactions to the effects of subdivision on food webs and entire communities. The only way to resolve this problem is to observe the response of entire communities to replicated manipulations of habitat fragmentation. It may be that theory can predict which species should be affected (and which should not) on the basis of dispersal rates and strengths of interactions with other species.

Although the experiments will be difficult, investigations of diffusive instability would be extremely interesting. These would need to be performed in relatively uniform environments (e.g. agricultural fields) and would require substantial modelling before a useful experiment could be designed. Ideally, one would like to have an estimate of the critical size of habitat necessary for patterning before embarking on a manipulative field study. Given such knowledge, one might be able to show that no patterning occurs if the habitat is too small, whereas consistent patterning arises in habitats sufficiently large.

In general, the most fruitful avenue for empirical studies of spatially distributed dynamics is an approach that entails a tight connection between the experiments and specific models (inspired by more general theory). A superb example of what can be gained by this approach is the analyses of competition between annual plants by Pacala & Silander (1990). Pacala (1986, 1987) first analysed the dynamics of competition by using models of varying degrees of abstraction, and found situations that did require spatial models, as well as situations for which dynamics could be captured by a simple representation of mean population densities changing through time. Pacala & Silander (1990) then applied both spatial and non-spatial models to field studies of competition; they found that indeed, spatial models were not necessary for the species under study because spatial clumping was weak and plant performance was especially plastic. The net result is not only well-developed spatial theory for plant competition, but a good understanding of when that theory is necessary and when it is not needed.

Finally, because field experiments concerning habitat subdivision or diffusive instability present vast logistical obstacles and are difficult to replicate properly, there is room for using laboratory microcosms as a testing ground (Forney & Gilpin 1989). This is especially true because the so-called classic experiments in this area (Huffaker 1958) are much more ambiguous than is commonly realized, and did not have the benefit of theory as a guide to their design.

(*b*) *Theoretical challenges*

So far, theoreticians have been busy examining yet another model in which habitat subdivision could alter dynamics, or yet another reaction-diffusion system in which diffusive instabilities could arise. We now need to reconcile this vast diversity of theory into a more unified form and to better address applications of theory to particular systems. More attention to highlighting when spatial theory is not needed would be a great aid to empiricists. It would also be especially useful if a common interpretation could be developed to approximate different 'clusters' of theoretical results, as has been so elegantly accomplished for host–parasitoid aggregation theory (Hassell & Pacala, this symposium). For instance, perhaps some measure of spatial asynchrony might summarize whether habitat subdivision could contribute to predator–prey stability. Another area in which it would pay to synthesize seemingly disparate results is the meeting ground between the spatial models I have reviewed and so-called 'disturbance models' (Fahrig 1989). Although 'spatial theory' and 'disturbance theory' tend to ask different questions, dispersal rates are key in both types of models (as the factor determining how connected are spatially separated population dynamics, or as the factor determining the rate at which disturbances are colonized). A final synthesis that has been repeatedly called for yet never achieved, is linking models of individual foraging behaviour (which predict how animals should search and use heterogeneous environments) with models for population interactions in heterogeneous environments (Hassell & May 1985).

There is need for original theoretical inquiry as well as consolidating existing results. Three relatively unexplored phenomena of potential importance are: (i) the observation that ecological interactions include ingredients acting at multiple scales (Powell 1989); (ii) the implications of nonrandom movement and mortality while animals actively search for habitats in fragmented landscapes, and (iii) the complications that might emerge in multispecies (or food web) interactions as opposed to pairwise interactions. Processes at multiple scales will be especially important in predator–prey interactions, where we often find long-range dispersal in response to regional variation in prey densities layered on top of foraging behaviour that adjusts to prey patchiness at a fine scale. Non-random search becomes an issue when we attempt to apply metapopulation models to conservation questions; such applications need to consider the extent to which details of 'island' geography determine the overall metapopulation dynamics (since it is the detail of habitat arrangement rather than total amount of habitat that is the key scientific question in conservation). Finally, it is important to establish how food web dynamics change in subdivided habitats, since single-species and pairwise species models cannot possibly capture the range of possible effects attributed to spatial subdivision. The limitations of pairwise theory is dramatically shown by analyses of diffusive instability in competitive interactions; whereas diffusive instability can be shown to be theoretically impossible for pairwise competitive interactions, diffusive instabilities easily arise in competitive systems that involve three or more species (Mimura 1984).

CONCLUSIONS

Theoretical support for the importance of habitat subdivision and spatially distributed dynamics is overwhelming. In contrast, experimental evidence is at best suggestive, and not at all illuminating regarding the precise mechanisms by which the spatial environment alters population and community dynamics. In the face of all the other factors that shape population dynamics, we simply do not know the relative role of spatial factors. Only a vigorous and theoretically informed experimental programme will be able to address this question, a question that is central to ecology because of its implications for biodiversity (Pickett & Thompson 1978), resource management (MacCall 1989), and conservation (Wilcove 1987; Quinn & Hastings 1988; Gilpin 1988).

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Discussion

A. Mullen (*Renewable Resource Assessment Group, Imperial College, London, U.K.*). In Professor Kareiva's paper published in the American Naturalist in 1987 he reported a behavioural mechanism whereby ladybirds tend to aggregate in regions of high prey abundance, through net migration. Wouldn't that stabilizing mechanism create a similar 'halo effect' to that he had described today arising from diffusive instability?

P. Kareiva. You are correct in pointing out that our continuum model of predator aggregation due to area restricted search (Kareiva & Odell 1987) does indeed produce a halo of predators surrounding aphid outbreaks. However, if you look carefully at that model you will see that predator movement has two components: (i) a diffusive component, and (ii) a taxis towards regions of increasing prey density. It is the diffusive component that produces the halo (if there were taxis alone predators would all end up piled on top of local peaks in aphid abundance). In fact, I think it is useful to think of something like diffusive instabilities arising in models with aggregation; in such models it will take more than a small perturbation to escape the inhibition due to predators, in part because the 'flux' or movement component of the model contributes to the inhibition. However, just as is the case with conventional diffusive instabilities, diffusion dissipates some of the inhibition and may allow the emergence of spatial patterning. Finally, it is worth emphasizing that most behavioural-based derivations of predator aggregation will yield partial differential equation models that include both a diffusion term and a taxis term.

R. Southwood (*Department of Zoology, University of Oxford, U.K.*). The model described by Professor Kareiva was also proposed by Readshaw (1964) as the mechanism underlying outbreaks of stick insects in Australian forests.

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