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The geometry of coexistence

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Understanding the processes that maintain diversity has been the focus of extensive study, yet there is much that has not been integrated into a cohesive framework. First, there is a separation of perspective. Ecological and evolutionary approaches to diversity have progressed in largely parallel directions. Second, there is a separation of emphasis. In both ecology and population genetics, classical theories favour local explanations with emphasis on population dynamics and selection *within* populations, while contemporary theories favour spatial explanations, with emphasis on population structure and interactions *among* populations. What is lacking is a comparative approach that evaluates the relative importance of local and spatial processes in maintaining genetic and ecological diversity. I present a framework for diversity maintenance that emphasizes the comparative approach. I use a well-known but little-used mathematical approach, the perturbation theorem for dynamical systems, to identify key points of contact between ecological and population genetic theories of coexistence. These connections provide for a synthesis of several important concepts: population structure (source–sink versus extinction–colonization), spatial heterogeneity (intrinsic versus extrinsic) in fitness and competitive ability, and temporal scales over which local and spatial processes influence diversity. This framework ties together a large and diverse body of theory and data from ecology and population genetics. It yields comparative predictions that can serve as guidelines in biodiversity management.

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ADDITIONAL KEY WORDS:—coexistence – polymorphisms – diversity – spatial processes – perturbations – spatial heterogeneity – temporal scale – selection – population structure.

CONTENTS

Introduction 2
Mathematical framework 3
    Perturbation theorem 3
    Biological interpretation 4
    A geometric metaphor for dynamical behaviour 5
Perturbations to monomorphic systems 5
    Allee effects and disruptive selection 5
    Multi-locus systems: epistatic selection 9
    Multi-species systems: priority effects and competitive exclusion 10

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- Time scale of perturbations 12
- Role of spatial heterogeneity 14
- Transition from weak to strong perturbations 14
- Perturbations other than dispersal 15
- Summary and predictions 16

Perturbations to polymorphic systems 17
- Transition from weak to strong perturbations 19
- Consumer-resource systems of high dimension 20
- Summary and predictions 22

Discussion 22
Acknowledgements 24
References 24
Appendix 1 28
Appendix 2 29

INTRODUCTION

Understanding the processes that maintain diversity is a central issue in ecology and evolutionary biology. The issue has been the subject of extensive study, but generalizations have been disproportionately few. Perhaps the most fundamental problem is the separation between ecological and evolutionary approaches to diversity. Implicit in this separation is the idea that processes that maintain diversity at lower levels of organization (e.g. alleles) are different from those that maintain diversity at higher levels of organization (e.g. species).

Yet, well-known explanations for diversity in genetics and ecology reveal a surprising amount of convergence. For example, both identify a basic dichotomy in the way local processes influence diversity.

On the one hand, local processes can bring about coexistence and enhance diversity. For instance, various forms of balancing selection such as heterosis, negative frequency-dependence, and variable selection over time or space promote the coexistence of alleles and genotypes (Futuyma, 1997; Hedrick, 1998). Density-dependent processes such as self-limitation reduce the strength of antagonistic inter-specific (or inter-genotypic) interactions and prevent competitive exclusion or overexploitation of resources (May, 1974; Maynard Smith, 1974). In the absence of forces that ameliorate antagonistic interactions, trade-offs can allow local coexistence. In competitive systems, trade-offs may arise between competitive ability and other life-history traits (Tilman & Pacala, 1993); in consumer-resource systems, trade-offs may occur between virulence and transmission efficiency (Levin & Pimentel, 1981; Anderson & May, 1982) or plant growth and resistance to herbivore pressure (Pacala & Crawley, 1992). Mathematically speaking, all of the above interactions are characterized by local dynamics that admit stable interior equilibria.

On the other hand, local processes can preclude coexistence and eliminate diversity. In such situations, the superior types (e.g. genotypes, species) increase to fixation at the expense of the inferior types. No trade-offs exist that may allow inferior types to coexist with superior types. In other words, local dynamics admit only boundary equilibria. When local dynamics are directional, as in competitive exclusion and directional selection, the genotype or species that is intrinsically superior (e.g. higher competitive ability or fitness) will exclude the others; when local dynamics exhibit threshold effects, such as in priority effects and disruptive selection, the genotype or species that is initially more abundant will displace all others (Begon, Harper & Townsend, 1996; Futuyma, 1997; Maynard Smith, 1998). Thus, systems with directional or threshold local dynamics are expected to be monomorphic.

This dichotomy suggests that the focus should be on the dynamical processes that influence diversity rather than on genetic versus ecological levels of organization. This brings us to the second problem. The classical approach to diversity emphasizes the role of local processes, while the contemporary approach emphasizes spatial processes (Wohrmann & Jain, 1990; Gilpin & Hanski, 1991; Hanski & Gilpin, 1997). Too few points of contact exist between the two approaches to determine how the interaction between local and spatial processes may shape diversity. For example, one would assume that spatial processes drive diversity in situations where local processes constrain it. Yet, it is not immediately clear as to what type of spatial structure and process should operate when local dynamics involve directional or threshold effects. Should the population structure be a source–sink type (Holt, 1985; Pulliam, 1988) or an extinction–colonization (Levins, 1969, 1970) type? What sort of spatial heterogeneity, intrinsic or extrinsic, would be required to maintain diversity? What are the temporal scales over which spatial processes should operate? And, what role, if any, do spatial processes and heterogeneity play in situations where local processes themselves drive diversity?

Clearly, there is much that needs to be integrated into a cohesive framework. The key to such a synthesis is a comparative approach that evaluates the relative importance of local and spatial processes in maintaining diversity.

I use perturbation theory (Hirsch & Smale, 1974; Guckenheimer & Holmes, 1983; Karlin & McGregor, 1972a, b; Levin, 1974, 1976) to establish key points of contact between ecological and population genetic theories on coexistence and diversity. These connections suggest a fundamental dichotomy in how diversity may be maintained in nature. The dichotomy is based on whether diversity is driven by local or spatial processes, the type of population structure and spatial heterogeneity required, and the temporal scales over which local and spatial processes operate. It leads to comparative predictions about diversity maintenance in patchy environments.

MATHEMATICAL FRAMEWORK

The perturbation theorem for dynamical systems (Hirsch & Smale, 1974; Guckenheimer & Holmes, 1983) provides the mathematical basis for the framework I present here. Karlin & McGregor (1972a) and Levin (1974) first pointed out the importance of the principle for biological systems. I extend their work to a broader framework that yields comparative predictions about the roles of local versus spatial processes, spatial heterogeneity, and space–time scaling in maintaining genetic and ecological diversity.

I begin with a description of the perturbation theorem and its biological interpretation. I then illustrate the application of perturbation theory to the two types of biological systems identified above: those in which local dynamics lead to stable polymorphisms, and those in which directional or threshold local dynamics lead to monomorphism.

The perturbation theorem

Let f be a vector field having a finite number of equilibrium points $x_1^*, x_2^*, \ldots, x_n^*$ (or periodic orbits $\lambda_1^*, \lambda_2^*, \ldots, \lambda_n^*$) of $x' = f(x)$. If $x_1^*, x_2^*, \ldots, x_n^*$ are hyperbolic (i.e. linearization in the neighbourhood of each equilibrium yields no eigenvalues of zero real parts in a continuous system, or of absolute value 1 in a discrete system, thus avoiding neutral stability), then each perturbation of f will have a unique equilibrium y_i^* ($i = 1, \ldots, n$) in the neighbourhood of each x_i^* that is both hyperbolic and has the same index (number of eigenvalues, including multiplicities, having real parts < 0 in a continuous system or < 1 in a discrete system) as x_i^*.

Similarly, if each periodic orbit λ_i^* is hyperbolic and has period τ, then there is $\varepsilon > 0$ such that each perturbation of f has a unique, hyperbolic periodic orbit near λ_i^* with the same index as λ_i^* and period in the interval ($\tau - \varepsilon$, $\tau + \varepsilon$).

The term perturbation refers to a perturbation of the vector field by the addition of a relatively small vector field (Abraham & Shaw, 1985). Such a perturbation is caused by a modification of the equations defining the dynamical system, and is hence distinct from perturbations of equilibria via modifications of the state variables (Rosen, 1970). Proofs of the theorem are provided in Hirsch & Smale (1974) and Guckenheimer & Holmes (1983).

Biological interpretation

Consider a spatially structured system consisting of n subunits and m possible types. The subunits can be niches or habitat patches within a population, or local populations and communities within a metapopulation or metacommunity. The m types represent alleles, genotypes or species.

Consider first an uncoupled system whose subunits undergo directional or threshold local dynamics. Each subunit admits a stable, monomorphic equilibrium. However, if the system is spatially heterogeneous different types may fix in different subunits. A stable polymorphism of all m types can occur at the system level if each type goes to fixation within at least one subunit. This can occur as long as the number of types do not exceed the number of subunits in the system ($m \leqslant n$).

Now consider a small perturbation to the above uncoupled system that leads to interactions among the different subunits. Examples of such coupling include dispersal (Levin, 1974, 1976; Amarasekare, 1998), gene flow (Lande, 1979; Slatkin, 1994), refuges from competitors, mutation, recombination or crossover probabilities (Karlin & McGregor, 1971, 1972a, b), small outcrossing probabilities in obligate inbreeders (Eshel, 1972), and storage effects such as seed banks (Chesson & Warner, 1981).

To make more concrete the idea of a small perturbation, let M be a matrix representing the interaction coefficients among subunits. For example, the element m_{ij} represents the interaction between subunits i and j. The perturbation specified by M would be considered small if M is sufficiently close to the identity matrix, i.e. the elements m_{ij} with $i \neq j$ are all sufficiently small as to allow the interaction among units to be slight. The matrix M is irreducible if there is a power M^k whose elements are all strictly positive (Karlin & McGregor, 1972a). Translated to biological terms this means that any type (e.g. genotypes, species) that is present in any of the subunits (e.g. niche, population, community) has a nontrivial probability, k generations into the future, of being present in any other subunit in the system.

The key outcome for coexistence is as follows: if the uncoupled system attains a locally stable equilibrium u^* with each type present within at least one subunit, and if the matrix of interaction coefficients is sufficiently small and irreducible, then the perturbation theorem applies and the coupled system will attain a locally stable equilibrium p^* near u^* in which coexistence of every possible type occurs in every subunit (see also Karlin & McGregor, 1972a; Levin, 1974, 1979).

The perturbation theorem also applies when local dynamics within subunits lead to locally stable polymorphic equilibria. In such situations, small perturbations that link the subunits lead to a stable polymorphic equilibrium in the neighbourhood of the original equilibrium.

In either case, the perturbation to the uncoupled system should be sufficiently small so as not to destroy its structural stability (Rosen, 1970; Hirsch & Smale, 1974; Guckenheimer & Holmes, 1983). Structural stability implies topological equivalence between vector fields of unperturbed and perturbed systems. For example, if the original system had an equilibrium to which nearby trajectories converge, so will the perturbed system. Such equivalence of vector fields is guaranteed only under small perturbations (Rosen, 1970; Guckenheimer, 1979; Abraham & Shaw, 1985). Biologically this means that the perturbation should not disrupt the characteristic dynamical behaviour of the community or population in question, i.e. it should not be so large that a species (or allele) that typically increases when rare goes extinct when rare. Habitat destruction exemplifies the kind of large perturbation that could disrupt the typical dynamical behaviour of a biological system.

A geometric metaphor for dynamical behaviour

The idea that small perturbations lead to stable polymorphic equilibria in the neighbourhood of the original equilibrium is most easily grasped if one visualizes dynamical behaviour in a geometric context. The geometric approach is particularly powerful in discovering common patterns across genetic and ecological systems. Rosen (1970) and Odell (1980) provide an excellent introduction to the topic.

PERTURBATIONS TO MONOMORPHIC SYSTEMS

I present a series of models from ecology and population genetics to illustrate how perturbations enhance local diversity in systems that are typically monomorphic. Perturbations can be of many different types (see above). I focus primarily on dispersal and gene flow since these spatial processes have important implications for diversity maintenance in fragmented landscapes.

Allee effects and disruptive selection in single species populations

Consider a patchy environment inhabited by a set of isolated populations each exhibiting Allee effects. The dynamics of a local population are described by:

$$\Delta x_i = [x_i\,(1 - x_i)(x_i - a)]\ \tau \tag{1}$$

where x_i is the density of the i^{th} population rescaled to vary between 0 and 1, and a is the threshold below which population growth in a patch becomes negative (Lewis & Kareiva, 1993; Amarasekare, 1998; Appendix 1). The quantity τ is the time metric, a composite of the per-capita growth rate, γ, and Δt, the time interval between successive generations. If the initial density is above a, the population increases to carrying capacity ($x_i^* = 1$). If the initial density is below a, the population declines to extinction ($x_i^* = 0$).

Allee effects typically arise due to difficulties in finding mates at low densities (Allee, 1931; Dennis, 1989; Lewis & Kareiva, 1993). This is especially problematic in situations involving reproductive incompatibilities between genotypes.

Allee effects have a profound consequence on diversity. A genotype or species cannot increase when rare, even when it may have a potential growth rate (or fitness) that is greater than a genotype or species that is already abundant. Hence, Allee effects tend to eliminate diversity from isolated populations.

Consider a perturbation that creates interactions among populations. The simplest mathematical representation of the perturbed system is two populations, each exhibiting Allee effects, linked by dispersal:

$$\Delta x_1 = \left[x_1(1 - x_1)(x_1 - a) - \beta_1 x_1 + \frac{(\beta_1 x_1 + \beta_2 x_2)}{2} \right] \tau \tag{2}$$

$$\Delta x_2 = \left[x_2(1 - x_2)(x_2 - a) - \beta_2 x_2 + \frac{(\beta_1 x_1 + \beta_2 x_2)}{2} \right] \tau .$$

The quantity β_i is the per capita emigration rate from population i scaled by the growth rate (Appendix 1). Individuals that emigrate from one patch immigrate to the other patch, with no loss in transit. This is equivalent to the island model of dispersal.

I use the discrete form of the equations to illustrate the generality of the perturbation principle to both discrete- and continuous-time dynamics. When dynamics are discrete, τ is the time interval between successive generations. As $\tau \rightarrow 0$, birth, death, emigration and immigration lead to continuous changes in population density, allowing studies of continuous-time dynamics.

Equation (2) has been studied in detail elsewhere (Amarasekare, 1998). A phase portrait suffices to make the points relevant to the present discussion (Fig. 1a and b). A small perturbation that links populations leads to a stable equilibrium with one population above the extinction threshold (a source, since population growth is positive; *sensu* Pulliam, 1988) and the other below it (a sink, since population growth is negative). Immigration from the source rescues the sink population from extinction. This rescue effect requires spatial heterogeneity in abundances that translates into spatial heterogeneity in fitness. For example, founder effects may initiate some populations above the extinction threshold and others below the threshold. The outcome is stable coexistence of source and sink populations, a situation impossible to achieve in the unperturbed system.

These results are generalizable to a multi-patch environment. The three-patch case is analysed in Appendix 1.

Source–sink dynamics can also enhance genetic diversity. The Allee model above is dynamically equivalent to a multiple-niche polymorphism model (Karlin & McGregor, 1972a, b; Barton & Clark, 1990). For example, consider two homozygous genotypes each locally adapted to a particular habitat type. Each homozygote will thrive in its favoured habitat, but experience an Allee effect in the less favoured habitat because of difficulties in finding mates of the same genotype. In isolated

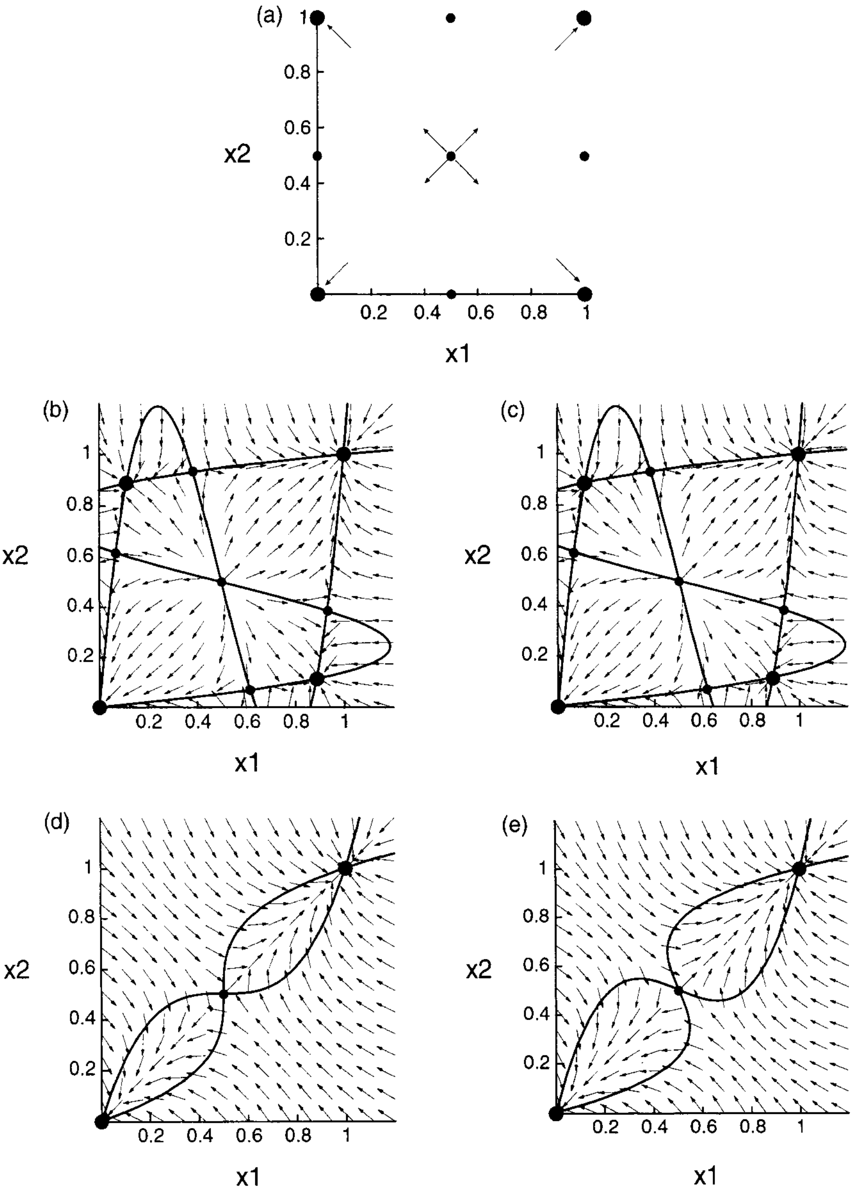

Figure 1. Phase portraits for a two-patch system undergoing Allee dynamics or disruptive selection. Panel *a* depicts equilibria for the uncoupled system ($\beta_1 = \beta_2 = 0$). Stable states are (0,0), (0,1), (1,0) and (1,1); (0.5,0.5) is an unstable node corresponding to the extinction threshold. Panels *b* and *c* show the effect of slight coupling on Allee dynamics ($\beta_1 = \beta_2 = 0.1$) and disruptive selection ($\beta_1 = \beta_2 = 0.2$). In both cases, the boundary equilibria (1,0) and (0,1) have shifted slightly off the axes as a result of the small perturbation. These correspond to a stable polymorphism. With a large perturbation (Allee system: $\beta_1 = \beta_2 = 0.5$; disruptive selection: $\beta_1 = \beta_2 = 0.7$) the polymorphism disappears and the system reverts to monomorphism (panels *d* and *e*). The large perturbation alters the topology of trajectories in the phase portrait. For example, the unstable node which is preserved under the small perturbation changes to a saddle following the large perturbation.

patches disruptive selection will operate, and the genotype better adapted to local conditions will fix. However, if such patches are linked by small amounts of gene flow, each genotype can maintain a small population in the less favorable habitat type. Source sink dynamics can maintain such polymorphisms even when the two homozygotes have equivalent fitness, as long as founder effects cause spatial variation in initial allele frequencies among patches (Christiansen, 1990).

Classical explanations for multiple niche polymorphisms result from spatially variable selection (Levene, 1953; Hedrick, Ginevan & Ewing, 1976; Hedrick, 1986). However, conditions for maintaining such polymorphisms can be quite restrictive (Maynard Smith & Hoekstra, 1980; Hoekstra, Bijlsma & Dolman, 1985). Limited gene flow can broaden the conditions for such polymorphisms in both random mating and inbreeding populations (Christiansen, 1975; Hedrick, 1990).

Partial assortative mating for autosomal dominant genes also creates threshold effects similar to disruptive selection (Karlin & McGregor, 1972a). The two phenomena are actually linked because niche differentiation often leads to assortative mating (Rice & Salt, 1988). For example, a homozygote locally adapted to its niche is more likely to mate with other individuals who utilize the same niche. Small perturbations to such mating systems also lead to stable polymorphic equilibria (Christiansen, 1990).

A third genetic example concerns underdominant chromosomal rearrangements. Certain types of translocations (e.g. reciprocal translocations, Robertsonian fusions) and inversions (e.g. pericentric inversions) lead to a fitness deficit in the heterozygote. Often the heterozygotes tend to be semi-sterile because 50% of their gametes are aneuploid (i.e. have either a duplication or deficiency of the arrangement) and lead to inviable zygotes (Lande, 1979, 1984). Individuals homozygous for the arrangement have normal fitness (Lande, 1979; Coyne, Aulard & Berry, 1991).

Consider a system of uncoupled patches each undergoing disruptive selection for a chromosomal rearrangement. The dynamics of a representative patch are given by:

$$\Delta x_i = [-x_i (1 - x_i)(1 - 2x_i)]\ \tau \tag{3}$$

where x_i is the frequency of the chromosomal rearrangement in the i^{th} patch (Lande, 1979). The time metric τ is a composite of Δt and s, the fitness deficit of the heterozygote relative to the homozygote. The only stable states in this model are fixation or loss of the rearrangement. These are separated by a threshold ($x^* = 0.5$) representing an unstable polymorphism.

This model illustrates the link between Allee effects and disruptive selection. When the rearrangement frequency is low most individuals are homozygous for the normal arrangement, making it difficult for individuals homozygous for the rearrangement to find mates of the same type. This difficulty is likely exacerbated by the fact that chromosomal rearrangements cause no obvious phenotypic effects other than reducing heterozygote fertility (Lande, 1979). Matings between the two homozygote types results in heterozygotes with a fitness deficit. These factors acting together create a positive feedback (Allee) effect that causes the rearrangement to decline further in frequency, leading ultimately to its loss from the population.

Consider now the same system of two patches, coupled by small amounts of gene flow:

$$\Delta x_1 = \left[-x_1(1 - x_1)(1 - 2x_1) - \beta_1 x_1 + \frac{(\beta_1 x_1 + \beta_2 x_2)}{2} \right] \tau$$

$$\Delta x_2 = \left[-x_2(1 - x_2)(1 - 2x_2) - \beta_2 x_2 + \frac{(\beta_1 x_1 + \beta_2 x_2)}{2} \right] \tau \qquad (4)$$

where β_i, $i = 1, 2$ is the fraction migrating between the two patches.

When there is spatial variation such that one patch has a rearrangement frequency above the threshold and the other below the threshold, small amounts of gene flow between patches lead to a stable polymorphism (Fig. 1c). The dynamical behaviour of the model is strikingly similar to the Allee model discussed previously. In each case, the threshold phenomena created by Allee effects or disruptive selection tend to eliminate diversity from local populations. Source–sink dynamics and spatial heterogeneity oppose this tendency and maintain diversity within local populations. The geometric approach reveals a mechanism for diversity maintenance that is common to both genetic and ecological systems.

This mechanism of diversity maintained by source–sink dynamics provides potential explanations for several puzzling observations from nature. For example, animal populations that exhibit partial assortative mating exhibit a high degree of polymorphism (Karlin & McGregor, 1972a) as do obligately selfing plant species (Allard *et al.*, 1968, 1993; Schoen & Brown, 1991; Bonnin *et al.*, 1996) and hermaphroditic animals (Stadler *et al.*, 1995; Viard, Doums & Jarne, 1997). Such polymorphisms in highly inbred organisms cannot be reconciled with the classical explanations of heterosis (Hedrick, 1998) or variable selection in time or space.

Similarly, chromosomal rearrangements typically involve negative heterosis (Lande, 1979, 1984; Coyne *et al.*, 1991), but polymorphisms for such rearrangements do exist in nature, albeit infrequently (Stone, 1955; Coyne *et al.*, 1991). More frequently however, one observes chromosomal races, populations of a given species that are fixed for alternative chromosomal arrangements (Lande, 1979). Moreover, closely related species often differ karyotypically due to fixation of rearrangements (Lande, 1979, 1984). The existence of such karyotypic differences implies an evolutionary transition from one chromosomal arrangement to another, which should be opposed by natural selection given the fitness deficit in the heterozygotes. However, small amounts of gene flow among populations can allow negatively heterotic arrangements to persist stably at frequencies above the extinction threshold. Over time, such rearrangements can be fixed within disjunct populations (Lande, 1979, 1984; Barton & Clark, 1990). More generally, stable polymorphisms exhibiting underdominance are a necessary starting point for understanding the evolution of assortative mating, linkage and dominance (Wilson & Turelli, 1986).

The discussion so far has focused on single species and single locus systems. The perturbation principle applies to multi-locus and multi-species systems as well. I briefly describe two multi-locus models and the relevant biological observations. I will consider multi-species systems in more detail.

Multi-locus systems: epistatic selection

Slatkin (1994) developed a model of complete epistasis. This model was motivated by the evolution of domesticated phenotypes in plants in the face of gene flow from wild relatives. Such evolution requires complex adaptations where several components have to be present simultaneously to accrue an increase in fitness. Local dynamics involve directional selection, and in the absence of gene flow the multilocus genotype that confers the complex adaptation goes to fixation. When perturbed by slight amounts of gene flow, however, the system attains multiple equilibria, one of which is a locally stable equilibrium corresponding to the coexistence of the adaptive genotype with others of lower fitness. This is a case where a perturbation enhances local diversity at the cost of preventing the evolution of an advantageous phenotype.

Asmussen, Arnold & Avise (1987, 1989) and Arnold, Asmussen & Avise (1988) have developed epistatic assortative mating models to explain how permanent non-zero cytonuclear disequilibria (non-random association between diploid nuclear genes and uniparentally transmitted cytoplasmic genes) can be maintained within hybrid zones. When there is no gene flow and assortative mating is not perfect, frequencies of both parental types go to zero (leaving a population of randomly mating hybrids) causing all cytonuclear disequilibria to also decay to zero (Arnold *et al.*, 1988). When modified to include migration of pure parental genotypes, the model predicts non-zero cytonuclear disequilibria as well as the maintenance of both parental types within the hybrid zone. These predictions provide an explanation for the observed disequilibria between nuclear loci and mitochondrial haplotypes in a hybrid population of *Hyla* tree frogs (Lamb & Avise, 1986).

In both these examples, gene flow perturbs systems with local epistatic interactions to produce stable polymorphic equilibria.

Multi-species systems: priority effects and competitive exclusion

In the classical Lotka–Volterra framework, the dynamics of two competing species are given by:

$$\begin{aligned} \Delta x &= [x\,(1 - x - \varphi_x \mathrm{y})]\ \tau \\ \Delta y &= [y\,(1 - y - \varphi_y \mathrm{x})]\ \tau \end{aligned} \tag{5}$$

where x and y are the densities of the two species scaled by the carrying capacity, φ_x and φ_y are the competition coefficients, and τ is the common time metric. When inter-specific competition is stronger than intra-specific competition (φ_x, $\varphi_y > 1$), local dynamics exhibit threshold effects. Then, a priority effect occurs such that the species that has the initial numerical advantage excludes the other species (Fig. 2a). When $\varphi_x < 1$, $\varphi_y > 1$ or vice versa, local dynamics will be directional such that the dominant competitor excludes all other species (Fig. 2b).

Now consider a two-patch system of competitors linked by dispersal. The dynamics are given by:

$$\begin{aligned} \Delta x_i &= \left[x_i\,(1 - x_i - \varphi_{x,i} \mathrm{y}_i) - \beta_x \mathrm{x}_i + \frac{(\beta_x \mathrm{x}_i + \beta_x \mathrm{x}_j)}{2} \right] \tau \\ \Delta y_i &= \left[y_i\,(1 - y_i - \varphi_{y,i}\, \mathrm{x}_i) - \beta_y \mathrm{y}_i + \frac{(\beta_y \mathrm{y}_i + \beta_y \mathrm{y}_j)}{2} \right] \tau,\ i, j = 1, 2;\ i \neq j. \end{aligned} \tag{6}$$

Here β_x and β_y are the species-specific emigration rates scaled by the respective growth rates. An island model of dispersal is again assumed. There are two cases to consider: threshold dynamics ($\varphi_{x,i}$, $\varphi_{y,i} > 1$; $i = 1,2$) previously studied by Levin

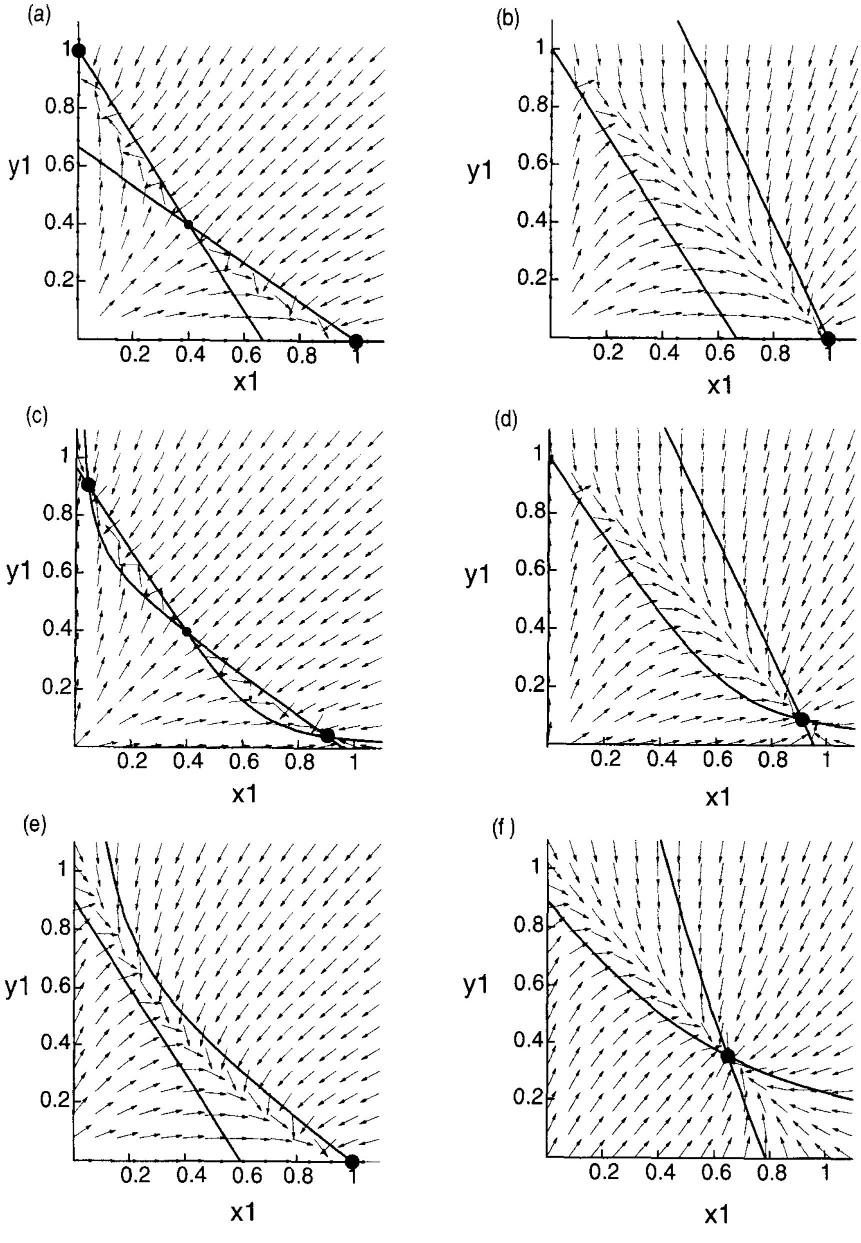

Figure 2. Phase portraits for competing species. Panels *a* and *b* depict the uncoupled systems with threshold ($\varphi_x=\varphi_y=1.5$) and directional ($\varphi_x=0.5$, $\varphi_y=1.5$) local dynamics. In panel *a*, stable states are the two boundary equilibria corresponding to the carrying capacity of each species in isolation. Panel *b* has a single globally stable state (1, 0). With a slight perturbation ($\beta_1=\beta_2=0.1$), stable coexistence of competitors becomes possible (panels c and d). Large perturbations ($\beta_1=\beta_2=0.2$) affect the two systems differentially. In the threshold system, a large perturbation leads to the loss of polymorphic equilibria (panel *e*). In the directional system, the polymorphic equilibrium persists under a large perturbation (panel *f*).

(1974), and directional dynamics ($\varphi_{x,i} < 1$, $\varphi_{y,i} > 1$; $i = 1,2$). For ease of mathematical representation, species are considered to be similar except for their initial densities in the threshold case (cf. Levin, 1974), i.e. $\varphi_{x,i} = \varphi_{x,j} = \varphi_{y,i} = \varphi_{y,j}$ and $\beta_x = \beta_y$. Relaxation of this assumption does not alter the conclusions.

The phase portrait is now multi-dimensional since there are two patches each with two species. It suffices for our purposes, however, to concentrate on a two-dimensional slice through the state space (Fig. 2c). This is the equivalent of having each patch linked to a permanent source population.

When local populations exhibiting priority effects are linked by small amounts of dispersal, stable coexistence of competitors occurs in each patch (Fig. 2c). As with Allee effects discussed previously, coexistence occurs via source–sink dynamics. Each species attains numerical dominance in one patch, but maintains a small number in the other patch via immigration. Spatial heterogeneity in initial abundances is required for coexistence.

When local dynamics are directional, small amounts of dispersal leads to stable coexistence of an inferior competitor with a superior competitor (Fig. 2d). Interestingly, the same result obtains in classical models of migration-selection balance (Wright, 1969). When there is directional selection for the dominant allele, immigration of the recessive allele leads to a stable polymorphism. Unlike in priority effects, spatial variation in initial abundances or frequencies is not sufficient for coexistence. There must be fixed differences among patches that lead to spatial heterogeneity in competitive rankings among species (i.e. $\varphi_{x,i} \neq \varphi_{x,j}$ and $\varphi_{y,i} \neq \varphi_{y,j}$), or fitness differences among competing genotypes. Alternatively, a permanent source population may exist, such as in a mainland-island situation, which may provide a source of immigrants for the inferior competitor.

Species coexistence in highly diverse plant communities is likely to result from such competition-migration balance. For example, tropical rainforests support large guilds of ecologically similar species (Hubbell, 1979; Hubbell & Foster, 1986), as do temperate grasslands (Tilman, 1994). Such diversity is most likely the result of immigration counteracting competitive exclusion (Hubbell, 1979; Hubbell, Condit & Foster, 1990; Tilman, 1994; Kinzig *et al.*, 1999). Similarly, input of seeds from neighboring habitats (spatial mass effect; Shmida & Ellner, 1984) can enhance local diversity in desert herb communities (Shmida & Whittaker, 1981).

More generally, weak coupling and spatial heterogeneity can bring about coexistence even when antagonistic interactions are non-competitive and indirect. For instance, multiple prey species that share a generalist predator may coexist in the face of apparent competition if each species is superior at withstanding predation in a subset of the patches and if coupling among patches is weak (Holt, 1984, 1993; Holt, Grover & Tilman, 1995).

Time scale of perturbations

One important feature of polymorphisms that result from perturbations is that they are not protected (Christiansen, 1990). If one allele is fixed in the population, or if a competitor is at its carrying capacity, other alleles or species cannot increase when introduced as rare. This is to be expected because local processes drive the system towards monomorphism, a force counteracted by perturbations such as

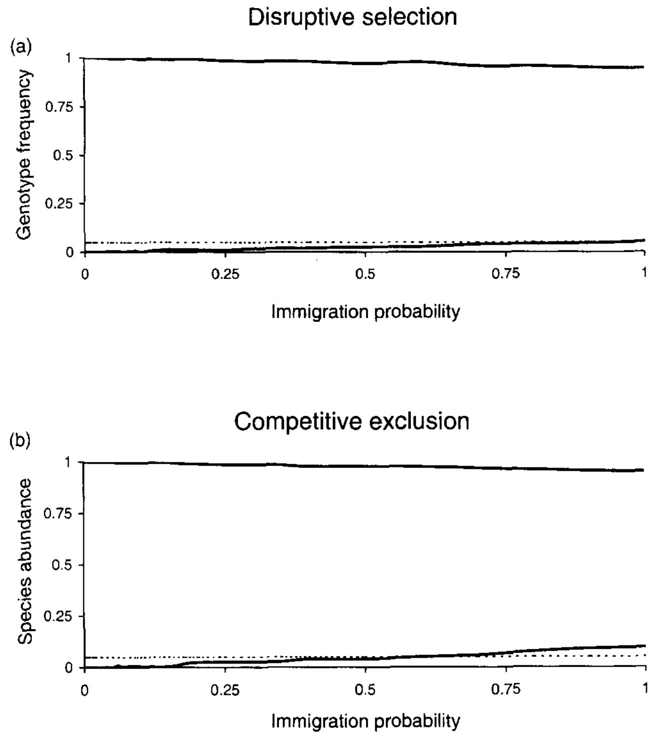

Figure 3. The relative time scales of local and spatial dynamics. Panel *a* depicts threshold local dynamics (disruptive selection), and panel *b*, directional dynamics (competitive exclusion). The y-axis gives the frequencies of two interacting genotypes (panel *a*), or the abundances of two competing species within a patch (panel *b*). The x-axis gives the probability that an immigrant arrives in the patch within a given generation. The dashed line depicts genotype frequency of 5% in panel *a*, and an abundance corresponding to 5% carrying capacity in panel *b*. When immigration is infrequent relative to selection and competition (immigration probability <0.25), the rarer genotype and the inferior competitor are eliminated from the population. Immigration occurring at intermediate time scales may prevent extinction, but the rarer genotype and the inferior competitor cannot maintain a frequency or abundance of 5%. When immigration occurs on the same time scale as selection and competition (immigration probability >0.75), a stable polymorphism results with both genotypes and species maintained within the patch. Parameter values are $\varphi_x = 1.5$, $\varphi_y = 0.5$, $\tau = 0.05$, and $\beta = 0.05$. Local extinction was simulated by setting to zero densities or frequencies falling below 0.001. Immigration was simulated as follows: immigration was allowed if a uniform random number was less than u (u [0,1]). For example, $u < 0.01$ implies immigration on the order of 100 generations, $u < 0.1$, immigration on the order of 10 generations and $u < 1$, immigration every generation. For each immigration probability, genotype frequency or species abundance at the end of 25 000 generations was recorded.

dispersal. This leads to an important question regarding the time scale of perturbations: how frequent should perturbations be relative to local dynamics in order to maintain stable polymorphisms?

Figure 3 illustrates the answer. Stable polymorphisms can be maintained only if perturbations such as dispersal and gene flow occur on the same time scale as local dynamics and selection. Perturbations occurring over longer time scales (e.g. that of extinctions and colonizations; Levin, 1976) cannot counteract the local tendency towards monomorphism.

Role of spatial heterogeneity

The majority of the examples I have presented come from biallelic or two-species systems. This is simply a matter of mathematical convenience. The perturbation principle is generalizable to polymorphisms with multiple interacting entities. If directional or threshold dynamics ensure fixation of one of *m* types within a patch, then a minimum of *m* patches is required to maintain a stable multiallelic or multispecies polymorphism (Karlin & McGregor, 1972a; Appendix 2). This suggests that in monomorphic systems subject to slight perturbations, local diversity will increase in proportion to the degree of spatial heterogeneity in the environment. In systems exhibiting threshold dynamics, local uniqueness (Levin, 1976, 1981) caused by spatial variation in initial allele frequencies or species abundances will suffice. Such intrinsic heterogeneity could result from founder effects or other random factors that are uncorrelated across populations. In systems exhibiting directional dynamics, local uniqueness requires extrinsic heterogeneity i.e. fixed differences in biotic or abiotic factors that create spatial variation in fitness or competitive rankings.

Transition from weak to strong perturbations

A point that has been stressed, particularly with respect to systems with threshold dynamics, is that stable polymorphisms result from *small* perturbations to an initially monomorphic system. This begs the question of what happens to polymorphisms during the transition from weak to strong coupling.

In systems with threshold local dynamics, large perturbations destroy polymorphic equilibria (Levin, 1974; Lande, 1979; Amarasekare, 1998; Figs 1d and e, 2e and f). Monomorphism results from a disruption of structural stability (Rosen, 1970; Guckenheimer, 1979; Freedman, 1987). A sufficiently large perturbation will destroy the topological conjugacy between the unperturbed and perturbed vector fields. For example, as the perturbation reaches a threshold magnitude each stable node merges with the adjacent saddle leading to the annihilation of both. This annihilation, termed a catastrophic event in dynamical systems theory (Hirsch & Smale, 1974; Guckenheimer & Holmes, 1983), leaves only the monomorphic boundary equilibria to which trajectories now converge. In biological terms, large perturbations destroy polymorphisms because they synchronize dynamics across patches, thus destroying the intrinsic spatial heterogeneity created by asymmetric initial conditions. For example, high dispersal will equalize genotypic abundances or competitor densities across patches, converting them effectively into a single, large patch within which local processes of disruptive selection or priority effects will dominate.

In systems exhibiting directional local dynamics, the influence of large perturbations depends on the nature of their interaction with local dynamics. If the interaction between local dynamics and dispersal leads to threshold effects, as happens with classical migration-selection models with directional selection for a recessive allele (Wright, 1931, 1969) and the more recent models of migration–epistatic selection balance (Slatkin, 1994), the transition from weak to strong coupling leads to the loss of the polymorphic equilibrium. If the perturbation does not lead to threshold dynamics as in competition–dispersal balance (Fig. 2f) or migration–selection balance with directional selection for a dominant allele (Wright, 1931, 1969), large perturbations have no impact on the polymorphic equilibrium. This is because the latter systems admit a single, globally stable equilibrium (e.g. fixation, competitive exclusion) in the absence of a perturbation. Unless the perturbation is so extreme as to cause extinction, the transition from weak to strong coupling cannot destroy topological conjugacy.

These considerations suggest that systems with threshold dynamics may be highly sensitive to the magnitude of the perturbation, while systems with directional dynamics may be relatively insensitive to such variation. This difference is directly related to the way in which spatial heterogeneity in fitness or competitive ability arises in the two systems. Intrinsic heterogeneity that characterizes threshold systems is generated by spatial variation in initial conditions, and can be destroyed by a perturbation that synchronizes local populations. In contrast, extrinsic heterogeneity that characterizes directional systems is generated by fixed variation in environmental factors and hence cannot be destroyed by a large perturbation. This suggests that local diversity maintained by perturbations to threshold systems may be lost more easily than that maintained in directional systems. For relatively simple models, the threshold level of perturbation at which local diversity is lost can be derived analytically (Karlin & McGregor, 1972a; Levin, 1974; Lande, 1979); for models admitting more complicated forms of local dynamics and selection, such thresholds have to be calculated numerically.

As noted at the beginning, perturbation theory envisions a spatially discrete (patchy) environment. An important issue therefore is the degree to which the above conclusions depend on the actual spatial structure of the environment. When local dynamics involve threshold effects and the environment is spatially continuous rather than discrete, perturbations may not always lead to coexistence (Levin, 1979; Durrett & Levin, 1994).

Perturbations other than dispersal

Although dispersal is the perturbation illustrated in the above examples, other perturbations such as refuges, storage effects such as seed banks (Chesson & Warner, 1981), and habitat destruction can have the same dynamical effect. For example, both the Allee and competition models can be interpreted in terms of a refuge from strong density-dependence. In the Allee model it is a refuge from the positive density-dependence that occurs at low densities; in the competition model it is a refuge from a strong competitor.

Habitat destruction is another important perturbation. I illustrate its effects using a patch occupancy model developed by Nee, May & Hassell (1996). Consider two mutualistic species. One (e.g. a plant) can survive within a habitat patch for some period of time but needs the other (e.g. pollinator or seed disperser) for reproduction and gene flow, whereas the second species needs the first for both survival and reproduction. Nee *et al.*, (1996) describe the dynamics of the system as follows:

$$\begin{aligned}\frac{dx}{d\tau} &= \alpha_p y + \alpha_d z - \beta_p z x\\ \frac{dy}{d\tau} &= \beta_p z x - \alpha_p y - \beta_d z y\\ \frac{dz}{d\tau} &= \beta_d z y - \alpha_d z. \end{aligned} \tag{7}$$

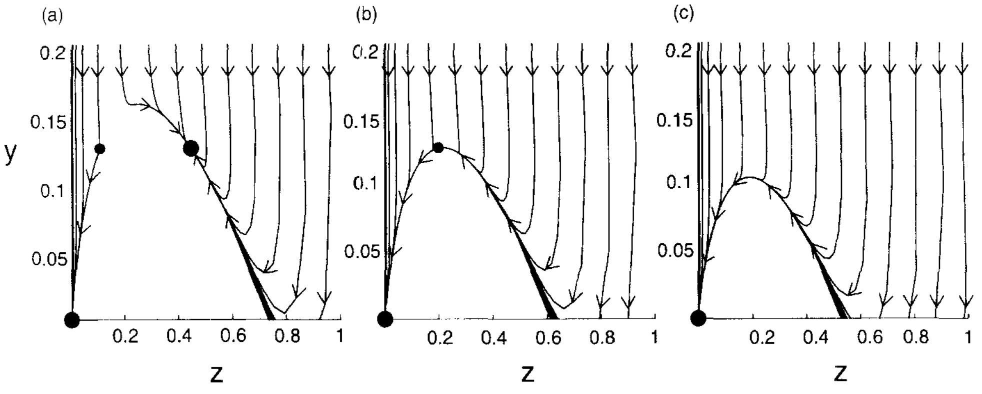

Figure 4. Phase portraits for a patch occupancy model of two mutualistic species. Under small amounts of habitat destruction (panel *a*, $h=0.8$), stable coexistence results. As a critical value of destruction is reached (the eradication threshold $h=0.68$, panel *b*) the two nontrivial equilibria merge and annihilate each other, leading to extinction of the entire metapopulation of mutualists ($h=0.6$, panel *c*). Parameter values are $\beta_p=\beta_d=4$, $\alpha_d=0.5$, $\alpha_p=1.5$.

Here x, y, and z refer respectively to the proportion of empty patches, proportion occupied by the plant only, and the proportion occupied by both plant and disperser. The sum $x + y + z$ equals h, the proportion of habitat suitable for occupation. When there is no habitat destruction, $h=1$. Quantities α and β refer to extinction and colonization rates respectively, and subscripts p and d to plant and disperser.

The phase portrait for this system (Fig. 4a) reveals multiple stable states corresponding to extinction and stable coexistence of mutualists, separated by a threshold (a saddle). The effect of habitat destruction on system dynamics is instructive. The mutualists continue to coexist under small amounts of habitat destruction, but as destruction reaches a particular threshold the coexistence equilibrium and the adjacent saddle merge and annihilate each other in a catastrophic event (Fig. 4b). This leads to extinction of the entire metapopulation of mutualists (Fig. 4c). This is a particularly illuminating example of the effect of large perturbations on systems exhibiting threshold effects, and as Nee *et al.* (1996) point out, a true catastrophe in the biological sense as well.

Summary and predictions

Stable polymorphisms can arise in genetic and ecological systems that are typically monomorphic, provided that the environment is spatially heterogeneous, perturbations exist that create weak coupling among local populations, and perturbations occur on the same time scale as local dynamics. Systems that exhibit threshold local dynamics are sensitive to the magnitude of the perturbation. Transition from weak to strong coupling destroys polymorphisms. Systems exhibiting directional dynamics are, for the most part, resistant to such transitions. These concepts apply to both discrete- (Karlin & McGregor, 1972a, b; Shmida & Ellner, 1984; Christiansen, 1990) and continuous-time systems (Levin, 1974, 1976, 1979; Lande, 1979; Amarasekare, 1998).

These considerations lead to three predictions. First, if source–sink dynamics are maintaining diversity, one would expect genotypes or species to be abundant in some locations of the landscape and to maintain small sink populations in other locations. This should lead to a U-shaped spatial distribution with few or no patches exhibiting intermediate abundances of frequencies. Second, one would expect dispersal to be frequent in that it should occur on the order of the generation time of the organism. In threshold systems one would also expect the number of dispersers exchanged per generation to be quite small. Third, if frequent dispersal is maintaining diversity in sink habitats one would expect isolation to lead to rapid loss of diversity.

PERTURBATIONS TO POLYMORPHIC SYSTEMS

Local processes that promote the coexistence of interacting entities include heterosis, variable selection over time and space, frequency-dependent selection, mutualisms, resource partitioning, and consumer-resource dynamics. These interactions are protected, i.e. genotypes or species can increase when rare. This is in direct contrast to the threshold and directional systems discussed above, where local processes lead to deterministic local extinction of entities that are either rare or have a fitness deficit. Since local processes can maintain polymorphisms even in the absence of perturbations, diversity is most likely lost via stochastic factors such as demographic stochasticity and random genetic drift. What role do perturbations and spatial heterogeneity play in such systems? I focus on consumer-resource systems because they represent a wide variety of biological processes, including plant-herbivore, predator–prey, host-parasite, and plant-pathogen interactions.

Consumer-resource systems exhibit the potential for oscillatory dynamics (Maynard Smith, 1974; May, 1974; Murray, 1993). There is typically a time delay between the growth rate of the resource and the numerical response of the consumer. This in turn leads to periods of overexploitation followed by crashes.

As an example, consider a closed population of predators and prey (modified slightly from Crowley, 1981) whose dynamics are given by:

$$\Delta x = \left[x(1 - x) - \frac{\alpha x y}{x + z} \right] \tau$$

$$\Delta y = \left[-\delta y + \frac{\alpha x y}{x + z} \right] \tau . \qquad (8)$$

Here x and y are the prey and predator densities respectively, scaled by the prey's carrying capacity, α is the maximum uptake rate, δ is the predator death rate relative to the prey growth rate, and z is the prey density beyond which the consumer functional response begins to saturate scaled by the prey carrying capacity.

When the predator nullcline crosses to the right of the hump in the prey nullcline (Fig. 5a), the outcome is a stable focus of predator and prey ($x^* = \delta z/\alpha - \delta, y^* = z(\alpha - \delta - \delta z)/(\alpha - \delta)^2$. However, this outcome is restricted to a limited range of parameter values. As α increases (or z decreases) the predator nullcline moves to the left of the hump in the prey nullcline (Fig. 5b). When α or z attain a critical value a bifurcation occurs, whereby the equilibrium becomes an unstable focus surrounded by a stable limit cycle (Crowley, 1981; Murray, 1993).

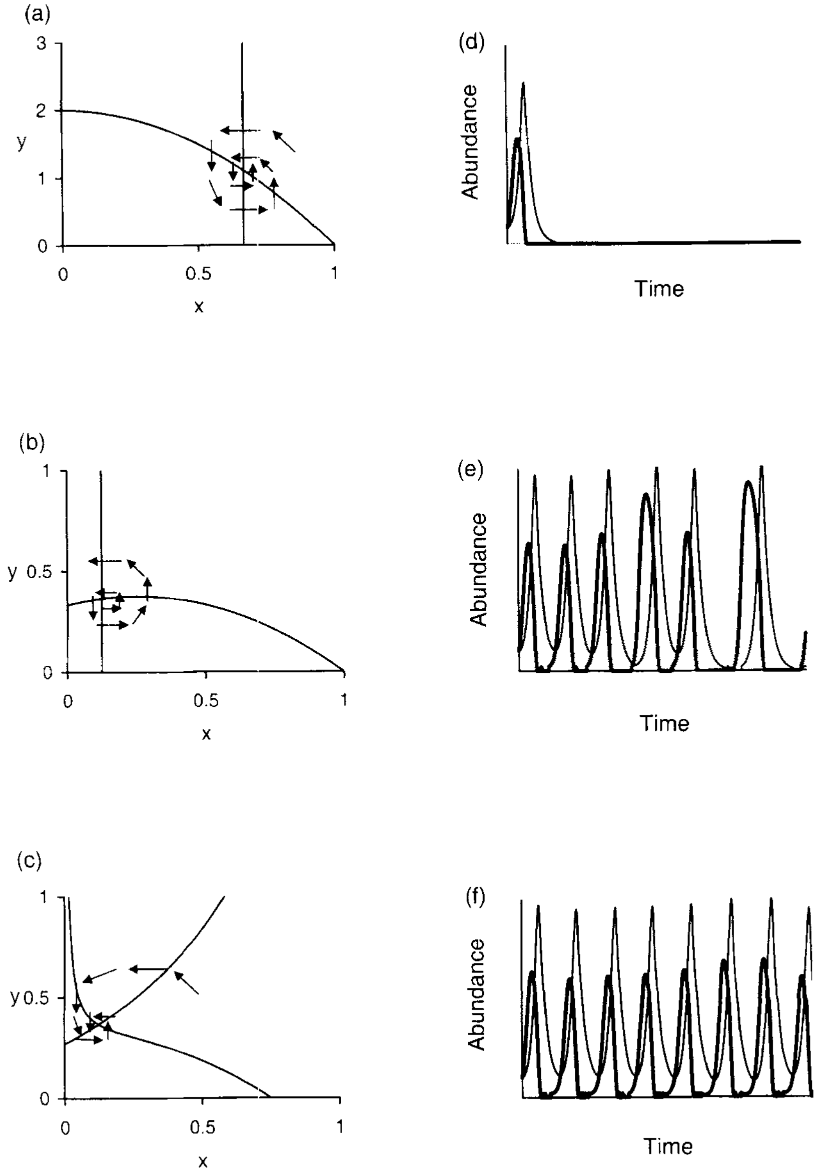

Figure 5. Phase portraits and the time series for a two-species consumer-resource interaction. Panels *a* and *b* depict the unperturbed system. Predators and prey attain a stable focus as can be seen from the tangential vectors that spiral inwards (panel *a*; $z=1$, $\alpha=0.5$, $\delta=0.2$). As certain critical parameters are varied, the system undergoes a Hopf bifurcation to periodic behaviour. This is depicted in panel *b* ($z=0.5$, $\alpha=1.5$, $\delta=0.3$) where the vectors are spiralling away from an unstable focus surrounded by a stable limit cycle. In panel *c* the predator–prey system in *b* is perturbed with prey and predator dispersal ($z=0.5$, $\alpha=1.5$, $\delta=0.3$, $\beta_x=0.3$, $\beta_y=0.8$). The bifurcation behaviour has been reversed by the perturbation. The unstable focus surrounded by a stable limit cycle has been converted to a stable focus. Panels *d*–*f* illustrate the role of extinction–colonization dynamics on the same predator–prey system. In the absence of immigration, demographic stochasticity can drive both prey and predators extinct. For a local extinction threshold of $x=y=0.01$ and parameter values of $z=0.18$, $\alpha=0.8$, $\delta=0.3$ and $\tau=0.01$, local extinction occurs in about 1000 generations. Rare colonization events that occur on the order of 1000 generations are sufficient to ensure the persistence of the predator–prey interaction (panel *e*). More frequent colonizations (e.g. on the order of 100 generations) have no effect

The limit cycle is stable in the sense that it attracts nearby initial conditions. In a deterministic world, the interaction should persist indefinitely. In the real world however, interacting species become susceptible to local extinction via demographic stochasticity when they go through periods of low densities. There are also situations in which consumers periodically drive their resources extinct, as demonstrated by classical models (Nicholson & Bailey 1935) and experiments (Huffaker, 1958; Huffaker, Shea & Herman, 1963; Pimentel, Nagle & Madden, 1963; Walde, 1991, 1994).

Perturbations can ensure the long-term persistence of such interactions. Unlike the directional or threshold systems discussed previously, perturbations do not have to occur on the same time scale as local dynamics. Immigration or colonization events that are infrequent relative to local dynamics are sufficient for long-term coexistence of consumers and resources (Fig 5d–f). Hence, the important population structure appears to be the extinction–colonization type rather than the source–sink type.

Transition from weak to strong perturbations

Small perturbations affect neither coexistence nor dynamics of consumer-resource systems that admit a stable limit cycle. They merely shift the system to another stable orbit in the neighbourhood of the original one (Hirsch & Smale, 1974; Guckenheimer & Holmes, 1983). Large perturbations simply modify the dynamics, without affecting coexistence. This impact on dynamics varies with the degree of complexity of the interaction. First, in simple consumer-resource models with linear functional responses and self-limitation in the consumer or resource, large perturbations tend to synchronize dynamics across linked populations. For example, predator–prey systems that oscillate independently are brought into phase by high rates of dispersal (Crowley, 1981; Holt, 1985; Murdoch *et al.*, 1992). Second, in consumer-resource systems that exhibit bifurcations (Rosenzweig & MacArthur, 1963; Rosenzweig, 1971; May, 1974; Murray, 1993), large perturbations can cause a reversal of bifurcation behaviour. An unperturbed system undergoing a stable limit cycle can be perturbed into one exhibiting a stable focus.

By way of illustration, consider the predator–prey model described by Equation (8). This population can be perturbed by linking it to other similar populations in the landscape via dispersal. For simplicity, assume that the perturbed population exchanges dispersers with other populations without affecting the dynamics of the latter (cf. Crowley, 1981). Also, let the other populations have prey and predator densities at the point equilibrium admitted by Equation (8). Relaxation of these assumptions does not influence the outcome (Crowley, 1981); it simply makes the analyses a great deal more complicated.

The dynamics of the perturbed system are given by:

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on the dynamics except to increase the minimum prey and predator densities (panel *f*). Colonization is simulated by adding 0.02 to the prey and predator densities if a random number between zero and one is less than 0.001 (colonization probability of 1 in 1000 generations; panel e) or 0.01 (colonization probability of 1 in 100 generations; panel *f*).

$$\Delta x = \left[x(1-x) - \frac{\alpha xy}{x+z} - \beta_x x + \beta_x \left(\frac{\delta z}{\alpha - \delta} \right) \right] \tau$$

$$\Delta y = \left[-\delta y + \frac{\alpha xy}{x+z} - \beta_y y + \beta_y \left(\frac{z(\alpha - \delta - \delta z)}{(\alpha - \delta)^2} \right) \right] \tau. \tag{9}$$

Here β_x and β_y are the prey and predator-specific emigration rates between the two patches. As previously, an island model of dispersal is assumed.

The phase portrait of the perturbed system is instructive (Fig. 5c). If an unperturbed population that exhibits a stable limit cycle is perturbed with prey and predator dispersal, it reaches a stable focus as long as prey dispersal is not too low and predator dispersal is intermediate (see Crowley [1981] for details). Hence, a perturbation of sufficiently high magnitude can convert predator–prey coexistence involving oscillations to one that involves a stable focus. This pattern has been observed for other predatory-prey models as well (Crowley, 1981; Holt, 1985; Murdoch *et al.*, 1992). Spatial heterogeneity is crucial. Damping of cycles does not occur if patches do not exhibit asynchronous fluctuations (Hilborn, 1975; Reeve, 1988; Taylor, 1988). Heterogeneity may arise from fixed differences among patches (Murdoch & Oaten, 1975; Murdoch *et al.*, 1992; Taylor, 1998) or from random variation in vital rates (Reeve, 1988) and initial abundances (Hassell, Comins & May, 1991, 1994; Comins, Hassell & May, 1992; Alder, 1993) that lead to phase differences in potentially identical environments (Levin, 1976, 1981).

Although not directly related to consumer-resource interactions, the parallels between perturbations to such systems and biological clocks is worth pointing out. Circadian oscillations leading to periodic activity in nocturnal organisms can be eliminated by high intensity stimuli such as light and temperature (Pavlidis, 1968; Winfree, 1974, 1975, 1980). The dynamical behaviour leading to the decay of circadian rhythms upon large perturbations (Winfree, 1980) is identical to that described here for consumer-resource interactions.

As can be seen from the above analyses, frequent dispersal and strong coupling may modify the nature of consumer-resource dynamics, but do not affect consumer-resource coexistence. Coexistence is mediated by local interactions in the short-term, and by extinction–colonization dynamics in the long-term. In fact, an extinction–colonization type population structure is necessary in antagonistic coevolutionary systems in which gene flow has to be sufficiently infrequent so as not to overcome the coevolutionary selection pressures exerted by interacting species (Slatkin, 1983; Frank, 1997).

Consumer-resource systems of high dimension

In communities with a large number of consumer-resource types (e.g. coevolving host and parasite genotypes, consumers that specialize on distinct resources), extinction–colonization dynamics may play an important role in maintaining local diversity. When the number of interacting genotypes or species is small, abundances are likely to be high and the opportunity for stochastic local extinction small (Frank,

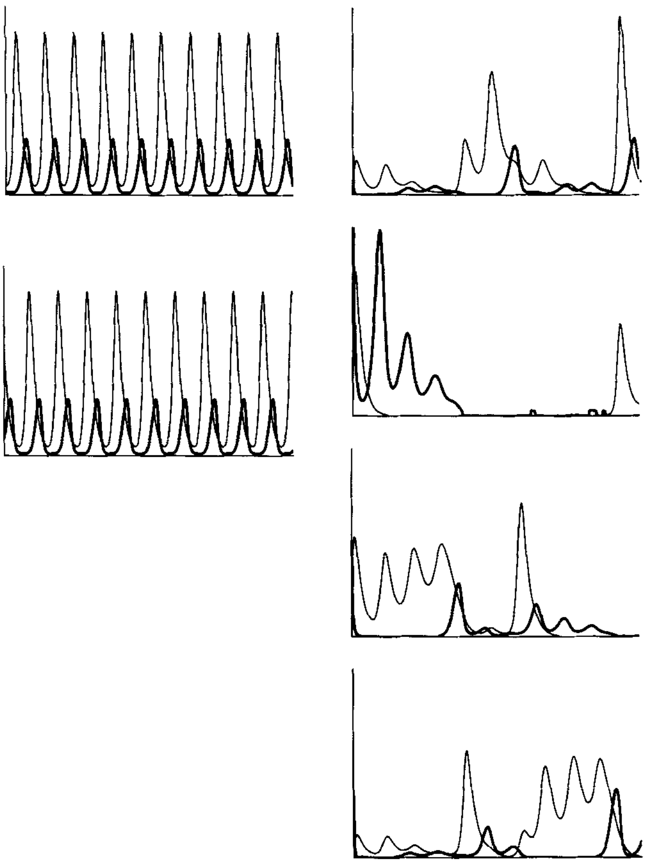

Figure 6. The role of extinction–colonization dynamics in consumer-resource communities of high dimension. The panels depict the dynamics of interacting hosts and parasites according to a model by Frank (1993, 1997): $\Delta h_i = [h_i\,(1 - H - (P - p_i))]\,\tau$, $\Delta p_j = [p_j\,(-s + b(H - h_j))]\tau$. The quantity h_i is density of the i^{th} host type scaled by the carrying capacity and p_j is density of the j^{th} parasite type scaled by the ratio of the parasite attack rate to the host growth rate. Quantities H and P are the total abundance of hosts and parasites respectively, s is the parasite mortality rate scaled by the host growth rate, b is the parasite birth rate per host scaled by the host growth rate and carrying capacity, and τ is the common time metric. The parameter values used are $\tau = 0.2$, $b = 2.4$ and $s = 0.4$. Local extinction and colonization were simulated as in Fig. 5. The two panels on the left depict host-parasite dynamics when the community consists of two host types and two parasite types. In each panel, the thick solid line represents host abundance, and the thin solid line, parasite abundance. When diversity is low, both hosts and parasites oscillate in a limit cycle, but abundances do not fall sufficiently low for local extinction to occur. Hence, extinction–colonization dynamics have little or no effect in maintaining host-parasite diversity. The four panels on the right depict host-parasite dynamics when the community consists of four host types and four parasite types. Since the average abundance of each type is lower, there is frequent local extinction of both host and parasite types. However, all eight types can be maintained within the community if there is facility for recolonization of locally extinct types. In contrast to the low-diversity community, the high-diversity community is driven by extinction–colonization dynamics (Frank, 1993, 1997). Similar results obtain for a generalized consumer-resource model (Frank & Amarasekare, 1998).

1993, 1997; Fig. 6). As the number of species or genotypes increase within a community, the average frequency or abundance of each type is likely to decline (Tilman & Pacala, 1993) and the potential for local extinction will increase (Frank

& Amarasekare, 1998). Isolated systems will lose local diversity over time. However, if there is facility for recolonization of locally extinct types, much of the local diversity can be maintained (Frank, 1993, 1997; Fig. 6). As consumer-resource diversity increases, there is a shift in control from local consumer-resource dynamics to extinction–colonization dynamics (Frank, 1993, 1997; Frank & Amarasekare, 1998).

Metacommunity models of consumer-resource interactions also find that extinction–colonization dynamics have a large influence on food chain lengths and local diversity (Holt, 1996, 1997). Spatial heterogeneity is important for maintaining diversity in high-dimensional consumer-resource systems, but unlike in the directional systems discussed above, fixed differences among local populations (extrinsic heterogeneity) are not necessary; asynchrony among interacting populations (intrinsic heterogeneity) may be sufficient (Frank, 1991).

Summary and predictions

As the preceding analysis suggests, local consumer-resource dynamics can maintain diversity in the short-term, but interacting species may become susceptible to stochastic local extinction during periods of low abundances. Extinction–colonization dynamics, rather than source–sink dynamics, are the important spatial process for long-term coexistence of consumers and resources. The data are consistent with this prediction. In consumer-resource systems that are not subject to local extinctions, spatial processes appear to have no effect on coexistence (Myers, Monro & Murray, 1981; Briggs, 1993; Murdoch *et al.*, 1996; Amarasekare, 2000a). Local processes appear to mediate coexistence as well as moderate population fluctuations in such communities (Harrison, Thomas & Lewinsohn, 1995; Murdoch *et al.*, 1996; Amarasekare, 2000b). In consumer-resource systems that are subject to local extinction, spatial processes of immigration and colonization are necessary for long-term coexistence (e.g. Huffaker, 1958; Huffaker *et al.*, 1963; Pimentel *et al.*, 1963; Lei & Hanski, 1998).

A second prediction is that an increase in consumer-resource diversity should lead to a shift in control from local consumer-resource dynamics to extinction–colonization dynamics. Comparative data required to evaluate the prediction are not available, but evidence exists that extinction–colonization dynamics are necessary for maintaining genotypic diversity in coevolutionary systems of high dimension (Gouyon & Couvet, 1985; Burdon & Jarosz, 1992; Thompson & Burden, 1992; Frank, 1997).

DISCUSSION

I have used perturbation theory to develop a framework for diversity maintenance in patchy environments. This approach encompasses both ecology and population genetics, and serves to bring together a large and diverse body of theory from both disciplines. It identifies a fundamental dichotomy in how diversity may be maintained in nature. This dichotomy yields comparative predictions that offer practical insights into conservation and restoration.

The basic dichotomy in diversity maintenance arises from the nature of interactions between local processes and perturbations such as spatial processes. The first type of diversity is driven by spatial processes. In systems characterized by threshold or directional local dynamics, competition and selection drive the system towards monomorphism. Given spatial heterogeneity in fitness or competitive rankings, dispersal or gene flow can lead to stable polymorphisms within an initially monomorphic population. Such polymorphisms, however, are unprotected. Genotypes or species that are intrinsically inferior or have a lower initial abundance cannot increase when rare. The long-term maintenance of local diversity requires that spatial processes operate on the same time scale as local dynamics and selection. Hence, population structure in unprotected interactions corresponds to a source–sink type in which the persistence of the interaction occurs because frequent dispersal continually rescues the inferior type (e.g. inferior competitor, genotype with a fitness deficit) from extinction. Since frequent gene flow swamps selection, there is little opportunity for evolution or coevolution within such source–sink systems.

Spatial heterogeneity that leads to source–sink dynamics can be of two types. Extrinsic heterogeneity arises from fixed differences in biotic or abiotic factors that lead to spatial variation in fitness or competitive ability. Intrinsic heterogeneity arises from founder effects or other random factors that create spatial variation in initial allele frequencies or species abundances. In unprotected interactions with threshold local dynamics, polymorphisms result from intrinsic spatial heterogeneity and are fragile to large perturbations; in systems with directional dynamics, polymorphisms result from extrinsic heterogeneity and are relatively robust to large perturbations.

The second type of diversity is driven by local processes such as balancing selection, resource specialization and consumer-resource dynamics. These processes lead to protected polymorphisms. Since interacting entities can increase when rare, diversity can be maintained locally even in the absence of spatial processes. Spatial processes are of overriding importance only when stochastic local extinction is likely, as in high-dimensional systems and those prone to oscillatory dynamics. In such situations, extinction–colonization dynamics can enhance both genetic and ecological diversity. Here, the population structure of importance is the Levins-type (Levins, 1969, 1970): dispersal is sufficiently infrequent to allow for population dynamics and coevolutionary feedback to proceed within local populations, but sufficiently frequent to allow for recolonization of locally extinct genotypes or species. Such a population structure can also counteract the loss of genetic diversity due to drift in small populations. Both extrinsic and intrinsic heterogeneity may operate in such systems, but intrinsic spatial heterogeneity alone is sufficient for maintaining diversity.

The above categorization provides a useful set of contrasts. Protected and unprotected interactions differ in whether they are driven by local or spatial processes, the time scales on which spatial processes are important, and in the type of population structure required for persistence or evolution of the interaction.

These contrasts suggest that anthropogenic perturbations are likely to have different impacts on the two types of diversity. For example, if frequent dispersal is maintaining unprotected interactions in sink populations, habitat fragmentation that isolates sources and sinks should lead to rapid loss of diversity. Since local processes maintain them at least in the short term, protected interactions may not be immediately affected by fragmentation. On the other hand, habitat loss is likely to disrupt local density- or frequency-dependent processes and increase the susceptibility of protected interactions to stochastic local extinction. Hence, habitat loss is likely to be more detrimental to protected interactions. One would also anticipate quite different restoration strategies. Protected interactions, once reintroduced, may establish without further intervention; unprotected interactions will require constant replenishment from a natural or artificial source. These implications for biodiversity management will be pursued in more detail elsewhere (Amarasekare, in prep.).

In conclusion, perturbation theory provides an interdisciplinary approach to understanding biodiversity. It serves to explain puzzling examples from nature, and to unite diverse conceptual approaches to studying diversity. It also highlights an important principle: while the details of genes, populations and species are important in defining the hierarchical structure of biological systems, the dynamical properties of these entities share a fundamental similarity that the details frequently seem to obscure.

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APPENDIX 1

(A) Model derivation for Allee local dynamics and dispersal

Local dynamics of a population exhibiting Allee dynamics can be described by the following model:

$$\Delta N_i = \left[\gamma_i \left(1 - \frac{N_i}{K}\right)\left(\frac{N_i}{K} - \frac{A}{K}\right)\right]\Delta t. \qquad (I.1)$$

The quantity N_i is the density of the i^{th} population, K is the carrying capacity, γ_i is the per capita growth rate, and A is the threshold below which population growth in a patch becomes negative due to Allee effects.

Equation (I.1) can be written in non-dimensional form (Murray, 1993). Non-dimensionalization reduces the system to a minimal set of parameters that also highlight the scaling relations among the various processes underlying the dynamics of the system.

With the following substitutions: $x_i = N_i/K$, $a = A/K$, $\tau = \gamma \Delta t$ we obtain the non-dimensional form of Equation (I.1), $\Delta x_i = [x_i(1 - x_i)(x_i - a)]\tau$, which is Equation (1) on page 5 of the main text.

Equation (2) can be derived in a similar manner. A two-patch system of interacting local populations can be described by:

$$\Delta N_1 = \left[\gamma N_1\left(1 - \frac{N_1}{K}\right)\left(\frac{N_1}{K} - \frac{A}{K}\right) - \alpha_1 N_1 + \frac{(\alpha_1 N_1 + \alpha_2 N_2)}{2}\right]\Delta t$$

$$\Delta N_2 = \left[\gamma N_2\left(1 - \frac{N_2}{K}\right)\left(\frac{N_2}{K} - \frac{A}{K}\right) - \alpha_2 N_2 + \frac{(\alpha_1 N_1 + \alpha_2 N_2)}{2}\right]\Delta t \qquad (I.2)$$

where α_i is the per capita emigration rate from population i. Spatial heterogeneity is expressed as differences in emigration rates between patches.

Non-dimensionalizing as previously, with the additional parameter $\beta_i = \alpha_i/\gamma$ we obtain Equation (2) in the main text:

$$\Delta x_1 = \left[x_1(1 - x_1)(x_1 - a) - \beta_1 x_1 + \frac{(\beta_1 x_1 + \beta_2 x_2)}{2}\right]\tau$$

$$\Delta x_2 = \left[x_2(1 - x_2)(x_2 - a) - \beta_2 x_2 + \frac{(\beta_1 x_1 + \beta_2 x_2)}{2}\right]\tau.$$

(B) Allee dynamics and dispersal—three patch case

The model can be extended to three patches as follows:

$$\Delta x_1 = \left[x_1(1 - x_1)(x_1 - a) - \beta_1 x_1 + \frac{(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3)}{3}\right]\tau$$

$$\Delta x_2 = \left[x_2(1 - x_2)(x_2 - a) - \beta_2 x_2 + \frac{(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3)}{3}\right]\tau$$

$$\Delta x_3 = \left[x_3(1 - x_3)(x_3 - a) - \beta_3 x_3 + \frac{(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3)}{3}\right]\tau. \qquad (I.3)$$

The key results for the two-patch model hold for the three-patch version as well. Under weak coupling, the boundary equilibria (0,0,1), (1,0,0), (0,1,0), (1,1,0), (1,0,1) and (0,1,1) are pushed slightly off the axes, yielding stable interior equilibria involving all three patches (Fig. A.1a–c). The existence of these equilibria require that at least one patch has an initial abundance above the extinction threshold. Immigration from this source patch rescues the other patches from extinction. As with the two-patch case, strong coupling synchronizes abundances among patches, thus destroying the interior polymorphic equilibria (Fig A.1d–f).

APPENDIX 2

Multi-allelic or multi-species polymorphisms in multi-patch environments

Consider a landscape containing n patches. The dynamics within each patch are directional (e.g. competitive exclusion, directional selection) or involve threshold effects (e.g. priority effects, disruptive selection), and do not yield equilibria that are neutrally stable. Provided that patches are linked by dispersal, how many patches would be needed to ensure a polymorphic equilibrium with *m* alleles at a locus, or *m* interacting species, within each patch?

Following Karlin and McGregor (1972b), I consider the two-patch, three allele/species case. The logic extends easily to the general case.

Given directional or threshold local dynamics, the only stable equilibria in the absence of a perturbation correspond to fixation of one allele (or species) and extinction of all others. For $m=3$ and $n=2$, there are $m^n=9$ stable equilibria which include all pairwise combinations of (1,0,0), (0,1,0), (0,0,1).

Consider the equilibrium with allele (species) 1 fixed in patch 1 and allele (species) 2 fixed in patch 2: (1,0,0), (0,1,0). If the patches are now connected, the perturbation theorem applies and a stable polymorphic equilibrium results. However, since the two patches can each contain only one allele (or species), the polymorphic equilibrium will necessarily be missing the third allele (species). Applying this logic to all pairwise combinations shows that all six equilibria that do not lead to global fixation involve exactly two alleles (species). Hence, a stable polymorphism with all three alleles (species) requires that the environment contain a minimum of three patches such that each allele (species) has the possibility, in the absence of a perturbation, to become fixed within at least one patch.

This result can be generalized as follows: for any multi-allelic or multi-species system involving threshold or directional local dynamics and inhabiting a patchy environment, a stable polymorphism with all alleles or species within a given patch is possible if and only if the number of patches in the environment ≥ the number of alleles or species.

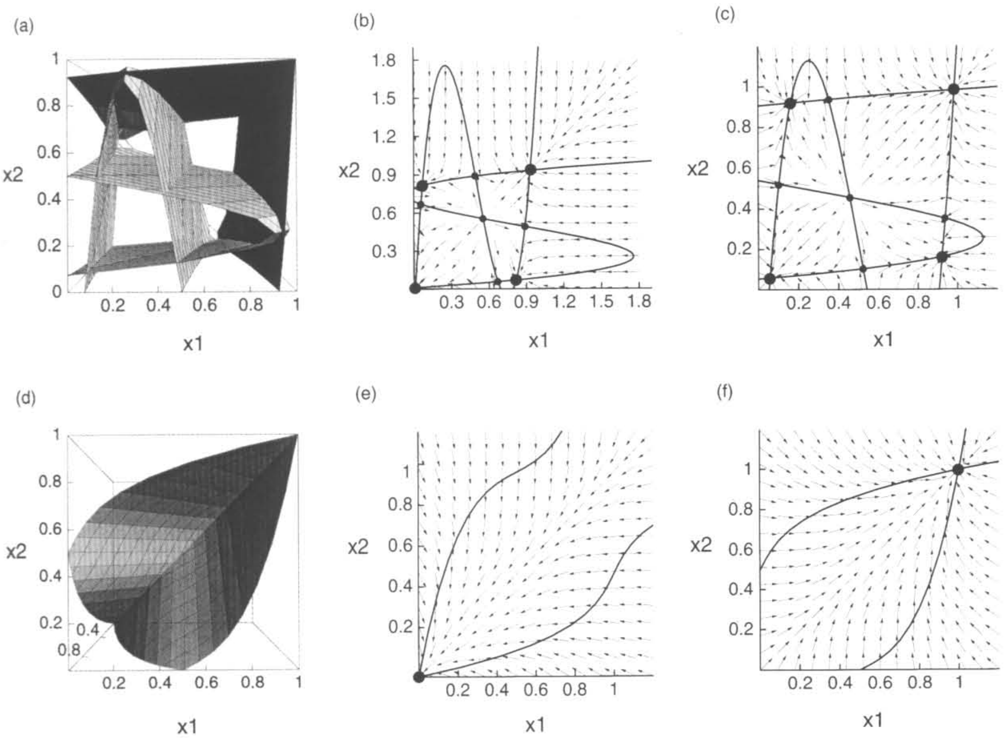

Figure A.1 Phase portraits for a three-patch system undergoing Allee dynamics and dispersal. Panels *a* and *d* depict the 3-dimensional phase plots for small and large perturbations respectively. Panels *b* and *c* depict 2-dimensional slices of the phase space for a small perturbation, and panels *e* and *f*, those for a large perturbation. As long as at least one patch is above the extinction threshold, weak coupling ($\beta_1 = \beta_2 = \beta_3 = 0.1$) leads to coexistence of all three patches as a source–sink system (panel *a*). The addition of a third patch increases the number of polymorphic equilibria from two (see Fig. 1*b*) to six. For instance, when the third patch has an initial abundance below the extinction threshold, the edge equilibria (1,0,0), (0,1,0) and (1,1,0) are perturbed to yield three polymorphic equilibria (panel *b*); when the third patch has an abundance above the extinction threshold, the edge equilibria (0,0,1), (1,0,1) and (0,1,1) are perturbed to yield three more polymorphic equilibria (panel *c*). A small perturbation of (0,0,1) leads to a source–sink system with one patch with an initial abundance above the extinction threshold maintaining both of the other patches below the extinction threshold. With strong coupling ($\beta_1 = \beta_2 = \beta_3 = 0.5$) all six polymorphic equilibria disappear (panel *d*). The only stable states are extinction (0,0,0) and carrying capacity (1,1,1), separated by a saddle (0.5,0.5,0.5). The stable manifold of the saddle defines the separatrix for the domains of attraction for the two stable states. When initial abundances of all three patches fall below the stable manifold, global extinction results (panel *e*); when initial abundances are above the stable manifold, all three patches attain carrying capacity (panel *f*).