Metapopulation theory, landscape models, and species diversity[1]

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Abstract: We construct a model that describes the interaction of multiple metapopulation processes with measures of landscape patch diversity, fragmentary grain, and patch availability. Landscape models corresponding to Voronoi tessellations formulated around two-dimensional point processes are suggested as alternatives to conventional neutral landscape models. A method for creating the configuration of suitable habitat composed of multiple types of patches in randomized landscapes is suggested, which utilizes perimeter polynomials associated with classical percolation theory. Landscape models are used to examine the influence of patch diversity, landscape grain, and total habitat availability on two measures of species performance that can be predicted from conventional metapopulation theory: the expected fraction of patches occupied by a species in the landscape (conditional prevalence), and the probability that a species will be represented in the landscape (representation). Results suggest that even when considering mutually non-interactive multiple metapopulation processes, the influence of landscape structure on species prevalence and representation depends in complicated ways on a combination of both species parameters and landscape parameters. Significantly, effects of changes in landscape structure on the distribution of a species cannot be anticipated from its pre-disturbance distribution.

Keywords: landscape models, multi-species metapopulations, habitat mosaics, Voronoi tessellations.

Résumé : Nous avons construit un modèle qui décrit les interactions entre les processus d'une métapopulation avec les mesures de la diversité en parcelles du paysage, le grain du morcellement et la disponibilité des parcelles. Les modèles du paysage comparables aux réseaux de Voronoi, basés sur les processus de points à deux dimensions, sont proposés comme une alternative aux modèles neutres conventionnels. Une méthode, créant des configurations aléatoires dans le paysage de plusieurs parcelles d'habitats adéquats au maintien des espèces, basée sur le périmètre polynomial de la théorie de la percolation, est proposée. Les modèles du paysage sont employés afin d'évaluer l'influence de la diversité en parcelles, du grain du morcellement et de la disponibilité des parcelles sur deux mesures de la performance des espèces qui peuvent être prédites par la théorie conventionnelle de la métapopulation : la valeur attendue de la fraction des parcelles occupées par une espèce dans le paysage (prédominance conditionnelle) et la probabilité qu'une espèce sera représentée dans le paysage (représentation). Les résultats suggèrent que, même lorsque l'on considère les processus mutuellement non-interactifs de la métapopulation, l'influence de la structure du paysage sur la prédominance et la représentation des espèces dépend, de façon compliquée, de la combinaison entre les paramètres des espèces et du paysage. Les effets de changement dans la structure du paysage sur la répartition d'une espèce ne peuvent pas être prévus par sa répartition avant une perturbation.

Mots-clés : modèles du paysage, métapopulations de plusieurs espèces, mosaique d'habitats, réseaux de Voronoi.

Introduction

Landscapes can be viewed as mosaics of different habitat types. These different types are often defined in terms of characteristic vegetative assemblages (Whittaker, 1978; Mucina & Dale, 1989; Feoli & Orloci, 1991), which might represent different stages of a successional cycle. Landscape ecology involves study of the spatial structure and temporal dynamics of these mosaics. Metapopulation theory recognizes that populations of organisms inhabiting these patches will be subject to local extinction events, and that regional persistence of species will depend on their dispersal and re-colonization of uninhabited patches of habitat. Spatial and temporal scales of these processes vary over many orders of magnitude depending on the autecology of individual species (Wiens, 1989). When viewing the dynamics of species assemblages, these variations in scale may be represented by hierarchically organized models. Problems of scale have largely frustrated a more useful fusion of metapopulation biology, with its preoccupation with the population dynamics of single species, and the ecology of landscapes, which by its nature takes a multi-species perspective (Wiens, 1997). Here we advance a formulation of these problems which combines several different existing approaches and permits consideration of generalized multiple metapopulation processes acting simultaneously at different scales. From atop this formulation we obtain an improved view of the difficulties and obstacles confronting the current construction of landscape ecology theory.

Conventional metapopulation theory in its starkest formulation represents the far end of a conceptual continuum of population models that begins with population processes so well mixed that space is simply irrelevant (May, 1974; Pimm, 1982), and extends through processes in which spatial

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domains are homogeneous but influential (Levin & Segel, 1985; Wilson, McCauley & De Roos, 1995; Bolker & Pacala, 1997), explicitly heterogeneous (Horn & MacArthur,1972; Pulliam, 1988) and ending with population processes that operate over spatial domains so heterogeneous that some parts of the domain are uninhabitable (Levins, 1969). At a landscape level, species ranges inevitably include areas so unsuited to a species' ecology that they may be viewed as uninhabitable, and the distribution of uninhabitable areas defines the configuration of suitable habitat. Habitat fragments can only support finite populations, and extinction is certain over some time scale (Lewontin & Cohen, 1969), whether through demographic or environmental stochastic events, biotic interaction, catastrophe, or transition of habitat from one that is suitable to one that is not. Species can persist only through a balance of these local extinction events with colonization. Habitat patches may be many things, for example small water bodies (*e.g.*, ponds, treeholes, lakes), individual trees in a forest or grassland, areas of forest of a certain age, forest gaps, entire watersheds, mountain tops, parks, etc. Landscapes may be viewed as contiguous tessellations of different habitats filling two-dimensional space. More of one habitat type means less of another. Ultimately, spatial allocation of habitat is a zero sum game.

Regional species richness is partly determined by evolutionary history, but is to some extent governed by ecological considerations, through a combination of habitat diversity, local extinction and intra and inter-regional colonization (Ricklefs & Schluter, 1994). A region's biota is composed of species that have withstood the test of time and have succeeded in persisting in the regional landscape. When habitats are structured and characterized by different vegetation types, their spatial configuration is likely to vary temporally, generating a complex mosaic of transient habitat patches, the dynamics of which are driven by some successional process. The ability of individual species to persist in such spatially and temporally changing landscapes depends on their ability to track (locate and exploit) suitable habitat as and when it occurs (Thomas, 1994). The relative connectivity of similar patches, and the permeability to species inhabiting the landscape as a whole therefore plays a central role in species distribution and abundance across landscapes (Dunning, Danielson & Pulliam, 1992; Taylor *et al.*, 1993; Andren, 1994), suggesting that patch shape and the texture of their agglomerates may be directly relevant to the long-term persistence of the assemblage.

Species dispersal abilities have evolved together with life-history strategies in response to natural landscape pattern, scale, and texture, and to temporal and spatial disturbance regimes that characterize different landscapes. Species whose dispersal properties or demographic dynamics are unsuited to a landscape will have been excluded, together with species that could potentially persist in such landscapes but that have adopted persistence strategies that render them uncompetitive relative to other species found in these regions. For some types of species, the natural characteristic size of induced patches in pristine landscapes seldom results in regular local patch extinctions, and for such species inter-patch dispersal will be a relatively unimportant element of regional persistence strategies.

However, while dispersal processes may or may not be influential in the determination of natural regional species richness, they are likely to become a great deal more important in the determination of the particular set of species that characterize a region subsequent to anthropogenically imposed landscape changes. We know appallingly little about dispersal and colonization abilities of different species, or how their resistance to local extinction depends on patch area and configuration (both the extents and limits of our knowledge of these problems are reviewed in Hanski & Gilpin, 1997). A finely tuned strategy that is successful for persistence in a landscape under its natural dynamics may perform far worse in one recently reconfigured by a new disturbance regime. Conversely, some strategies unsuited to the natural landscape structure and dynamics may perform far better subsequent to anthropogenic modification, resulting in species range expansions, invasions, and emergence of "pest" problems.

Habitat diversity has long been considered an important determinant of γ-diversity. Landscapes subdivided into a number of different habitats are inevitably more likely to support more diverse species assemblages than those that are not. However, such habitat heterogeneity implies a decreased absolute extent of any one habitat type, existence of habitat edge, plus a degree of fragmentation, all of which are often associated with detrimental impacts on persistence of individual species' populations. An interesting paradox arises: the existence of a mosaic of habitat patches is critical to the maintenance of species diversity in the landscape as a whole, yet the resulting fragmentation potentially threatens the persistence of many populations of constituent species within the co-existing assemblage. Clearly, maintenance of the appropriate spatial "texture" of such habitat mosaics is likely to be an important component of a landscape's capacity to support diverse species assemblages.

In what follows we suppose that the observed species assemblage on a landscape is some (possibly dynamic) subset of a larger regional species pool. The regional species pool is the set of species with at least some physical access to the landscape. We focus on two important components of species diversity on the landscape. The first we term "conditional prevalence", the percentage of patches comprised of suitable habitat for a particular species that are in fact occupied by that species. The second is the probability that any member of the regional species pool is represented somewhere (anywhere) in the landscape, which we refer to as "representation." We consider three separate landscape indices. The first is the degree of habitat fragmentation, or "graininess." Landscape grain is a measure of the extent to which available habitat is broken up into larger numbers of patches of smaller size. The second is habitat diversity, the number of different habitat types present on the landscape-more different types of habitat implies reduced availability of each one. The third is habitat availability, which is inversely related to the fraction of the landscape unusable to the regional species pool. We develop our model in three modules relating to landscape, metapopulation dynamics, and species properties, and describe results of a simplistic transparent analysis, followed by a more complicated numerical demonstration of the model's possible behaviour.

Material and methods

We proceed by describing the three modules; all parameters are summarized and defined in Table I.

LANDSCAPE MODEL

Our landscape model is closely related to a family of so-called neutral landscape models (see Gardner *et al.*, 1987; With, 1997; With & King, 1997) that derive from physical percolation theory (reviewed in Stauffer & Aharony, 1992). It differs slightly in that the model need not be viewed as lattice based, but is formulated around an underlying two-dimensional point process (akin to that employed by Doak, Marino & Kareiva, 1992).

Consider a region defined by some area (A) of landscape. Suppose that this entire region may be totally divided into similarly sized, discrete non-overlapping cells or "tiles" each of which can be classified into one of z distinct types characterized by some relevant ecological property (perhaps a distinctive vegetation assemblage, for example). We refer to these distinct classifications as cell types. The total area of the ith cell type is denoted a_i. Add one further category (category 0) which is of a type that is not usable by any member of the regional species pool, bringing the total number of categories to $z + 1$. Examples of what such landscapes might look like are shown in Figures 1a and b.

We have:

$$A = a_0 + a_1 + a_2 + ... + a_z \qquad [1]$$

This can be rewritten $A = \sum_{i\in\Theta} a_i$ as where Θ is the set of all cell types,

and

$$1 = f_0 + f_1 + f_2 + ... + f_z \qquad [2]$$

where $f_i = a_i/A$ and is the fraction of the landscape consisting of cell type i. Thus a proportion, f_0, of this region is totally uninhabitable by any members of the regional species pool.

Define a graininess, Γ, for this region. Graininess is density of cells. Following Turner *et al.* (1991), landscape grain is the smallest spatial scale over which the landscape is assumed to be homogeneous. With a large number of very small cells, graininess is high; graininess is lower when there are fewer larger cells. Γ is a density and may take any positive value.

The total number of cells of all types is now $A\,\Gamma$. The number of cells of type i is $a_i\,\Gamma$. The probability that a cell is of type i is of course f_i, and the average area of a single cell is $1/\Gamma$.

A species' habitat is defined as the set of all cells comprising a set of types. Let Ω_j denote the set of cell types constituting habitat of the jth species. A specialist species may only exist in habitat of a single type, whereas the habitat of a more generalist species would be composed of several different cell types. Assume that generalists are equally adept at using all types of cells constituting their habitat.

Obviously, these cells can be organized into an almost infinite number of spatial configurations. However, for some tractability, assume that cell types are randomly distributed with respect to one another through space. This could be modeled as follows: assume that centroids of all

TABLE I. Parameters used in the model

Parameter	Definition
A	total area of landscape modelled
a_i	total area of the ith cell type
z	total number of inhabitable cell types
Θ	the set of all cell types
f_i	the fraction of total landscape comprised of the ith cell type
Γ	the density of cells in the landscape
Ω_j	the set of cell types comprising habitat of the jth species
p_j	the proportion of the landscape comprised of habitat inhabitable by the jth species
p_c	the critical percolation threshold above which a habitat patch spanning the whole landscape is likely to be encountered
n_j	the expected number of patches of habitat in the landscape inhabitable by the jth species
d_k	perimeter polynomial equal to the probability that a randomly selected cell will be part of a cluster of k cells all inhabitable by the jth species (depends on p_j)
γ_j	density of habitat patches consisting of cell types inhabitable by the jth species
h_j	the average area of patches consisting of cell types inhabitable by the jth species
g	a physical constant determined by the dimensionality of the landscape (for two-dimensional landscapes, $g = 11/8$)
w_j	CONDITIONAL PREVALENCE: the proportion of available patches potentially inhabitable by the jth species, that are inhabited by the jth species
m_j	the rate at which the jth species colonizes suitable vacant patches of habitat from occupied patches
e_j	the rate of local extinction of the jth species from occupied patches of habitat
E_j	the regional extinction rate of the jth species
S	the number of species in the regional species pool
R_j	REPRESENTATION: the probability that the jth species will be represented in the landscape
C	the regional colonization rate (assumed common to all species)
r_j	the maximum distance at which an unoccupied patch may be colonized from an occupied patch by the jth species
μ_j	the rate at which the jth species can colonize unoccupied patches within a distance r_j of an occupied patch
k_j	the expected time to local extinction of the jth species in a patch of unit area - a parameter likely to be proportional to population density and constancy
x_j	a measure of how fast average local population lifetime of species j increases with patch area

A superscripted asterisk indicates a quantity at equilibrium.

A Γ cells are distributed according to a simple two-dimensional Poisson process with density Γ. Cells are formed by assigning to a given centroid all space nearer to that centroid than to any other. The resulting mosaic is known as a Voronoi tessellation. Voronoi tessellations may be formed around any point process in any dimension, but Voronoi tessellations arising from two-dimensional Poisson point processes have been well studied (see reviews by Miles, 1972; Stoyan & Stoyan, 1994; Moller, 1994). Assign each cell to the ith type ($i = 0... z$) with probability f_i. The problem of habitat configuration is now described by a multi-state percolation process on a two-dimensional Voronoi tessellation. Multi-state percolation has been used in landscape modelling only recently (*e.g.*, With & King, 1997). An example of a six-state Voronoi tessellation is shown in Figure 1a, and at half the graininess in Figure 1b.

Suppose for example that in the landscape shown in Figure 1, a chosen species can inhabit two different cell types (say cell types 2 and 3). Habitat available to this species in the region shown in Figure 1b is shaded in
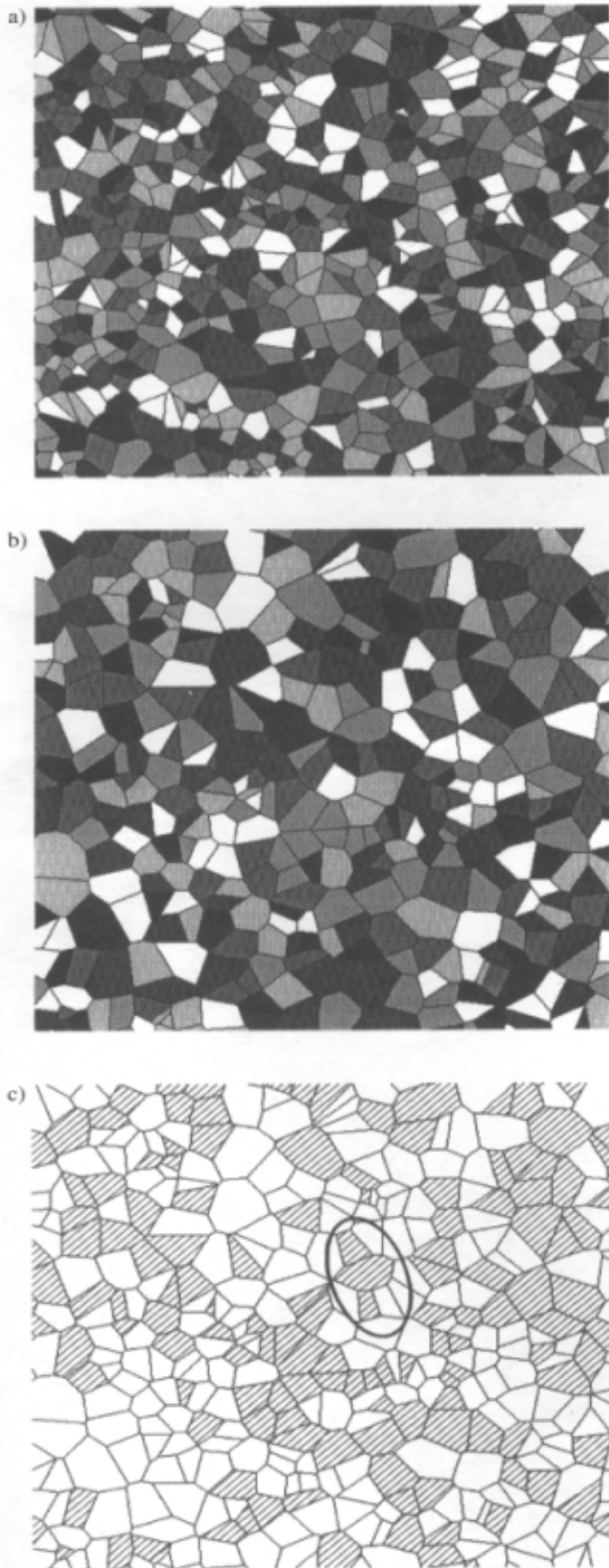
FIGURE 1. a) Voronoi tessellations constructed around single two-dimensional Poisson point processes. Each edge in the landscape perpendicularly bisects a line (not shown) connecting two neighboring centroids (centroids not shown) at its mid-point. Each cell in the tessellation has been designated one of six types (denoted by shading) with probability 1/6; b) the same as a) but using a Poisson process of half the density; c) same as b) but cells of two types have been hatched (all others are white). A habitat patch comprising three cells is enclosed within the oval.

Figure 1c. If usable cell types share borders with each other in the Voronoi tessellation, they form part of larger spatially contiguous regions that we term habitat patches. Two questions may now be asked about this regional mosaic: i) how many discrete patches of habitat are available to this species, and ii) what is the average size of a patch of habitat? (Note that although we know the average size of individual cell types, habitat patches can also be formed by fusion of multiple cells, and because different species may inhabit some of the same cell types, the patch structure perceived by each species can overlap in complicated ways with those recognized by other species.) These questions are addressed specifically by physical percolation theory. On average, cells in mosaics formulated in this manner have six sides. In the physics literature such lattices are known as triangular (hexagonal might be more intuitive), and are specifically addressed by a wide range of percolation theory (Stauffer & Aharony, 1992).

The proportion of the landscape that contains habitat suitable for the jth species equals p_j and is equal to

$$\sum_{k \in \Omega_j} f_k$$

which is the sum of all elements of the set of usable cell types, Ω_j ($\Omega_j \subseteq \Theta$). For our chosen species above, p_{chosen} is $f_2 + f_3$. If p_j is greater than a critical value then a large patch of continuous habitat is almost certain to span the region. This threshold is the so called critical "percolation threshold" (usually referred to as p_c; Stauffer, 1979). For triangular lattices this threshold is 0.5. Assuming that $p_j < p_c$, the expected number of habitat patches, n_j, in the region is given by:

$$n_j = \Gamma A \sum_{k=1}^{\infty} p_j^k d_k (1 - p_j) \qquad [3]$$

The functions d_k are termed perimeter polynomials and are related to the density of cell conglomerates comprising k cells; they originate from low-density series expansions. These functions become cumbersome but acquire extremely low values for large values of k, so long as p_j is quite small relative to p_c. They are given for a variety of lattice types for k up to 14 in Sykes & Glen (1976). If p_j is small, the probability that more than 14 cells all usable by the jth species form a contiguous cluster is quite low. For example when $p_j = 0.2$, the probability that a randomly selected landscape cell is part of a habitat patch comprising 14 contiguous habitable cells is less than 6.2×10^{-5}, but as p_j rises to 0.333, this probability becomes 5.75×10^{-4}. For larger values of p_j nearer the percolation threshold, various numerically established scaling relationships can be used in place of series expansions (see Stauffer, 1979).

Density of habitat patches (γ_j) for species j is:

$$\gamma_j = \frac{n_j}{A} \approx \Gamma p_j \qquad [4]$$

This approximation is good for low values of p_j.

Average size of each habitat patch (h_j) is given approximately by:

$$h_j = \Gamma^{-1} (1 - \frac{p_j}{p_c})^{-(g+1)} \approx \Gamma^{-1} \qquad [5]$$

(see Essam, 1972) where p_c is 0.5, and g is a constant valid for any structure of fixed dimensionality (for two-dimensional lattices, $g = 11/8$). Once again the approximation is good for low values of p_j.

METAPOPULATION MODEL

Consider the modified Levins (1969) metapopulation model:

$$\frac{dw_j}{dt} = m_j(\cdot)w_j(1 - w_j) - e_j(\cdot)w_j \qquad [6]$$

where w_j is the probability that a patch of species j habitat is occupied, $m_j(\cdot)$ is a function that describes the rate at which the jth species can colonize vacant habitat patches locally from occupied habitat patches, and $e_j(\cdot)$ is the rate of local extinction of species j from occupied patches. Dots inside parentheses indicate that these parameters may themselves be complicated functions of many landscape and species specific parameters. Setting $dw_j/dt = 0$ we get the expression for the expected fraction of available patches occupied by the jth species (conditional prevalence) at equilibrium, w_j^*:

$$w_j^* = 1 - \frac{e_j(\cdot)}{m_j(\cdot)} \qquad [7]$$

Equation 6 describes the deterministic average dynamics of patch occupancy probabilities. In reality, patches are either occupied or not, and local extinction and colonization are discrete events occurring stochastically at rates governed by $m_j(\cdot)$ and $e_j(\cdot)$. Therefore all occupied habitat patches might undergo local extinction before any colonization event takes place, with the result that a species becomes regionally extinct in all habitat patches in the landscape. Nisbet & Gurney (1982) derive an approximate expression for the regional extinction rate of the jth species (E_j) given the local dynamics in equation 6:

$$E_j^* \sim e_j(\cdot)\exp\left(\frac{-w_j^{*2}n_j}{2(1 - w_j^*)}\right) \qquad [8]$$

This expression is derived from a model in which all habitat patches are assumed equally accessible; however, it is quite robust to different local colonization processes (Gurney & Nisbet, 1978).

Given this non-zero rate of regional extinction, regional species diversity can only be maintained by balancing regional colonization. We assume that the landscape region has associated with it a set of species containing S members that we will refer to as the regional species pool. These species regularly or irregularly have, at least potentially, a chance of taking up residency in the landscape (*i.e.*, they have some physical access to it). Populations of these species within the region will go regionally extinct at some rate, E_j which may be very low. This regional extinction process is countered by colonization of species from the regional species pool that are not currently extant within the region. This colonization rate, C, is simply the rate at which a species enters the landscape from some exterior source and may also be extremely low. We assume that species richness observed in the region is a long-term balance resulting from regional extinction and regional colonization

rates over time, and that the probability of a species being represented on the landscape (its representation) is given by:

$$R_j^* = \frac{C}{C + E_j^*} \qquad [9]$$

SPECIES MODEL

Simplistically, a species possesses two important descriptive functions that relate directly to its ability to persist in landscape mosaics, *i.e.*, the rate at which occupied habitat patches in the landscape go extinct, $e_j(\cdot)$, and the rate at which populations in occupied patches succeed in local colonization of unoccupied patches, $m_j(\cdot)$. To maintain a degree of population sustainability at a regional level, rates of local colonization must exceed those of local extinction; the greater this excess the greater will be the conditional prevalence. However, different species can persist in a landscape at the same levels of conditional prevalence in very different ways, and these are differentiable by the turnover time of local populations. In Figure 2, we characterize a regional species pool with nine "species types." Types 1, 2, and 4 are unable to persist in the region for which local extinction and colonization rates have been evaluated; types 3, 5, and 7 have low conditional prevalence, 6 has a medium conditional prevalence and types 8 and 9 are highly prevalent. Represented species with very low extinction rates (type 7) do not persist as a result of classical metapopulation dynamics, whereas those with both high
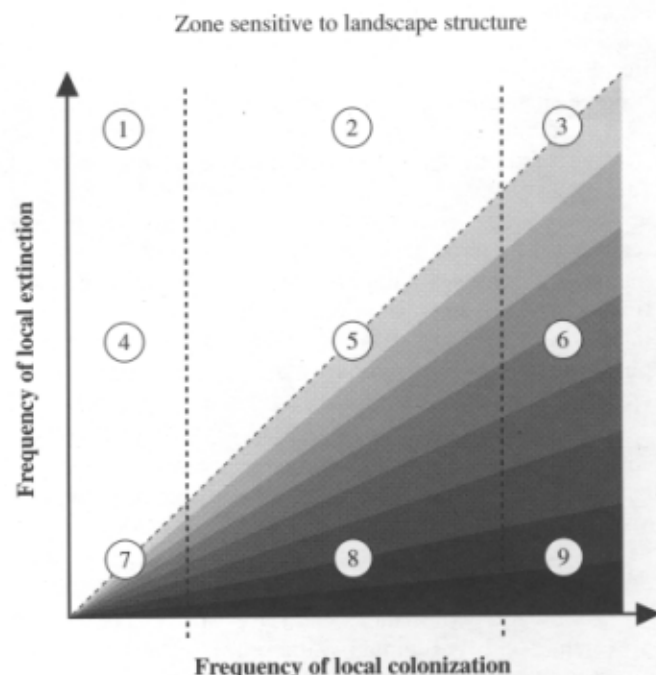

FIGURE 2. Species may be characterized by the frequency with which sub-populations are founded (x-axis) and become locally extinct (y-axis). Conditional prevalence is indicated by the intensity of shading (light gray - low, dark gray - high). Different types of species may maintain the same percentage of patch occupancy (which we refer to as conditional prevalence) with very different rates of local exinction and colonization; hence species types 3, 5, and 7 are rare in the landscape for which this Figure is constructed, but species type 3 has high population turnover rates, and species type 7 has very low population turnover rates. Species type 8 and 9 display high conditional prevalence (they are widespread).

local colonization rates and conditional prevalence (types 6 and 9) are unlikely to be critically sensitive to changes in landscape structure. The status of types 2, 3, 5, and 8 is potentially sensitive to modifications of landscape structure.

Suppose that the jth species is equally likely to colonize any empty habitat patch within a radius r_j of an occupied habitat patch at rate μ_j. Assume that patch configuration corresponds to that predicted by our landscape model. Given a habitat patch density of γ_j, we would expect to find $\gamma_j \pi r_j^2$ habitat patches within a circle of radius r_j distance units. We can then write $m_j(\cdot)$ as:

$$m_j(\cdot) = \gamma_j \pi\, r_j^2 \mu_j \qquad [10]$$

Note that in this deterministic formulation, the square of the maximum radius of dispersal (r_j^2) and the rate of this dispersal (μ_j) are functionally equivalent parameters.

Extinction rates of occupied habitat are conventionally modelled (Hanski, 1994a; Cooke & Hanski, 1994) as inverse functions of habitat area. Habitat area is used as a surrogate for population size. Thus

$$e_j(\cdot) = \frac{h_j^{-x_j}}{k_j} = \frac{1}{k_j}\left[\frac{1}{\Gamma}(1-\frac{p_j}{p_c})^{-(g+1)}\right]^{-x_j} \qquad [11]$$

where k_j is the expected lifetime of a population in a patch of unit size and $x_j \neq 1$ permits a non-linear relationship between extinction rate and patch area. The rationale for this formulation is that k_j can be chosen to be large for high density or stable populations, and low for lower density or highly fluctuating populations. If $x_j = 1$, then extinction rates are directly proportional to patch area; $x_j > 1$ accounts for disproportionate increases in extinction rates as patches become smaller, as $x_j \to 0$ extinction rates become independent of patch area. Expected population lifetime is the inverse of this local extinction rate, and when plotted against area (on logged axes) increases linearly with area at rate x_j with intercept 10^{k_j} (see Figure 3). Species can resist local extinction in two ways: they can have a large intercept, k_j, corresponding to high and/or constant population density, or high slope, x_j, corresponding to rapidly increasing resistance to local extinction with increasing patch area. At low values of p_j, extinction rates are approximated by $e_j(\cdot) \approx \Gamma^{x_j}/k_j$.

This formulation of species population dynamics enables every species to be described by three key population parameters: i) r_j, a measure of rate or distance of individual dispersal; ii) k_j, average time to local extinction for occupied habitat patches of unit area; and iii) x_j, the rate at which time to local extinction increases with habitat area.

Landscape perturbations can affect species conditional prevalence and its regional extinction rate, and therefore affect its likely representation in different ways. In considering the effects on species j of a change to an (undefined) landscape property X, we are interested in only three quantities: i) rate of change of local colonization rate with X, $\partial m_j(\cdot)/\partial X$; ii) rate of change of local extinction rate with X, $\partial e_j(\cdot)/\partial X$, and iii) rate of change of density of habitat patches with X, $\partial \gamma_j/\partial X$. These quantities affect conditional prevalence and regional extinction rates. Figure 4 shows that the relationship between conditional prevalence and
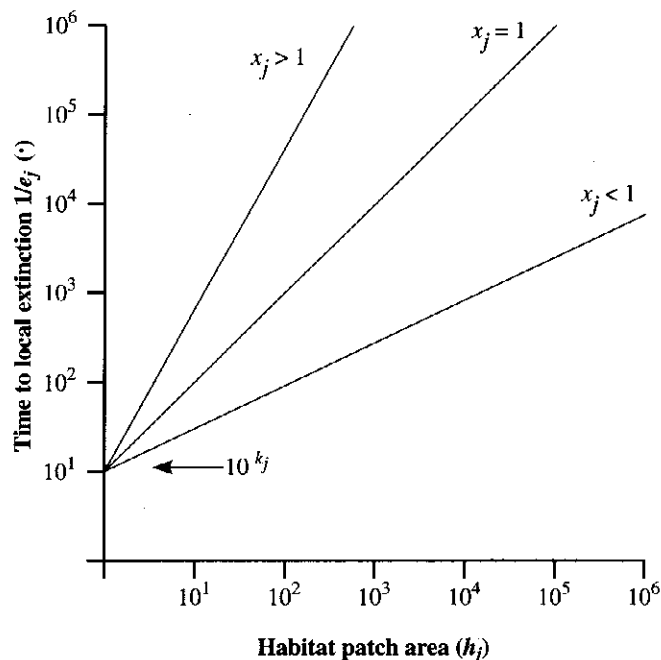

FIGURE 3. Log-log plots of different local extinction rates as functions of patch area (equation 11). For any given patch area, population lifetimes are determined by both the value of the slope (x_j) and intercept (k_j). A population might be less vulnerable to local extinction (higher k_j) than another because it exists within the same area at higher density or with more stable population dynamics.

regional extinction rates may not be straightforward under some circumstances both conditional prevalence and regional extinction rate can potentially decline.

Results

LANDSCAPE FRAGMENTATION

Pure landscape fragmentation occurs when existing levels of habitat availability are held constant but cells become smaller and more numerous. In our model this is accomplished by varying the grain of the landscape using the parameter controlling cell density (Γ). Note that functions defined in equations 10 and 11 are both influenced by the value of Γ, and this dependency can be denoted using the notation $m_j(\Gamma)$ and $e_j(\Gamma)$. Consider a landscape as perceived by the jth species. Let the landscape in its pristine state be characterized by a grain denoted Γ_0. The conditional prevalence of species j in the pristine landscape is given by $w^*_j = 1 - [e_j(\Gamma_0)/m_j(\Gamma_0)]$, but the response of this prevalence to fragmentation is determined by the relative magnitudes of the partial derivatives of $m_j(\Gamma)$ and $e_j(\Gamma)$ taken with respect to Γ. Assuming that p_j is sufficiently small that habitat patches are mostly composed of only single cells, these derivatives can be approximated by:

$$\left.\frac{\partial e_j(\Gamma)}{\partial \Gamma}\right|_{\Gamma_0} \approx \frac{x_j \Gamma_0^{x_j-1}}{k_j} \qquad \left.\frac{\partial m_j(\Gamma)}{\partial \Gamma}\right|_{\Gamma_0} \approx \mu_j p_j \pi\, r_j^2 \quad [12a\text{-}b]$$

The effect of fragmentation on representation would also require knowledge of:

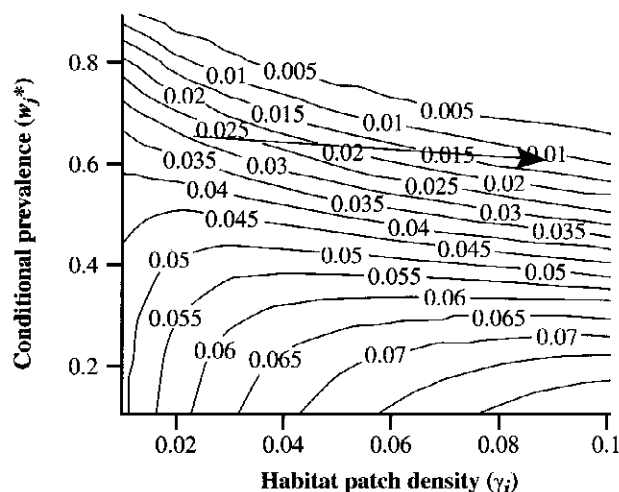$$\left.\frac{\partial \gamma_j(\Gamma)}{\partial \Gamma}\right|_{\Gamma_0} \approx p_j \qquad [12c]$$

FIGURE 4. Contour diagram of the typical relationship between habitat patch density (γ_j, x-axis) and the equilibrium regional extinction rate, E_j^*, as a function of conditional prevalence, (w_j^*, y-axis) as determined by equation 8. The general relationship is robust over most parameter combinations, although the exact topography obviously varies (other parameters chosen: $e_j(\cdot)$ given by equation 11, $A = 100$, $k_j = 1.0$, $x_j = 0.1$, $p_j = 0.1$, $p_c = 0.5$ and defined in Table I). The sensitivity of regional extinction rates (E_j^*) to changes in habitat patch density (γ_j) is dependent on x_j. Note that under some circumstances, regional extinction rates can decrease with decreasing conditional prevalence (see arrow).

The behaviour of each derivative in equations 12a-c is influenced by a largely independent suite of parameters, and knowledge of conditional prevalence characteristic of Γ_0 is not informative of any one of them. Effects of fragmentation on species prevalence cannot be anticipated from knowledge of only their pre-disturbance prevalence, but depend on relative magnitudes of a positive effect (increase in patch density) and a potentially negative effect (increased local extinction rates in smaller patches). Widespread species whose susceptibility to local extinction increases rapidly as population size falls (high x_j) could experience sharp decreases in conditional prevalence subsequent to fragmentation. Alternatively, if x_j is low, fragmentation can actually increase conditional prevalence through increased rates of local colonization. Moreover, the relationship between conditional prevalence and regional extinction rate is not simple. Decreases in conditional prevalence can be associated with increased representation if the number of suitable patches increases enough. How different types of species (as described in Figure 2) might react to fragmentation is difficult to generalize. Some possibilities are indicated in Figure 5. Different species respond differently to fragmentation in ways that are hard to predict. Species characterized by values of $x_j > 1$ are more vulnerable to effects of fragmentation than those for which $x_j < 1$, but it is always possible to construct fragmentation scenarios over at least some range of Γ values for which such a generalization is not valid. Conditional prevalence decreases as a result of fragmentation if rates of local extinction increase faster than local rates of colonization (i.e., if $x_j \Gamma_0^{x_j-1}/k_j > \mu_j p_j \pi r_j^2$). The only robust generalizations are that when $x_j = 1$ all these derivatives are independent of Γ, and that increases in local extinction rates resulting from the reduced average area of habitat patches are precisely compensated for by the increased density of patches in the landscape. Under
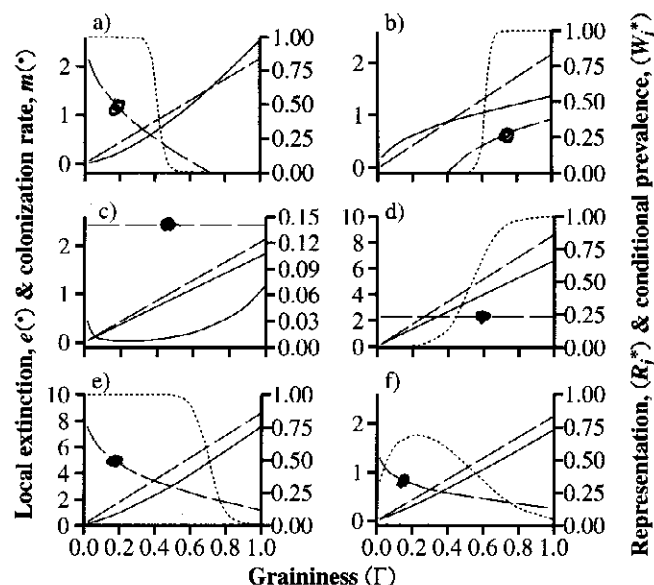

FIGURE 5. a-f) Effects of changing landscape grain (Γ) on species local extinction (e_j ($\cdot$) from equation 11, solid line) and colonization functions (m_j ($\cdot$) from equation 10, dashed line) on the left axes, and representation probabilities (R_j^* from equation 9, dotted line) and condition prevalences (w_j^* from equation 7, dashed-dotted line) on the right axes. a) $r_j = 4$, $k_j = 0.5$, $x_j = 1.5$; b) $r_j = 4$, $k_j = 0.5$, $x_j = 0.5$; c) $r_j = 4$, $k_j = 0.5$, $x_j = 1.0$; d) $r_j = 8$, $k_j = 0.14$, $x_j = 1.0$; e) $r_j = 8$, $k_j = 0.2$, $x_j = 1.32$; f) $r_j = 4$, $k_j = 0.54$, $x_j = 1.15$; (other parameters: $A = 10\,000$, $\mu_j = 1$, $C = 0.001$, $S = 100$, $z = 100$, $f_i = 0.01$ for all $i > 0$. Each species is capable of inhabiting five different habitat types. Parameters are defined in Table I). The take-home message from this figure is that even the qualitative effects of changes in landscape grain on species conditional prevalence and representation are highly sensitive to the exact shapes of functions governing local extinction and colonization rates.

these circumstances, conditional prevalence remains unaffected by fragmentation, although population turnover times increase.

HABITAT SUBSTITUTION

What happens as the number of different types of cells (z) in the landscape is increased, while average total cell density (Γ) remains fixed? Obviously, the density of cells of any one type (γ_j) must decrease. As a result, local colonization rates fall together with conditional prevalence while regional extinction rates increase. However, the increased number of cell types in the landscape may permit representation of a greater number of species from the regional species pool. Thus species richness can be expected to increase until the density of habitat patches particular to each species decreases to such low levels that lower conditional prevalences and higher regional extinction rates counter the positive influence of increased patch type diversity. Examples are shown in Figure 6.

HABITAT REMOVAL

Effects of habitat removal (such as those resulting from human usurpation) can be explored by increasing the unusable fraction of the landscape, f_0. If grain, Γ, is held constant then cell areas remain constant, but because the proportion of landscape that contains suitable habitat for the jth species (p_j) declines, the number (n_j) and/or average area (h_j) of habitat patches will decrease. Therefore our analysis predicts that habitat removal always results in lowered con-
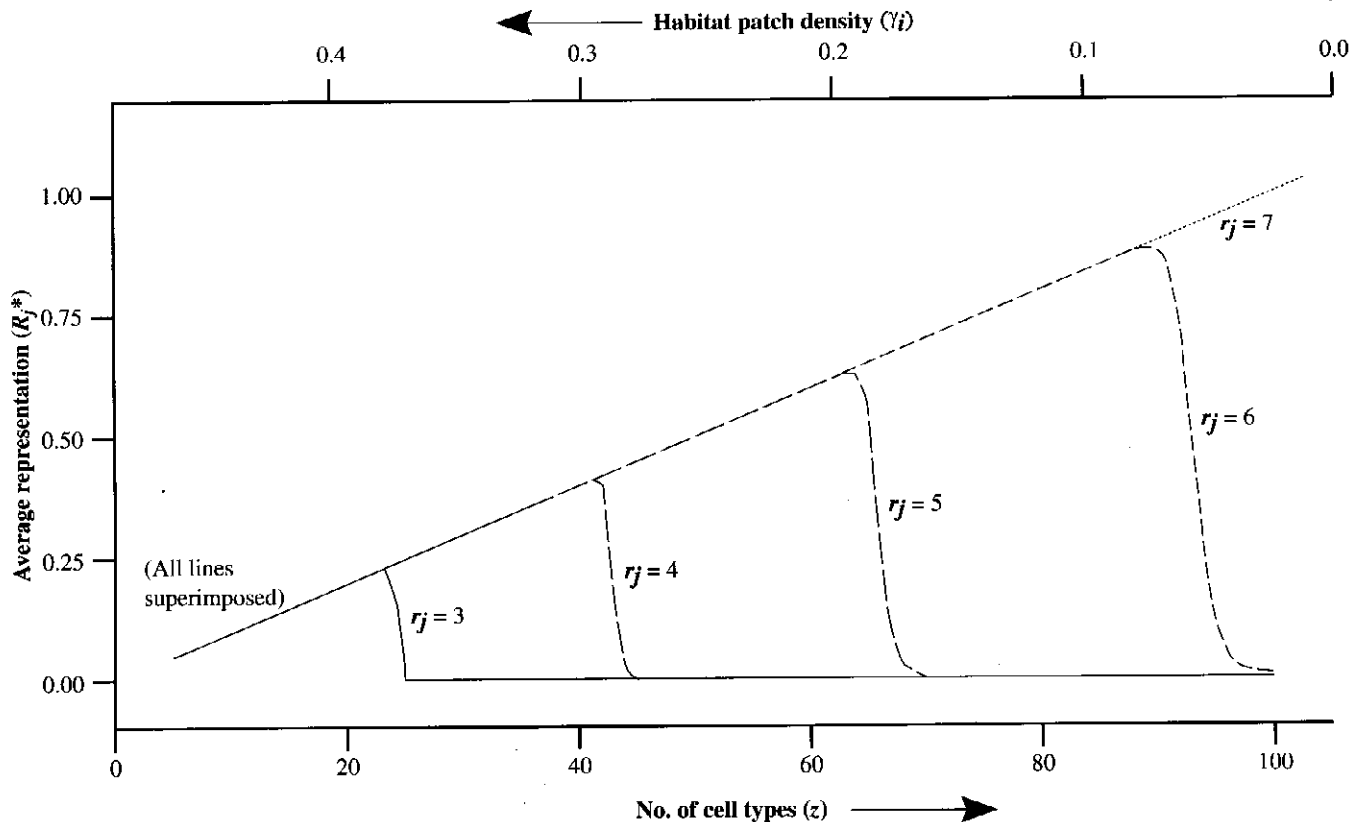
FIGURE 6. Effects of habitat substitution. Number of different cell types (z) is increased (lower x-axis) while holding constant overall cell density (Γ), with the effect that the density of habitat patches (γ_j) decreases (upper x-axis). Ultimately, effects of these landscape changes on species reduces their conditional prevalence with a consequent increase in their regional extinction rates. However, landscapes with a greater diversity of cell types potentially support a greater subset of the regional species pool. Observed average representation is a balance of these opposing influences—maximum representation can occur at an intermediate value of cell diversity. As expected, more vagile species (higher r_j) and those with lower local extinction rates maintain higher conditional prevalences and are more likely to be represented in landscapes with less habitat, thus the habitat diversity that maximizes overall species diversity increases with species vagility. ($x_j = 1, k_j = 1, \mu_j = 1, S = 100, C = 0.001, \Gamma = 5, f_i = 1/z, i > 0$, each species in the regional species pool is assumed to be able to use a single different habitat type. Parameters defined in Table I).

ditional prevalence, increased regional extinction rates, and reduced representation. Spatially explicit formulations of this model with realistic configurations of habitat patches would permit different patches of the same habitat type to be ranked in order of the effect of their removal on the species assemblage.

MODELLING HETEROGENEOUS SPECIES ASSEMBLAGES: THE SPECIES CUBE

A three-dimensional parameter space is defined, within which every member of the regional species pool can be positioned. The three axes of this volume correspond to the three characteristic species parameters: the species density parameter, k_j; the species vagility, r_j; and the way in which local extinction rates change with habitat area, x_j. We term this parameter space the "species cube." The capacity of different landscapes (constructed under our formulation, containing up to z different habitable cell types) to accommodate members of such a species cube is easily examined with more complex computation. For example, let the three characteristic parameters for S members of the regional species pool be random variables drawn from specified uniform distributions, so that the density of species in the parameter volume is even throughout. Assign to each

member of this hypothetical species pool a particular combination of usable cell types, Ω_j, ($\Omega_j \subseteq \Theta$, $\Theta = \{1... z\}$). The probability that different members of this species pool will be represented in a variety of landscapes can now be examined directly.

In Figure 7, results of such an exercise are illustrated. Species are designated "present" if they have a greater than 50% chance of representation. Figure 7a shows that, as predicted, regional diversity is maximized at an optimum number of different habitat types in the landscape. Beyond this optimum, habitat types are not present in sufficient quantity across the landscape to support sustainable populations of species able to persist in less habitat diverse landscapes. Figure 7b shows the subset of this species pool present in a particular landscape containing 22 different cell types. In this example, represented species are more vagile and maintain denser local populations. Figures 7c and d illustrate changes in the represented species pool after a four-fold increase in fragmentation. Additional species able to invade this landscape (Figure 7c) are vagile, with lower values of x_j (thus less impacted by changes in the average area of habitat patches), and can persist with populations at lower density than their pre-fragmentation associates. Species that are lost (Figure 7d) as a result of the
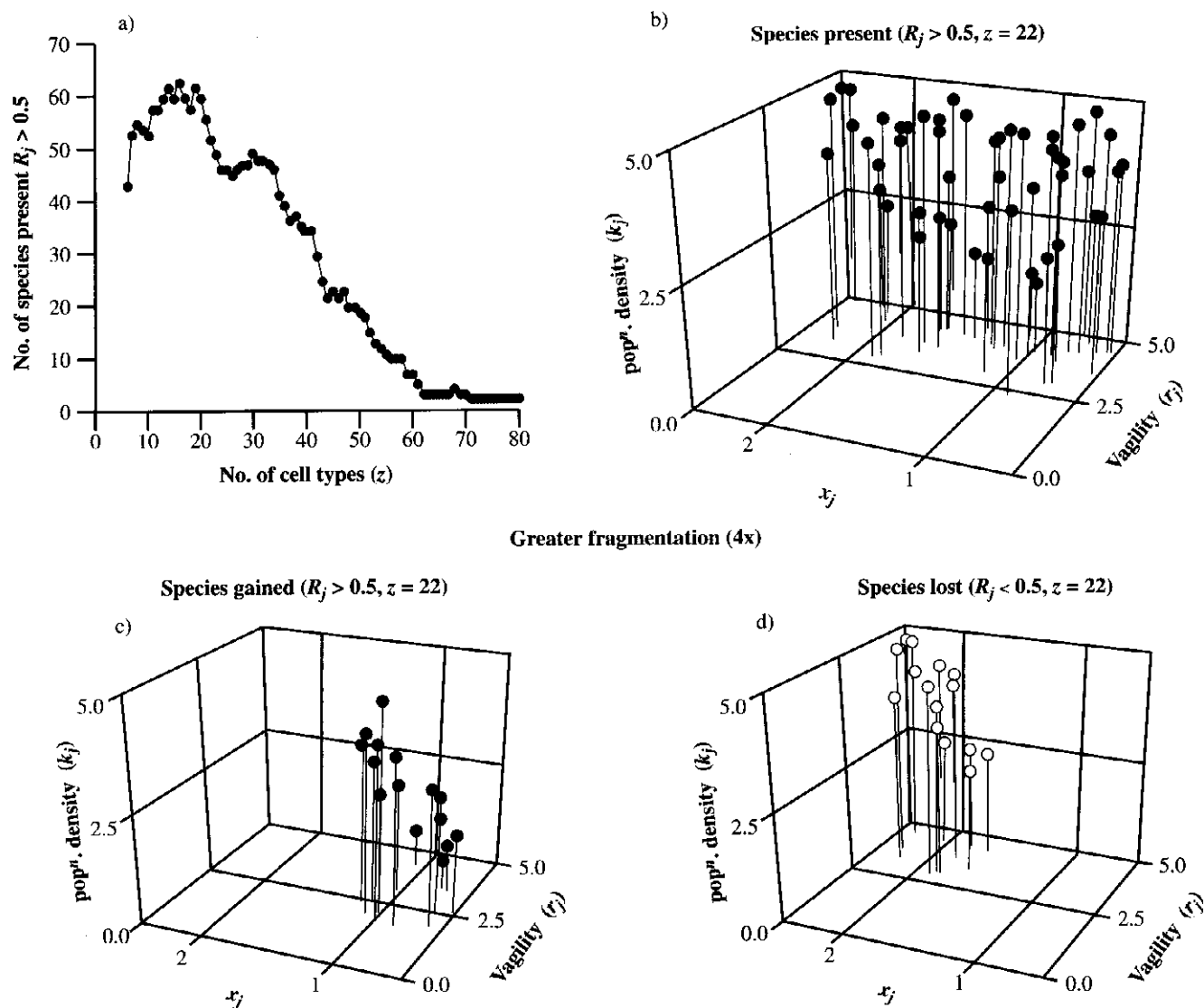
FIGURE 7. The species pool is composed of 800 members. Each species is characterized by a maximum dispersal distance (r_j), density parameter (k_j) and sensitivity to fragmentation (x_j), drawn from uniform distributions (0, 10), (0, 5) and (0.5, 2.5) respectively. Each species is a specialist, equally likely to be capable of inhabiting any one of 80 different cell types. Species are judged to be "present" if its representation (R_j) exceeds 0.5. Figures 7a and b are evaluated for a landscape with $\Gamma = 2.0$. Figure 7a shows how the expected number of species represented in the landscape varies as a function of increasing the diversity of cell types (habitat subsitution), Figure 7b shows positions in species parameter space (the "cube") of those members of the regional species pool represented on a landscape with 22 different cell types. Positions in the species parameter cube of species gained and lost in the landscape after a four-fold fragmentation are indicated in Figures 7c and d. (Other parameters $A = 10$, $f_0 = 0$, $\mu_j = 1$ for all j, parameters defined in Table I).

fragmentation are characterized, as would be expected, by sensitivity to smaller habitat patches (higher values of x_j).

Discussion

Our model analysis suggests three main sets of conclusions. First, the effect of pure habitat fragmentation (that is, in the absence of habitat removal) can either enhance or reduce species prevalence depending on the relative sensitivity of its dispersal abilities and local extinction proneness to landscape grain. When local extinction events are not overly sensitive to small patch areas, high landscape grain may permit existence of species that would otherwise be precluded from the region as a result of low vagility. Existing levels of species prevalence are uninformative of

the consequences of landscape fragmentation. Changes in a species' conditional prevalence are usually inversely proportional to accompanying changes in regional extinction rates, but because increasing landscape grain actually increases the number of discrete habitat patches, species prevalence and representation need not be influenced in the same direction. Second, high levels of habitat diversity only result in high levels of regional diversity if areas of habitat are represented in usable sized portions. Regional species representation can be optimized at an intermediate level of cell type diversity. Third, habitat removal always lowers conditional prevalence, increases regional extinction rates, reduces representation, and decreases species diversity.

Despite the complexity of our model, it is grossly simplistic in many ways. Most injurious is the assumption that

species are not impacted by interspecific interactions. This criticism can be made of all single-species metapopulation models, but it becomes less easy to forget in a multi-species model. However inclusion of species interactions in multi-species metapopulations has received attention (reviewed in Holt, 1997) and is computationally straightforward. Species can be placed in competitive hierarchies, such that competitively dominant species may displace competitively inferior species from occupied patches, and only empty patches and those containing competitively inferior species are available for colonization. Predator-prey interactions can be included by defining usable predator habitat as the subset of their normal habitat also occupied by suitable prey species. Trophic webs of arbitrary complexity can be considered in this way. These approaches have allowed some analytic insight (Holt, 1997). Usually competitively superior species are assumed to be habitat specialists with lower dispersal prowess than their more generalized competitors. Such assumptions permit a plethora of counter-intuitive observations to be made (Nee & May, 1992; Tilman *et al.*, 1994); however, grounds for these assumptions are currently little more secure than those justifying omission of interspecific interactions altogether.

Our measures of representation and conditional prevalence are not informative of actual population abundances because within-patch population dynamics are not considered explicitly. This simplification is justified when migration and extinction processes are not highly sensitive to variation in local population density or when within-patch dynamics occur on much faster time scales than between-patch processes, so that populations exist for the most part at a single characteristic density. However, by introducing correlations between parameters governing a species' metapopulation dynamics, some accommodation for this simplification can be made. For example, imposing a positive correlation between expected lifetime of local populations in patches of unit area (k_j) and rate of dispersal from occupied patches (u_j) for all species in the regional species pool serves to relate characteristic population densities to dispersal rate, and causes species with high rates of dispersal to go locally extinct less often. There is certainly no reason to suppose that species are uniformly distributed thoughout the species cube.

The negative impact of fragmentation on species distribution and abundance has been often documented (Macnally & Bennett, 1997; Bowers *et al.*, 1996; Hinsely *et al.*, 1996; Lacy & Lindenmayer, 1995; and Hanski *et al.*, 1995, to name only a few). Separating effects of habitat fragmentation from habitat removal usually requires carefully designed experimentation, and can lead to equivocal results (*e.g.*, Wolff, Schauber & Edge, 1997; Johannesen & Ims, 1996, but see Fahrig, 1997). Clearly, negative effects of pure fragmentation can arise through a diverse array of mechanisms (demographically stochastic local extinction, reduced mating success, inbreeding depression, decreased survival rates mediated through limitations of food, shelter, increased predation, disperser mortality, etc.). Any tendency of fragmentation to increase species representation and/or prevalence are probably at least as diverse. As pointed out by Doak, Marino & Kareiva (1992), studies do not always fully

elucidate the precise ecological mechanisms by which populations are influenced by fragmentation, but the plethora of ecological mechanisms responsible for these patterns could perhaps be categorized into many fewer classes of explanation (for example, perhaps corresponding implicitly to the value of parameters k_j and x_j in our model).

The method of habitat assembly results in larger contiguous habitat patches for more generalized species, but a weakness of our model is that all cell types are of the same approximate size. This results from using a simple planar Poisson point process around which to construct the Voronoi tessellation. Voronoi tessellations can be constructed around any point process, and a Neyman-Scott process is a useful alternative to the simple planar Poisson process (see Stoyan & Stoyan, 1994; or Cox & Isham, 1980, for a detailed treatment). A Neyman-Scott process assumes that so-called "parent points" are distributed according to a simple planar Poisson process of specified intensity, but that around each parent point, a certain number of daughter points are scattered according to some other intensity and spatial distribution, which might for example be normal, or another Poisson. By varying the ratio of parent/daughter intensities, and the number of daughter points around each parent, a wide variety of point patterns with different clumping characteristics can be generated. When Voronoi tessellations are constructed around these point fields, areas of increased point intensity are characterized by smaller cells. If desired, the designated type of each cell can then be correlated with its area. Examples are given in Figures 8a and b. Development of theory that explicitly accounts for second moments of patch areas in landscapes remains a problem that theoreticians should address. Some anthropogenically imposed landscape features are linear, such as easements and boundaries, and might best be modelled with a Poisson line tessellation generated by randomly bisecting a plane (Figure 8c). Analytic results exist for these tessellations and are discussed in Miles (1964) and Stoyan & Stoyan (1994).

Many landscape studies have shown that habitat edge is an important predictor of species performance on landscapes (Gates & Gysel, 1978; Roland, 1993; Fritz & Merriam, 1996; Abowers *et al.*, 1996; Didham *et al.*, 1998). If areas of landscape comprising patch boundaries are themselves habitat for members of the regional species pool, this is an additional reason why fragmentation may result in increased prevalence of these species. Configuration of edge habitat types can be examined within the context of multi-state Voronoi tessellations by low series expansions corresponding to patch edge, similar to those used here for patch area (see Stauffer, 1979 and references therein).

Voronoi diagrams are attractive because they constitute a parsimonious method of map making (along lines suggested by Kendall, 1971). If the ecology of a region is known only from an established limited set of points, then this knowledge is transformed into an approximate map by construction of the accompanying Voronoi tessellation. Cells within tessellations are attributed to the same "type" as the point around which cell boundaries were constructed. An adaptive point sampling program could be constructed
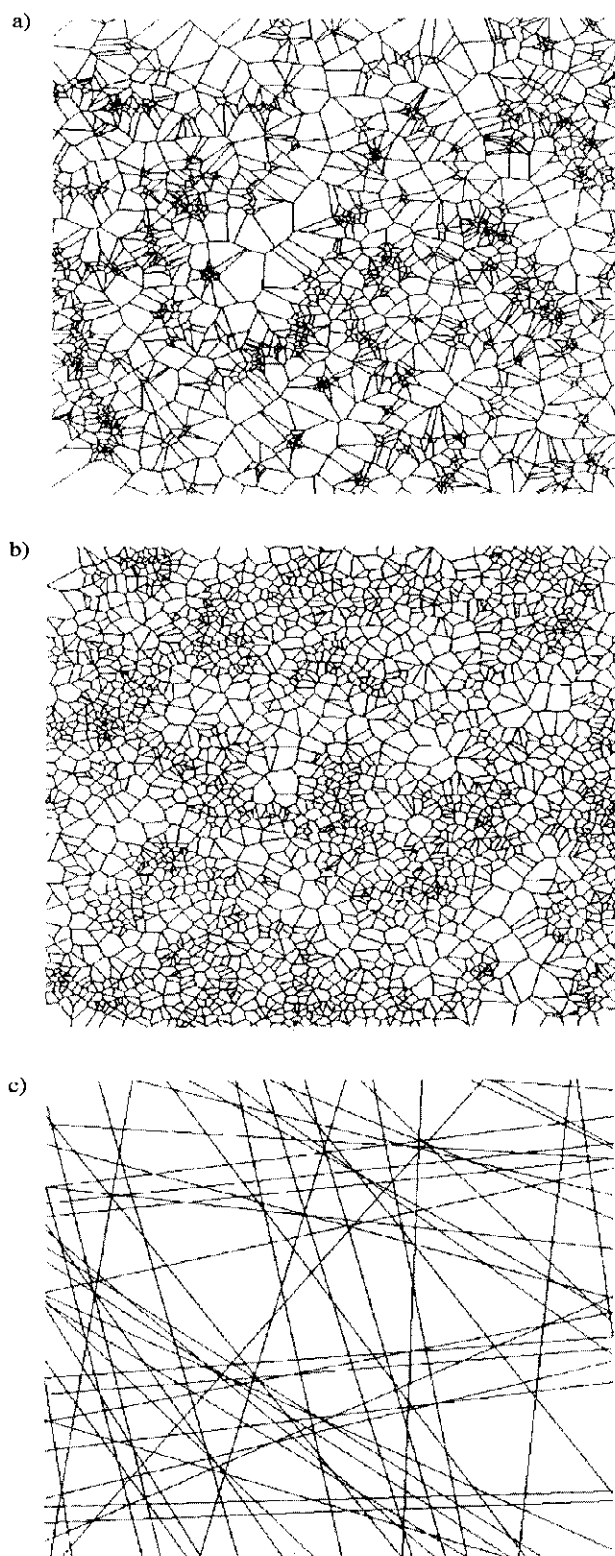
a)

b)

c)

FIGURE 8. Alternative landscape models. a-b) Voronoi tessellations constructed around point fields formed by Neyman-Scott processes. In cases a and b, parent points are scattered according to a primary Poisson process with the same density, a fixed number of daughter points (in this case 10) are then scattered around each parent point according to a second Poisson process with density 100 x (a) and 6 x (b) that of the parent process. c) A Poisson line field: points at which random lines intersect with a single fixed line form a linear Poisson process; intersecting angles are independent and have a known distribution function.

whereby additional sampling was focused in those parts of the region believed (on the basis of preliminary sampling) to contain increased environmental or vegetative gradients.

A critical component to understanding regional species persistence is the parameters contained in the function governing local population extinction rate. Methods to recover these parameters from incidence data exist, and values of x_j ranging between ~0.2 to ~2.5 (with a probable positive correlation with body size) have been suggested (Hanski, 1994a,b; Cook & Hanski, 1995; see also Didham *et al.*, 1998; Schoener & Spiller, 1992). Alternatively, expected time to population extinction might not depend on patch area, but be determined instead by the timescale of a successional process that transforms suitable habitat into unsuitable habitat. If transition probabilities of patches proceeding from one state to another are Markov, and can be described by a matrix akin to a Leslie matrix (Horn, 1975), then the areas of the landscape in each state (the a_i values) are given by elements of the eigenvector associated with the leading eigenvalue of this matrix. The expected time that a patch remains in a particular state is given by one over the sum of probabilities of the patch undergoing transition from its existing state to some alternative state. We can think of no reason why these sorts of temporal patch dynamics and local extinction functions could not be considered within the general framework outlined here, except that the successional process would have to take place within the essentially static outline of original patch boundaries.

We have presented results in the context of species responses to changing landscapes, but our results are not limited to considerations of such change. Results of our analysis address how the interaction of landscape and species properties influences species diversity. They suggest that even assuming the most simplistic of possible models and in the absence of interspecific interactions, the influence of landscape on the representation of the regional species pool may depend in counter-intuitive ways on several elusive species parameters. Thus the results suggest that two regions containing similar habitat but characterized by different measures of landscape grain might differ substantially in their capacity to represent different species. This observation is relevant at all spatial scales. For small invertebrates, this might apply to the spatial distribution of individual host plants (Singer, 1972; van der Meijden, 1979; van der Meijden *et al.*, 1992), for larger species it might apply to the distribution of old-growth forest across an entire biome (Lamberson *et al.*, 1994; Andersen & Mahato, 1995). Differences in grain structure might arise from application of a disturbance agent or process at different spatial scales. Similarly, our model predicts that a region could contain within it so many habitat types that each of them is present, but in configurations unable to support species specialized to them. Such landscapes could appear to be unsaturated with respect to the regional species pool.

Our analysis offers a sharp reminder that metapopulation theory, while usually focused on the dynamics of species that are declining within landscapes, provides a clear theoretical basis for how landscape changes may facilitate invasion by previously unrepresented members of the

regional species pool. In fact, when studying heterogeneous species assemblages using the "species cube," greater species richness was often observed after landscape perturbations, not before. While fragmentation is often regarded as detrimental to population endurance, there are scenarios in which particular species may benefit from it (Didham *et al.,* 1998). In addition to predictions of single species (non-interactive) models, spatial fragmentation can foster coexistence of interactive multi-species complexes, particularly when trade-offs are required between different life-history strategies (Lavorel, O'Neill & Gardner, 1994; Tilman, 1994; Comins & Hassell, 1996). The extent to which effects of interspecific interactions on single-species population dynamics may be successfully subsumed into parameters of single-species population models is likely to determine in large part the degree of insight that theory can provide to this line of enquiry.

Landscape ecology represents ecology studied at one of its larger scales. As a result, it is tempting to view it as, in some sense, a sum of multitudinous smaller processes. Therefore any "theory" of landscape ecology might, in the same sense, be a "meta-theory," *i.e.,* a polymerous chain of existing models. Many ecologists would probably share a tendency to view with some skepticism the predictions of theory based on such implausibly long chains of assumptions. We fully share this skepticism, but caution that what might be skeptically regarded in its entirety, should not be less critically evaluated when presented piecemeal. If we accept that populations fluctuate, we need to accept the likelihood that they undergo local extinction; local extinction events are likely to be balanced by colonization events. If we even equivocally accept the metapopulation paradigm, we must also accept the likelihood that many such metapopulation processes operate simultaneously at the landscape level across a range of spatial scales. We must not avoid higher-level implications of processes less questionably accepted in simpler form. Part of the value of ecological theory is that it forces such rigor upon us. Complete extension of theory is necessary to establish its credible bounds. Important lessons remain to be learned by staying within these bounds, and from knowing when we stray too far beyond them. A bridge between landscape ecology and population dynamics currently requires a disagreeable and unconvincing number of spans, each with its own peculiar fragilities. Until theoreticians can devise longer, more robust spans, it is likely to remain a bridge too far.

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