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6. Communities in Patchy Environments: A Model of Disturbance, Competition, and Heterogeneity

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All landscapes are to some extent patchy. The biological heterogeneity of communities on patchy landscapes reflects the time scales of local biotic interactions and abiotic disturbance, the time and space scales of dispersal, and (especially) the interaction of these scales. To investigate these factors, we examine here a simple model that provides a framework for building models of patchy communities directly from hypotheses about time scales. The model has numerous applications (Caswell and Cohen, 1991, in preparation); here we focus on the interplay of competition and disturbance as well as the kinds of biological heterogeneity that can be maintained by that interplay.

Our model describes a landscape composed of an effectively infinite set of effectively identical patches. Species colonize these patches, interact, are affected by abiotic disturbance, and eventually become locally extinct. Each of these processes has a characteristic temporal scale, in terms of which we describe the stochastic dynamics of individual patches and the resulting statistical properties of the landscape. Because we assume that all patches are identical, we are providing only the bare minimum of *environmental heterogeneity*—that produced by the independence of the patches. Our focus is on heterogeneity generated by the biological processes.

Consideration of the interaction of competition and disturbance has led to two important ecological concepts. The first is the idea of *fugitive species*

(Hutchinson, 1951), which persist regionally even though they are excluded locally by nonfugitive or *equilibrium species.* Fugitive species rely on disturbance to perturb the process of local competitive exclusion and cannot persist in its absence. The existence of fugitive species makes it impossible to infer competitive dominance from relative abundances; depending on the rates of disturbance, dispersal, and within-patch interactions, fugitive species may be much more common than competitive dominants.

The second concept is the maximization of species diversity at an intermediate disturbance frequency (Connell, 1978a,b; Huston, 1979). If disturbance is too rare, local competition proceeds to equilibrium and fugitive species are eliminated. If disturbance is too frequent, it eliminates all species and produces a desert. At intermediate frequencies, the combination of fugitive species and equilibrium species produces a maximum in species diversity.

The relation between disturbance and diversity is likely to be affected by resource supply rates or productivity. Huston (1985), in a discussion of coral reef communities, proposed that at high light intensities rapid coral growth should lead to rapid competitive exclusion and require a higher frequency of disturbance to maintain diversity than at lower light intensities. Discussions of the possible role of disturbance in maintaining high species diversity in deep-sea benthic communities (e.g., Dayton and Hessler, 1972; Grassle and Sanders, 1973; Rex, 1981, 1983) have emphasized the apparent low frequency of disturbance in the deep sea. However, it is known that growth rates and productivities in these communities (hydrothermal vents excluded) are low. Thus it is entirely possible that the time scale on which disturbance frequency must be measured is different in the deep sea.

Diversity enhancement is at odds with the concept of *biotic impoverishment* (Woodwell, 1983): that disturbance leads to shortened food chains, decreased diversity, and dominance by the handful of species hardy enough to resist the disturbance. Biotic impoverishment is a well documented response to radiation, pollution, and overgrazing.

At least two resolutions exist to this apparent contradiction. First, the disturbances that lead to biotic impoverishment tend to be chronic, whereas those leading to enhancement tend to be transient at any one spot. Whether disturbance leads to diversity enhancement or biotic impoverishment might depend on disturbance frequencies. Second, some disturbances, especially anthropogenic ones, delay recolonization for a long time. Levin and Smith (1984), for example, found that whereas defaunated sediment in the Santa Catalina basin was recolonized slowly, as is usually the case in the deep sea, defaunated sediment enriched by kelp was essentially uncolonized by macrofauna for the duration of their study. Such delays in recolonization may keep disturbance from enhancing diversity. Evolutionarily novel disturbances such as toxic waste are more likely to have long-lasting residual effects, which may make them more likely to produce biotic impoverishment than to enhance diversity.

Model Structure

Consider a patchy landscape inhabited by N species, $S_1, S_2, \ldots, S_N$. The landscape consists of an infinite set of physically identical patches. The state of a patch is determined by the presence or absence of each of the N species; there are thus 2^N possible states for each patch. These states can be conveniently numbered from 1 to 2^N by adding 1 to the binary representation of the presence and absence of each species. Consider two competing species, of which S_1 is locally superior to S_2, and let 0 denote absence and 1 denote presence. We then have

Species 2 (loser)	Species 1 (winner)	State
0	0	X_1
0	1	X_2
1	0	X_3
1	1	X_4

We denote the possible states of a patch by X_s, $s = 1, 2, \ldots, 2^N$. The proportion of all patches that are in X_s, is denoted by x_s; the state of the landscape is given by a vector $\mathbf{x}$, the elements of which give the proportion of patches in each of the states. This definition of the state of the landscape assumes that the spatial arrangement of the patches is unimportant, so that any landscape with a specified proportion of its patches in each state is effectively identical to any other such landscape.

The dynamics of the community are described by a nonlinear, discrete-time Markov chain

$$\mathbf{x}(t+1) = \mathbf{A}_\mathbf{x}\mathbf{x}(t) \tag{1}$$

where $\mathbf{A}_\mathbf{x}$ is a column-stochastic matrix whose elements may depend on the vector $\mathbf{x}$. An element $a_{rs}(\mathbf{x})$ of $\mathbf{A}_\mathbf{x}$ gives the transition probability from X_s, to X_r.

The transition probabilities a_{rs} are calculated from hypotheses about the time scales of interspecific interactions, dispersal, and disturbance. In general, the rate of a process is given by the inverse of the time scale on which that process occurs.

Colonization plays an important role in these models because any satisfactory description of the colonization process renders the model (1) nonlinear. The probability that a patch is colonized by S_i in $(t,t+1]$ depends on the proportion of patches in the landscape in which S_i is present. Thus the entries a_{rs} that depend on colonization are functions of the current state vector **x**.

We make the following hypotheses about competition, dispersal, and disturbance.

1. Disturbance follows a Poisson process, with a time scale (mean time between disturbances) given by τ_d. The expected number of disturbances per unit time is τ_d^{-1}, and the probability of at least one disturbance in the interval $(t,t+1]$ is

$$p_d = 1 - e^{-\tau_d^{-1}} \tag{2}$$

2. The rate of competitive exclusion is specified by τ_c, the mean time required for S_1 to exclude S_2. If the probability of exclusion during the interval $(t,t+1]$ is p_c, the time required for exclusion (t_c) follows a zero-truncated geometric distribution, with

$$P(t_c = k) = p_c(1-p_c)^{k-1} \qquad k = 1, 2, \ldots \tag{3}$$

The mean time required for exclusion is then $\tau_c = E(t_c) = p_c^{-1}$. Thus

$$p_c = \tau_c^{-1} \tag{4}$$

3. Colonization follows a Poisson process. The mean number of colonists of species i, $i = 1, \ldots, N$, arriving in a vacant patch in $(t,t+1]$ is proportional to the frequency of occurrence of species i. The constant of proportionality (the *dispersal coefficient*) d_i combines the effect of the production of offspring by populations in the occupied patches and the success at dispersal of those offspring. Let f_i denote the frequency of S_i; e.g., in our two-species example $f_1 = x_2 + x_4$ and $f_2 = x_3 + x_4$. The conditional probability of at least one colonist arriving in a patch, given that the patch is vacant, is then

$$C_i = 1 - e^{-d_i f_i} \tag{5}$$

4. Either or both species may colonize a vacant (X_1) patch; the winning species S_1 may also colonize a patch (X_3) containing S_2, but the losing species S_2 may not colonize a patch (X_2) that contains the winning species.
5. Disturbance affects only patches containing species. Thus empty patches (X_1) are not subject to disturbance while colonization is in progress.

Each of these hypotheses may be modified, but this simple model allows us to demonstrate the approach in the context of disturbance and competition.

A directed graph showing the possible transitions among the community states is shown in Figure 6.1. The corresponding transition matrix $\mathbf{A_x}$, which determines the dynamics in equation (1) is

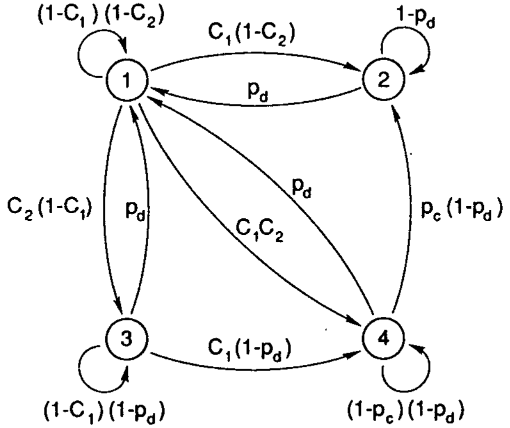

Figure 6.1. State transition graph for the two-species competition model. See text for definitions of states and notation.

$$\begin{pmatrix} (1-C_1)(1-C_2) & p_d & p_d & p_d \\ C_1(1-C_2) & 1-p_d & 0 & (1-p_d)p_c \\ (1-C_1)C_2 & 0 & (1-C_1)(1-p_d) & 0 \\ C_1C_2 & 0 & C_1(1-p_d) & (1-p_d)(1-p_c) \end{pmatrix} \tag{6}$$

where the C_i values are given by equation (5).

Analysis

The analysis of this class of models is challenging only because of the nonlinearity introduced by the dependence of colonization probabilities (equation 5) on the current state $\mathbf{x}(t)$, through f_i. If not for that nonlinearity, the model would be a linear, finite-state Markov chain, and standard methods would tell us everything there is to know about it.

The nonlinear model has several potential classes of dynamic behavior. The simplest is convergence of $\mathbf{x}(t)$ to a stable fixed point $\hat{\mathbf{x}}$. Once the community reaches such a fixed point, the matrix **A** is constant, and standard Markov chain methods can be applied. The nonlinear difference equation (1) may in principle also possess periodic, quasiperiodic, and chaotic attractors. We have no a priori reason to rule out these possibilities, but after extensive numerical investigation we have never found any of them. We conjecture that this model always has at most a single fixed point in the interior of the unit simplex, and that this fixed point attracts all initial vectors in the interior of the simplex.

Fixed Points and Stability

The existence of at least one fixed point in the closed unit simplex (including its boundaries) is guaranteed by the Brouwer fixed point theorem. Depending on the parameter values, some of these fixed points are on the boundaries, corresponding to landscapes in which one or more species are absent. Conditions guaranteeing the existence of an interior fixed point are difficult to obtain.

The stability of fixed points is surprisingly difficult to analyze. The simplest possible model, with one species and two states, can be reduced to a one-dimensional map of the interval (Caswell and Cohen, in preparation). In this model, if the dispersal rate is less than the disturbance rate, 0 is the only fixed point. If the dispersal rate is greater than the disturbance rate, there is an interior fixed point that is always globally stable. However, we have been unable to extend this proof to higher-dimensional models.

As an alternative, we carried out a numerical search for *un*stable equilibria, randomly sampling parameters from the sets $d_1 \epsilon (0,10)$, $d_2 \epsilon (0,10)$, $p_d \epsilon (0,1)$, and $p_c \epsilon (0,1)$. For each parameter set, we used a nonlinear equation-solving routine (part of the GAUSS software package, Aptech Systems, Inc., Kent, WA 98064) to find as many fixed points as possible. The local stability of these points was evaluated by calculating the linear approximation to the system at that fixed point and evaluating the eigenvalues of the resulting Jacobian matrix. If all the eigenvalues are less than 1 in magnitude, the fixed point is stable.

Examination of several thousand samples from the parameter space revealed no unstable interior fixed points. It is not a proof but it is the best we can do now.

Model Output

The output of the four-state model (or its generalizations) is surprisingly copious, considering its simplicity. It includes the following.

1. *State frequencies*. The immediate output of the model is the vector of equilibrium state frequencies $\hat{\mathbf{x}}$, which provides the basic description of the landscape. The other output variables are calculated from $\hat{\mathbf{x}}$.

2. *Species frequencies*. The frequency (or prevalence) of species i is given by the sum of the state frequencies for the states in which that species is present.

3. *Alpha diversity*. Local (or alpha) species diversity is measured by the mean number of species per patch. For our two-species example,

$$\alpha = x_2 + x_3 + 2x_4 \tag{7}$$

The variance in alpha diversity provides one measure of spatial heterogeneity in community structure. For the two-species example it is

$$V(\alpha) = x_2 + x_3 + 4x_4 - \alpha^2 \tag{8}$$

4. *Beta diversity*. Beta diversity measures spatial heterogeneity in species composition. It can be measured in a number of ways, one of the simplest being the entropy of the state frequency vector.

$$\beta = -\sum_{s=1}^{2^N} x_s \log x_s \tag{9}$$

A value of $\beta = 0$ corresponds to a homogeneous landscape. In practice, beta diversity is usually considered only in terms of the biological component of heterogeneity, with empty patches being ignored. We refer to it as biological beta diversity, and calculate it as

$$\beta_b = -\sum_{s=2}^{2^N} \left(\frac{x_s}{\sum_{j=2}^{2^N} x_j} \log \left(\frac{x_s}{\sum_{j=2}^{2^N} x_j} \right) \right) \tag{10}$$

A value of $\beta_b = 0$ corresponds to a landscape in which all occupied patches are homogeneous, although there may be some heterogeneity due to the presence of empty patches.

5. *Species–area slope*. Increasing the number of patches in a sample increases the number of species collected. The shape of the curve relating the number of species to the number of patches, or area, is sometimes used as a measure of diversity. It is possible to calculate the expected number of species found in any specified number of patches by a simple extension of the calculation of alpha diversity above. There are $(2^N)^k$ possible combinations of states in a sample of k patches (e.g., for $k = 2$, the two patches are respectively in states X_1 and X_1 with probability x_1^2, X_1 and X_2 with probability $x_1 x_2, \ldots, X_4$ and X_4 with probability x_4^2), each of which yields a specific number of species. The average taken over this distribution gives the expected number of species in a sample of k patches.

6. *Interspecific association patterns*. The equilibrium state vector $\hat{\mathbf{x}}$ contains all the information necessary to calculate the association between any pair of species. A number of association indices are available. One of the simplest in the two-species case is the log odds ratio

$$\log \left(\frac{x_1 x_4}{x_2 x_3} \right) \tag{11}$$

which is positive when the species tend to occur together, zero when they are independently distributed, and negative when they tend to occur alone. Association indices are discrete analogues of spatial niche overlap measures, indicating the extent to which the species co-occur in space.

7. *Rates of community change*. Along with the equilibrium state vector $\hat{\mathbf{x}}$, the model provides the equilibrium Markov matrix $\mathbf{A}_{\hat{\mathbf{x}}}$, which describes the dynamics of the landscape. Because these dynamics are described by a homogeneous Markov chain, it is easy to calculate a variety of measures of rates of community change. An ecologist following the fate of patches within this landscape might find some types of patch to be ephemeral, whereas others persist for long times. Certain developmental pathways (e.g., an empty, disturbed patch changing to a patch occupied by only the competitive dominant) might be traversed rapidly, others slowly. Insight into these dynamic patterns can be obtained from the following measures.

a. *Turnover rates*. Although the landscape reaches an equilibrium, characterized by $\hat{\mathbf{x}}$, the individual patches change state continually. The probability of remaining in state s from t to $t+1$ is given by a_{ss}. Thus the residence time in state s is geometrically distributed with mean $(1-a_{ss})^{-1}$; the turnover rate is the inverse of this mean residence time. The mean turnover rate for a randomly selected patch is then

$$\sum_{s} \hat{x}_s(1-a_{ss}) \tag{12}$$

b. *First passage times*. Consider a patch in state j. How long, on the average, does it take before this patch first reaches state i? This first passage time provides some insight into the apparent rates of "succession" in this landscape. For example, a landscape in which the mean time required to go from state X_1 (recently disturbed) to state X_2 (occupied by the dominant competitor) is short appears to undergo a much more rapid succession than a landscape in which this time is long. Let m_{ij} denote the mean first passage time from state j to state i. This value is given by the (i,j) entry of a matrix $\mathbf{M}$ given by

$$\mathbf{M} = (\mathbf{\Pi}_{dg})^{-1}(\mathbf{I} - \mathbf{Z} + \mathbf{Z}_{dg}\mathbf{E}) \tag{13}$$

where $\mathbf{\Pi}$ = a matrix each of whose columns is $\hat{\mathbf{x}}$, $\mathbf{Z} = [\mathbf{I} - (\mathbf{A}_{\hat{\mathbf{x}}} - \mathbf{\Pi})]^{-1}$, and $\mathbf{E}$ = a matrix of ones (Iosifescu, 1980, theorem 4.7). $\mathbf{\Pi}_{dg}$ and $\mathbf{Z}_{dg}$ denote matrices containing the diagonal elements of $\mathbf{\Pi}$ and $\mathbf{Z}$.

The mean recurrence time for a state is the mean first passage time from that state to itself and is given by the diagonal elements m_{ss} of $\mathbf{M}$. The formula simplifies for these elements to $m_{ss} = 1/\hat{x}_s$. It is also possible to calculate the mean passage time to state j from a randomly selected patch by taking the mean of m_{ji} over the stationary distribution $\hat{\mathbf{x}}$ (Iosifescu, 1980, p. 135).

$$\sum \hat{x}_i m_{ji} = \frac{z_{jj}}{\hat{x}_j} \tag{14}$$

c. *Smoluchowski recurrence time*. The recurrence times m_{ss} may be heavily influenced by the fact that the patch may *stay* in state s from t to $t+1$, in which event the recurrence time is 1. The Smoluchowski recurrence time θ_s of state X_s is the time elapsing between *leaving* state X_s, and the next return to state X_s. Its mean is given by the following (Iosifescu, 1980, p. 135).

$$E(\theta_s) = \frac{1-\hat{x}_s}{\hat{x}_s(1-a_{ss})} \tag{15}$$

Like the recurrence time, this index gives some insight into the rates of community development. $E(\theta_1)$ gives the mean time elapsing between colonization of a patch and its return to the disturbed state.

The Smoluchowski recurrence time can also be calculated for *sets* of states, defined as the mean time between leaving that set and the next return to it. This measurement is particularly useful for sets of states defined by the presence of a species; the recurrence time for such a set of states gives the mean time elapsing between the local extinction of a species (for whatever reason) and its next reappearance. Let χ denote the set of states under consideration. Then, as noted by Iosifescu (1980)

$$E(\theta_\chi) = \frac{1-\sum_{s\in\chi}\hat{x}_s}{\sum_{s\in\chi}\hat{x}_s \sum_{r\notin\chi} a_{rs}} \tag{16}$$

d. *Rate of convergence*. The dominant eigenvalue λ_1 of $\mathbf{A}_{\hat{\mathbf{x}}}$ is 1; the corresponding eigenvector is proportional to $\hat{\mathbf{x}}$. An idea of the rate of convergence to the landscape equilibrium can be had from the largest subdominant eigenvalue λ_2 of $\mathbf{A}_{\hat{\mathbf{x}}}$. The smaller $|\lambda_2|$, the more rapidly the landscape converges to the equilibrium $\hat{\mathbf{x}}$. This analysis applies only to arbitrarily small perturbations from $\hat{\mathbf{x}}$; the rate of convergence from larger perturbations reflects the nonlinearity of the full model.

Relation to Other Approaches

A variety of complementary approaches have been used to study community dynamics in space and time. Each has its advantages and disadvantages. Our models lie at one end of a spectrum: Space, time, and the state of individual cells are all discrete. At the other extreme are partial differential equation models (e.g., Dubois, 1975; Wroblewski, 1977; Okubo, 1978), in which space, time, and state are continuous. Such models, especially when coupled with fluid mechanics for description of aquatic systems, can provide detailed insight into specific situations (Wroblewski, 1977), but they are complex, analytically intractable, and computationally difficult. It is not easy to obtain general theoretical insight from them.

Reaction-diffusion models (Levin, 1974, 1976; Yodzis, 1978), in which space is discrete but each patch contains a continuous model for species abundances, are intermediate in complexity. However, their detail can still make their results difficult to interpret (Levin, 1976).

Our models are closely related to deterministic differential equation models for patch state frequencies (e.g., Levins and Culver, 1971; Horn and MacArthur, 1972; Vandermeer, 1973; Slatkin, 1974; Hastings, 1977, 1978, 1980; Crowley, 1979; Acevedo, 1981; Greene and Schoener, 1982; Hanski, 1983, 1985; Caraco and Whitham, 1984). The state variables in these models are the proportions of patches in each of several states. Analysis typically focuses on the conditions for stability of the equilibria of the resulting equations, with an emphasis on conditions favoring coexistence.

Some of the early models in this category (Levins and Culver, 1971; Horn and MacArthur, 1972; Vandermeer, 1973) are written as differential equations in species frequencies. Unless each patch can be occupied by only a single species, or species occupy patches independently (which usually contradicts the hypothesis that the species interact) such patch state frequencies do not define a probability distribution and the models cannot correspond to a Markov chain (Slatkin, 1974).

More recently—certainly since Slatkin (1974)—these models have been written in terms of patch state frequencies, which sum to 1. The resulting models are nonlinear continuous time Markov processes. With the exception of Caraco and Whitham (1984), however, these studies have by and large failed to take advantage of the stochastic formulation underlying the deterministic models to get additional insight into community structure and dynamics.

The analysis of patchy community dynamics in terms of Markov chains was introduced by Cohen (1970). He considered a linear Markov chain describing transitions between four states defined by the presence and absence of two species at the equilibrium of Lotka-Volterra competition equations. Our nonlinear formulation of community models in terms of Markov chains defined by the time scales of within-patch processes is a combination of that proposed by Cohen (1970) and Caswell (1978).

Results

To examine the behavior of this model, we conducted a numerical experiment. The model parameters were varied over all 120 combinations of the elements of the following sets.

$d_1 \varepsilon \{1,10\}$
$d_2 \varepsilon \{1,10\}$
$p_c \varepsilon \{0.01, 0.1, 1\}$
$p_d \varepsilon$ {10 values, log-uniformly spaced between 0.001 and 1}

Relying on the presence of a single stable fixed point for the model, we iterated the model (1) until $\mathbf{x}(t)$ converged to a fixed point $\hat{\mathbf{x}}$. The elements of $\hat{\mathbf{x}}$ give the proportions of the various states to be expected in a large landscape; the corresponding matrix $\mathbf{A}_{\hat{\mathbf{x}}}$ describes the transition dynamics of patches in such a landscape. The results of this experiment are shown as a series of figures. Most plot the response variable as a function of disturbance probability for several values of some other variable.

State Frequencies

The state frequencies $\hat{x}_s$, $s = 1, \ldots, 4$, are plotted as a function of p_d, in Figure 6.2. The frequency $\hat{x}_1$ of empty patches is nearly proportional to p_d, with only a small amount of variation generated by the different values of d_1, d_2, and p_c used in the experiment. This finding suggests that the fre-

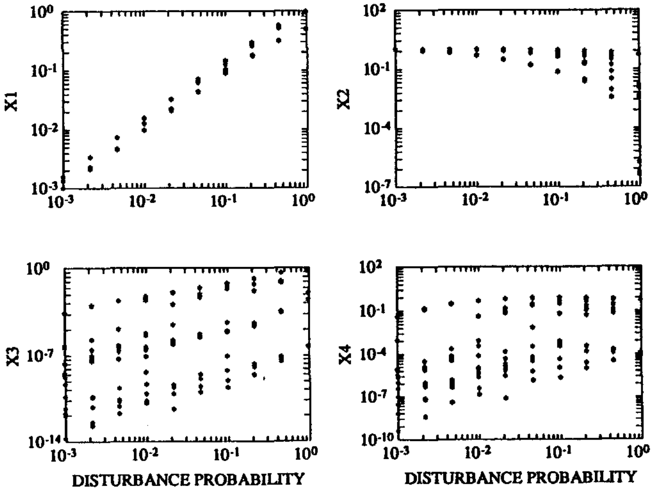

Figure 6.2. Equilibrium state frequencies x_s, $s = 1, \ldots, 4$, plotted as functions of the disturbance probability for the results of the numerical experiment described in the text.

quency of empty patches could be used as an index of disturbance probability in natural systems.

At low disturbance frequencies, $\hat{x}_2 \approx 1$ and almost all patches are occupied by the dominant competitor. As p_d increases, $\hat{x}_2$ decreases and becomes more variable as the dispersal rates and competitive exclusion rates come to play a part in determining community structure.

At any given disturbance frequency, the frequencies $\hat{x}_3$ and $\hat{x}_4$ of patches containing the inferior competitor vary over six to eight orders of magnitude, depending on the rates of competitive exclusion and dispersal. This variability is reflected in the variety of community patterns generated by the model.

Species Frequencies

The frequency f_1 of the winning competitor is independent of the losing competitor. Thus the dynamics of S_1 can be described by the one-species, two-state model described above: $f_1 > 0$ if and only if $d_1 > p_d$, and f_1 declines with increasing disturbance frequency independently of p_c (Fig. 6.3).

The losing competitor S_2 is a genuine fugitive species. In the absence of disturbance, it is eventually excluded by S_1 in every patch. In the presence of disturbance, however, it can persist and reach high frequencies. Figure 6.4 shows some results. When $d_1 = d_2$, f_2 is usually maximized at an intermediate frequency of disturbance. Numerically, it appears that f_2 begins to increase above 0 when

$$p_d > \frac{p_c}{d_2} \tag{17}$$

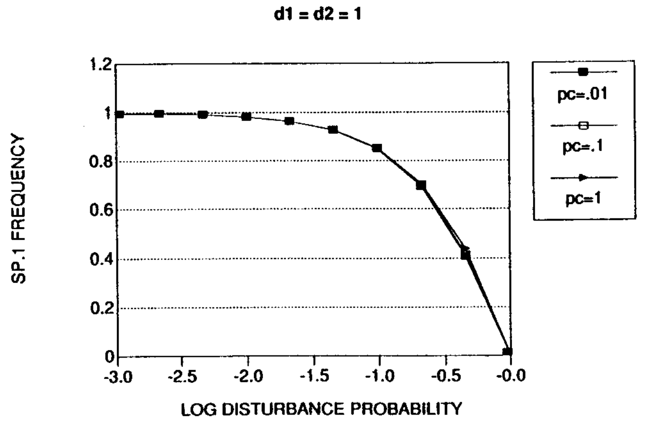

Figure 6.3. Equilibrium frequency f_1 of the winning competitor as a function of the disturbance frequency and the rate of competitive exclusion.

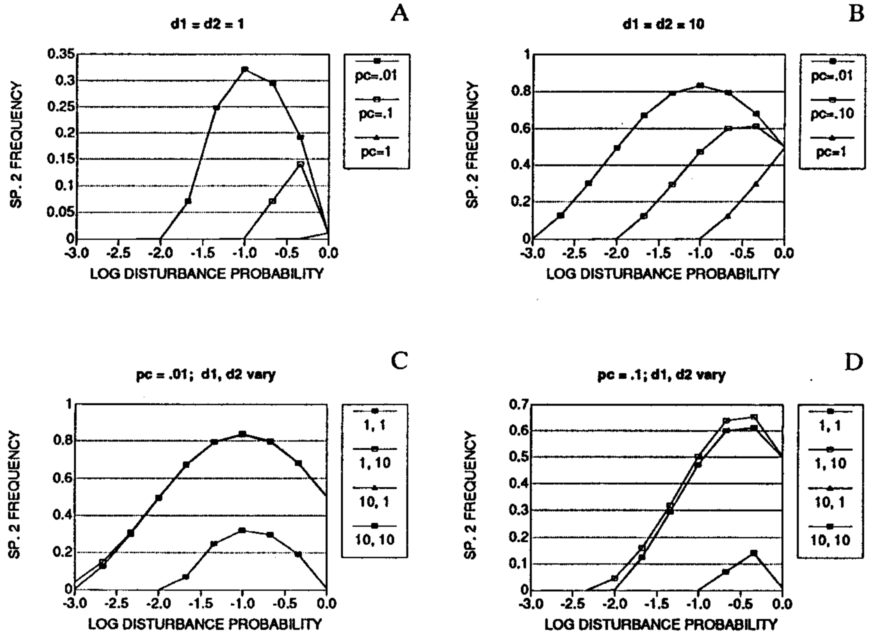

Figure 6.4. Equilibrium frequency f_2 of the losing competitor as a function of the disturbance frequency, dispersal rates, and rate of competitive exclusion. In (A,B) dispersal rates are fixed and competitive exclusion rates vary. In (C,D) competitive exclusion rates are fixed and dispersal rates vary.

Thus the minimum disturbance frequency required to maintain the fugitive species is directly proportional to the rate of competitive exclusion and inversely proportional to the dispersal rate of the fugitive. The disturbance frequency at which f_2 is maximized increases with p_c.

It is apparent from Figure 6.4A,B that the dispersal rate has an important positive influence on f_2. Fugitive species are often characterized as producing large numbers of propagules, but it is often also assumed that a fugitive species must have a dispersal advantage over the superior competitor. This assumption is not true (Fig. 6.4C,D). If d_2 is high enough, the relative values of d_1 and d_2 have no impact on f_2. If d_2 is lower ($d_2 = 1$ in our calculations), a dispersal advantage on the part of the superior competitor prevents the fugitive from persisting.

Diversity Enhancement

The interaction of competition, disturbance, and dispersal in this model is capable of enhancing local species diversity at intermediate disturbance frequencies. Figures 6.5 and 6.6 show the results.

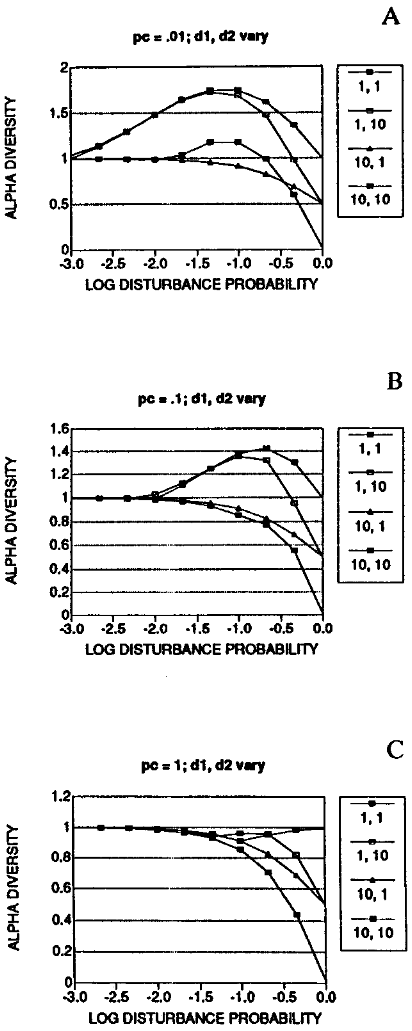

Figure 6.5. Mean alpha diversity as a function of the disturbance probability and dispersal rates (d_1, d_2) for three rates of competitive exclusion.

When dispersal rates are low and equal ($d_1 = d_2 = 1$), alpha diversity is enhanced only when competition is slow ($p_c = 0.01$) (Fig. 6.6A). When the fugitive species has a dispersal advantage ($d_1 = 1$, $d_2 = 10$), diversity is enhanced (by as much as 80%) for $p_c = 0.01$ and $p_c = 0.1$ (Fig. 6.6B) but not for the fastest rate of exclusion. The same pattern holds when $d_1 = d_2 = 10$, so it apparently depends more on an adequate dispersal rate for the fugitive species than on the dispersal advantage per se. When the winning competitor also has a dispersal advantage ($d_1 = 10$, $d_2 = 1$) there is no trace of diversity enhancement, regardless of p_c (Fig. 6.6D).

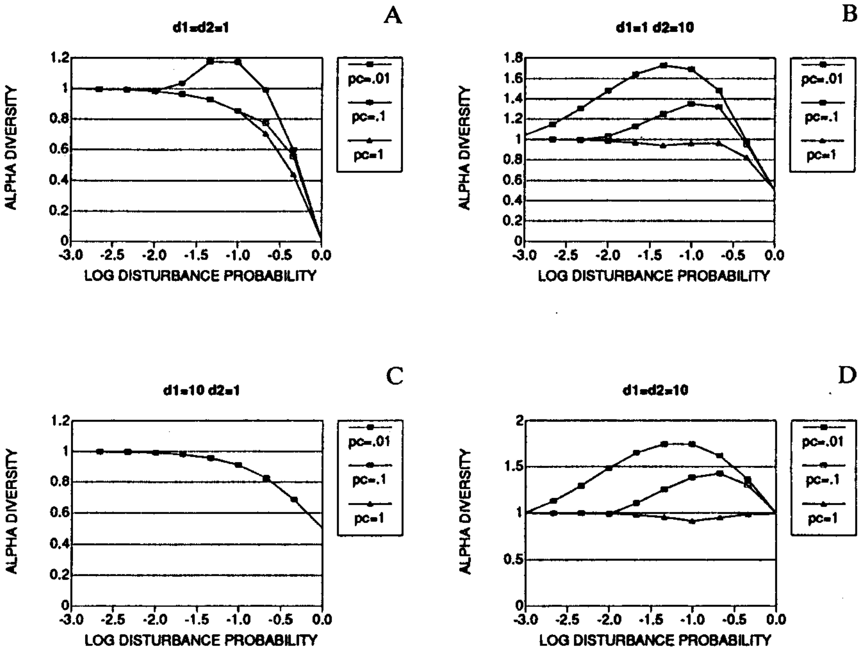

Figure 6.6. Mean alpha diversity as a function of the disturbance probability and rate of competitive exclusion for four combinations of dispersal rates.

Spatial Heterogeneity

In the absence of disturbance, this model converges to a uniform landscape, with every patch occupied by S_1. Disturbance and the processes of colonization and interaction that follow disturbance create spatial heterogeneity in local community structure. The three measures of spatial heterogeneity—beta diversity (equation 9), biotic beta diversity (equation 10), and the variance in alpha diversity are highly correlated with each other and show similar patterns. Here we show the results for β_b (Fig. 6.7).

When dispersal is low ($d_1 = d_2 = 1$) (Fig. 6.7A), β_b generally increases with disturbance probability and decreases with the rate of competitive exclusion. At the other extreme, when $d_1 = d_2 = 10$ (Fig. 6.7D), β_b is maximized at a disturbance frequency $p_d \approx p_c$. The patterns when d_1 and d_2 differ are more complex. When the fugitive species has a dispersal advantage ($d_1 = 1$, $d_2 = 10$) (Fig. 6.7B), β_b shows a bimodal pattern for slow exclusion rates and a peak at high disturbance rates for faster exclusion rates.

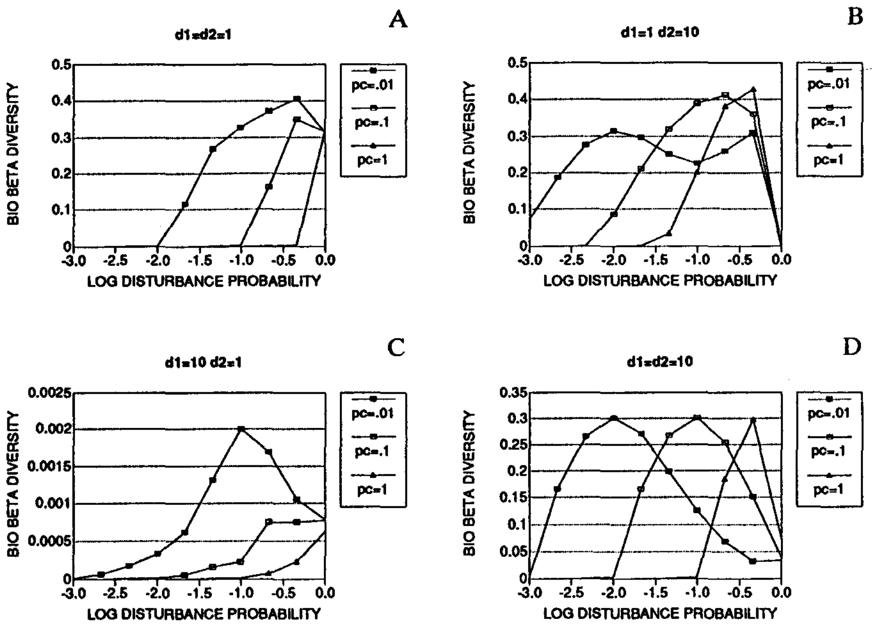

Figure 6.7. Biotic beta diversity (β_b) as a function of the disturbance frequency and the rate of competitive exclusion for different combinations of dispersal rates.

When the fugitive has a dispersal disadvantage, β_b is low (Fig. 6.7C), reflecting the nearly complete absence of S_2 in this situation.

Interspecific Association

The landscape-level pattern of association of two species tells remarkably little about their local interaction. In this case, the two species are pure competitors, and their association, were it to reflect that fact, would be negative. Figure 6.8 shows the results, and it is clear that association may be either positive or negative, depending on the parameters.

In general, association is more positive when the winning competitor has a high dispersal coefficient. Association tends to increase with p_d (Fig. 6.8A,B), although when the winning competitor has a dispersal advantage it decreases again at high values of p_d (Fig. 6.8C). When d_1 is high, association is positive over the entire range of disturbance probabilities. When d_1 is low, the association appears negative or positive, depending on the rate of disturbance.

Rates of Community Change

An observer following the fate of a randomly selected set of patches within the landscape described by this model would see continual change as patches are disturbed and colonized and as species interact with and exclude each other. The rates of this process of change can be measured in several ways.

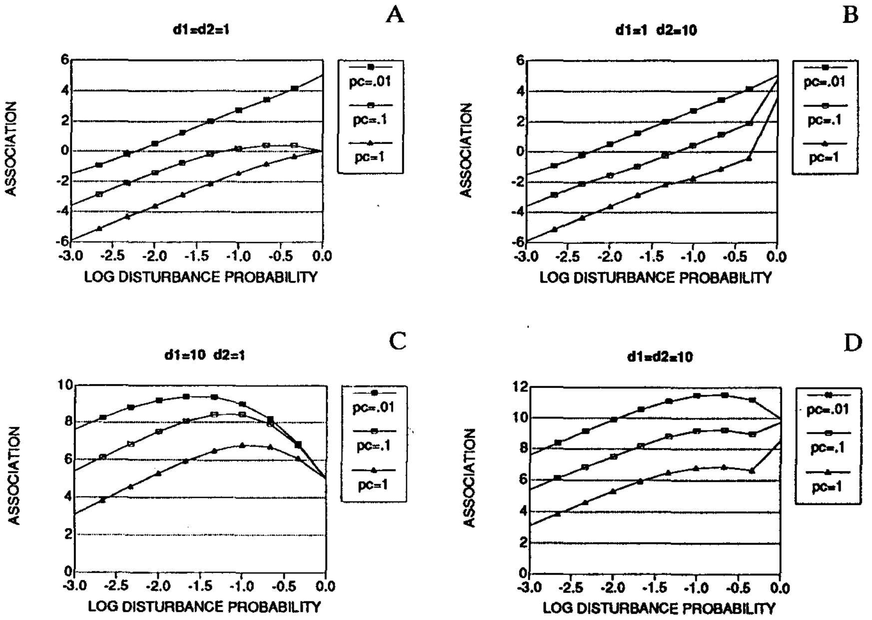

Figure 6.8. Interspecific association, measured by the log odds ratio, as a function of disturbance frequency and competitive exclusion rates for various combinations of dispersal rates.

Mean Turnover Rates

The mean turnover rate is an overall measure of the rate of community change, regardless of direction. In this model, it is determined almost completely by disturbance rate and in fact is nearly equal to the disturbance rate except when disturbance is so frequent relative to dispersal ability that the species begin to be driven to regional extinction (Fig. 6.9).

First Passage Times

The entries m_{ij} of the first passage time matrix **M** give the expected time required for a patch to reach state X_i for the first time, given that it starts in state X_j. Here we examine m_{i1}, $i = 1, \ldots, 4$: the mean first passage times from the disturbed state.

The mean first passage time from X_i to itself (*recurrence time*) is $\hat{x}_i^{-1}$. Thus $m_{11} = \hat{x}_1^{-1} \approx p_d^{-1}$. The mean first passage times from X_1 to X_2, X_3, and X_4 are shown in Figures 6.10 and 6.11.

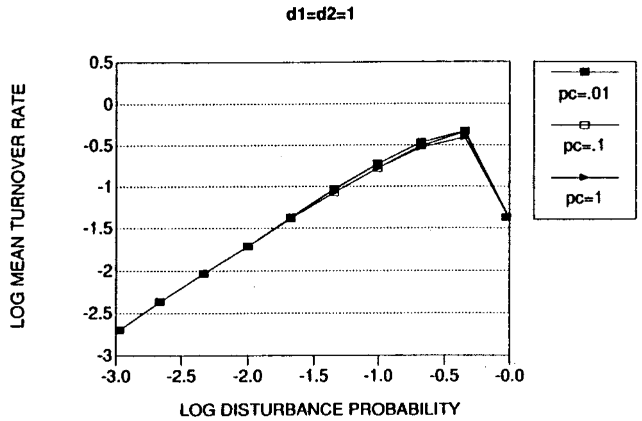

Figure 6.9. Log of the mean turnover rate as a function of disturbance frequency and competitive exclusion rate for low dispersal rates. The patterns for other dispersal rates are almost identical, except that they lack the drop in turnover rate at the highest disturbance probability. This drop reflects the fact that both species are being driven to extinction because their dispersal rates cannot match the disturbance rate.

State X_2 is the local equilibrium for this system, the "climax" of the two-species successional process described by the model. The mean first passage time m_{21} is thus a measure of how long an empty patch should take to reach the climax. At low dispersal rates ($d_1 = d_2 = 1$), m_{21} is low and insensitive to p_d, except when competitive exclusion is slow (Fig. 6.10A). In that case, there is a sudden increase in m_{21} when p_d exceeds p_c (thus permitting the persistence of S_2). Finally, m_{21} increases again, regardless of p_c, as p_d increases enough to begin to eliminate both species.

At high dispersal rates ($d_1 = d_2 = 10$) the pattern is similar (Fig. 6.11A). There is a sudden increase in m_{21} when p_d exceeds p_c. Then there is a plateau where m_{21} is inversely proportional to p_c, reflecting the fact that most patches arriving in X_2 must go through X_4, and that the transition from X_4 to X_2 is determined by p_c. Finally, when p_d is large, m_{21} increases again as the reduction in f_1 caused by the disturbance rate inhibits colonization by species 1.

The mean first passage time m_{31} to X_3 decreases with increasing p_d (Figs. 6.10B and 6.11B), as this state can be reached only by colonization of empty patches by the fugitive species. It also tends to increase with increasing p_c because when competition is more rapid the frequency, and hence the colonization probability, of the losing competitor is less.

Finally, the mean first passage time to X_4 also decreases with increasing p_d and with decreasing p_c. Like X_3, X_4 is reachable only by colonization of empty patches (by both species in this case). Thus it is reached more rapidly when empty patches are more common and when colonization is rapid enough to fill them with both species. The colonization rate increases with decreasing p_c and with increasing dispersal rates for both species (Figs. 6.10C and 6.11C).

This survey of mean first passage times reveals a wealth of patterns. The most reasonable candidate for a measure of the "rate of succession," m_{21}, suggests that there is a relatively sharp threshold value of disturbance frequency that, once exceeded, switches the community from one in which

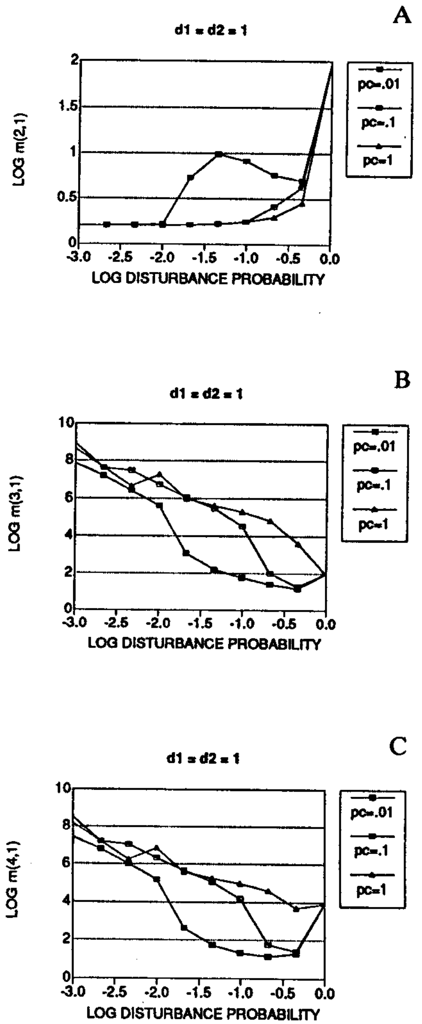

Figure. 6.10. Mean first passage times from state X_1 to states X_2, X_3, and X_4, for low dispersal rates ($d_1 = d_2 = 1$).

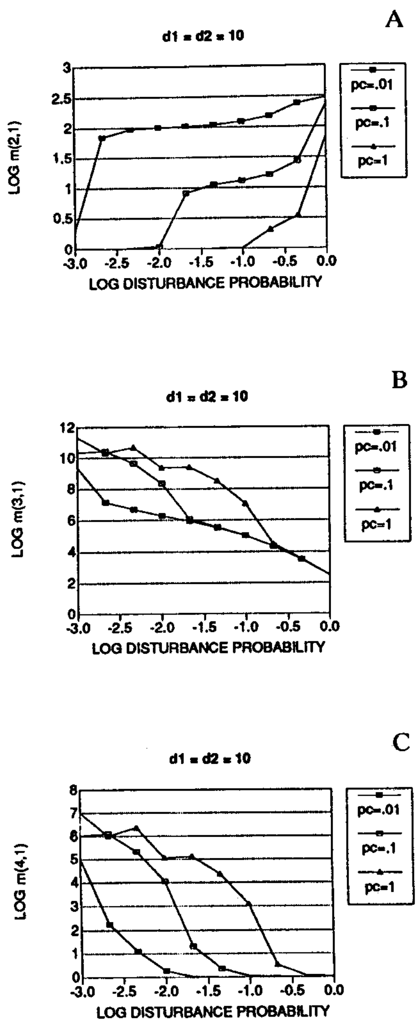

Figure 6.11. Mean first passage times from state X_1 to states X_2, X_3, and X_4 for high dispersal rates ($d_1 = d_2 = 10$).

succession proceeds almost immediately to its climax to one in which succession is much slower. In the latter case, a patch may cycle through disturbed and preclimax states many times before it reaches the climax state.

Smoluchowski Recurrence Time

The Smoluchowski recurrence time θ_i for state X_i measures the expected time between leaving X_i and returning to it for the first time. It is thus a measure of the rate at which a patch state recurs but without counting patches that remain in their present state.

In this experiment, $\theta_i \approx m_{i1}$, $i = 1, \ldots, 4$, which implies that the process of returning to a given state includes a passage through X_1, and that most of the variation in θ_i reflects variation in the time required to get from X_1 back to X_i. That time, of course, is measured by m_{i1}.

Convergence Rate

The rate of convergence of community structure, as measured by the second eigenvalue of $\mathbf{A}_{\hat{x}}$, shows a remarkable lack of variation compared to the variation in the other parameters. This fact suggests that the likelihood of a community being near its equilibrium distribution is independent of the parameter values, and hence observed differences between communities reflect differences in equilibria (at the landscape level) rather than differences in the rate of approach to equilibria.

Discussion

The results of this chapter demonstrate that the time scales of disturbance, dispersal, and competitive exclusion can interact to produce a variety of patterns in patchy communities. Studies of diversity, spatial heterogeneity, interspecific association, and rates of community change must take these time scales into account in order to make any sense of observed patterns of community structure.

Our results allow us to examine the relation between disturbance, rate of competitive exclusion, and alpha diversity, as discussed by Huston (1985). Figure 6.12 shows alpha diversity as a function of disturbance frequency and rate of competitive exclusion. In our model, diversity is maximized at intermediate disturbance frequencies and at low rates of competitive exclusion. At high enough disturbance rates, the competitive exclusion rate effect disappears. The value of p_d, which maximizes diversity, increases in log-log fashion with p_c. Huston (1985) proposed a somewhat different relation, in which diversity is maximized at intermediate values of p_d and p_c.

These results have important implications for discussions of diversity in low disturbance environments (e.g., of deep-sea benthic diversity). Alpha diversity is determined not by the disturbance rate per se but by that rate in relation to the rate of competitive exclusion. In environments characterized by low rates of competitive exclusion (e.g., low productivity, low growth rates), even very low rates of disturbance can significantly enhance species diversity and community heterogeneity. Comparisons between environments differing in disturbance frequency must also take into account differences in the rate of competitive exclusion.

We can also examine the apparent dichotomy between biotic impoverishment and diversity enhancement. The rate at which a disturbed patch

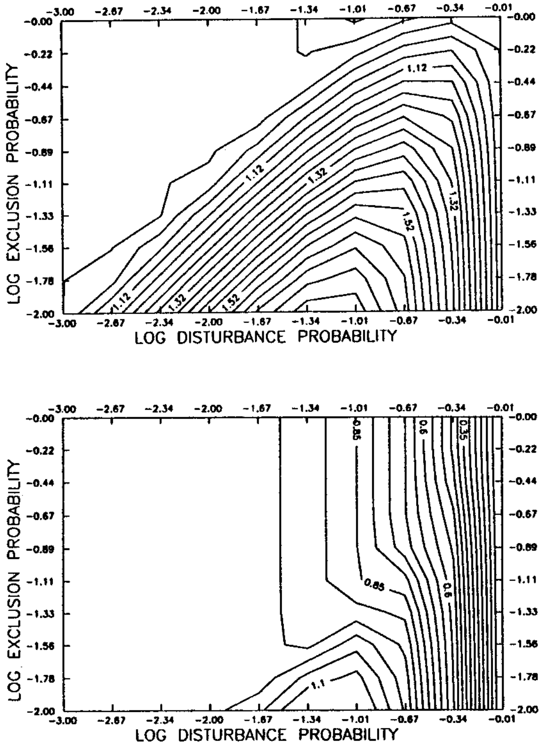

Figure 6.12. Contours of alpha diversity as a function of disturbance probability and the rate of competitive exclusion for high dispersal ($d_1 = d_2 = 10$) (top) and low dispersal ($d_1 = d_2 = 1$) (bottom) communities. In both graphs, diversity is at a minimum in the upper right corner.

recovers and becomes available for colonization influences whether the main effect of disturbance is diversity enhancement or biotic impoverishment. To illustrate this point we augment the basic model by adding a fifth state, corresponding to disturbed patches that are unavailable for colonization.

Unavailable	S_2	S_1	State
0	0	0	1
0	0	1	2
0	1	0	3
0	1	1	4
1	0	0	5

The graph for this model is shown in Figure 6.13, with the corresponding matrix $\mathbf{A_x}$.

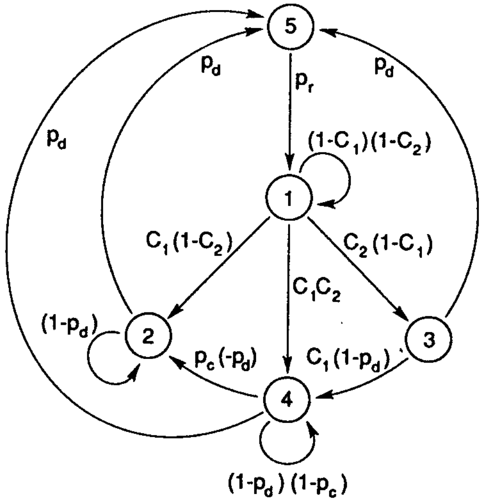

Figure 6.13. Transition graph for the residual effects model. Disturbance produces patches in X_5 that are unvailable for colonization until a recovery period (characterized by the recovery rate p_r) has passed.

$$\begin{pmatrix} (1-C_1)(1-C_2) & 0 & 0 & 0 & p_r \\ C_1(1-C_2) & 1-p_d & 0 & p_c(1-p_d) & 0 \\ C_2(1-C_1) & 0 & (1-p_d)(1-C_1) & 0 & 0 \\ C_1C_2 & 0 & C_1(1-p_d) & (1-p_d)(1-p_c) & 0 \\ 0 & p_d & p_d & p_d & 1-p_r \end{pmatrix} \tag{18}$$

The rate of recovery of disturbed patches is given by p_r; all other parameters are as in equation (6).

The rate of recovery determines the response of diversity to disturbance (Fig. 6.14A). Even when dispersal is high and competitive exclusion slow, diversity is enhanced by disturbance only if the rate of recovery is high enough. If recovery is slow enough ($p_r = 0.01$ in this example), disturbance leads only to biotic impoverishment.

This biotic impoverishment reflects the increasing proportion of patches in X_5 as disturbance becomes more frequent (Fig. 6.14B). At least in this case, in which dispersal rates are high ($d_1 = d_2 = 10$), it appears that $x_5 \approx p_d/p_r$ for low disturbance frequencies. As p_d increases, x_5 eventually approaches 1, the sooner the lower the value of p_r.

Summary

We have presented a simple modeling framework for studying the interaction of the rates of disturbance, dispersal, and competitive exclusion

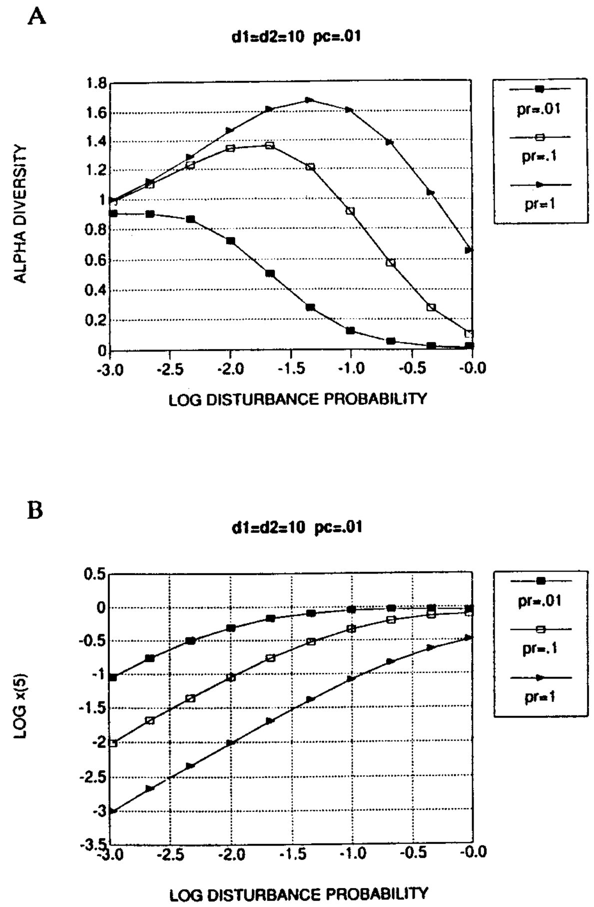

Figure 6.14. Alpha diversity (A) and log x_5 (B) for the residual effects model as a function of the disturbance rate and the rate of recovery (p_r) of disturbed patches.

in a patchy environment. The model is a nonlinear Markov chain, the transition probabilities of which are derived from hypotheses about the aforementioned rates. The state of a patch is defined by the presence and absence of the two competing species and the state of the landscape by the probability distribution of patch states. Numerical studies strongly suggest that the model has, at most, one stable fixed point in the interior of the unit simplex; this fixed point represents an equilibrium community at the landscape level, although equilibrium is never attained at the level of the individual patch. The output of the model includes species frequencies, alpha and beta diversity, interspecific association patterns, and measures of community change.

The model shows that disturbance can generate heterogeneity, both spatially and temporally, in patchy communities. The resulting patterns depend strongly on the relation between the time scales of the interacting processes.

The results are used to examine the relation between productivity and the phenomenon of diversity enhancement by disturbance. A single model can account for both diversity enhancement and biotic impoverishment, depending on the relations among its parameters.

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