

Red, White and Blue: Environmental Variance Spectra and Coexistence in Metapopulations

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Environmental variability, in the form of disturbance, is critically important for metapopulations. Their spatial subdivision makes possible the regional coexistence of inferior competitors (fugitive species) that are unable to persist locally. It is known that such coexistence depends on the frequency of disturbance relative to the rates of dispersal and competitive exclusion. In this paper, the effects of the spectral “color” of the environmental variation in a simple two-species competition model are considered. A simple two-state Markov chain is developed to describe the environment; its single parameter can be tuned to give a power spectrum that emphasizes low frequencies (red) or high frequencies (blue), or that contains all frequencies equally (white). Coupling this to a nonlinear Markov chain model for two competing species, this study considers the interacting effects of disturbance frequency and the spectrum on the frequency of the losing competitor, local species richness, spatial heterogeneity (beta diversity), and the Smoluchowski recurrence time for patch states. In general, a red spectrum makes coexistence more difficult and reduces local diversity. However, the details of the patterns depend on the rates of dispersal and competition.

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1. Introduction

Abundance, coexistence and diversity in metapopulations depend on the combined effects of disturbance, ecological interactions and dispersal. Disturbance is particularly important because the spatial subdivision of a metapopulation makes it possible for a species to persist regionally without being able to persist locally. This “nonequilibrium” or “fugitive” coexistence is a major contributor to species diversity.

In our previous studies of nonlinear Markov chain metapopulation models for interspecific competition (Caswell & Cohen, 1991*a, b*, 1993; Barradas & Cohen, 1994) we found that

- diversity can be maximized at intermediate disturbance frequencies;
- the disturbance frequency maximizing diversity depends on the time scale of local interspecific competition;

- contrary to popular opinion, regional persistence as a fugitive species does not necessarily require a dispersal advantage to compensate for local competitive inferiority; and
- patterns of beta diversity and turnover and recurrence times respond in complicated ways to disturbance frequency.

In this paper we extend these analyses to consider the spectral properties, as well as the frequency, of environmental variability. These properties characterize the temporal scaling, or autocorrelation pattern of the environment.

The importance of temporal scaling has been emphasized by Steele (1985, 1991, Steel & Henderson, 1984, 1994) in a comparison of marine and terrestrial ecosystems and their responses to environmental variability. Steele (1985) noted that atmospheric data (temperature and other variables) exhibit variance

spectra well described by "white noise" (i.e. equal variances at all frequencies) down to frequencies of $\approx 0.02 \text{ yr}^{-1}$. By contrast, long-term records of abiotic variables (e.g. temperature) from the ocean yield spectra in which the variance is much greater at low than at high frequencies; such spectra are referred to generically as "red" (Monin *et al.*, 1977).

The importance of this difference lies in the dynamic consequences of perturbing ecological systems by red and white noise. On the basis of simulations of a simple predator-prey system, Steele & Henderson (1984) concluded that red noise produces dynamics in which the system jumps back and forth between qualitatively different equilibria, while perturbation by white noise leads to variation around a point between the two equilibria. They argued that long-term historical records of marine fish populations show the kind of abrupt variation predicted from red noise perturbations (although this has been challenged by Sinclair, 1988).

A general model for this effect has been developed by Kitahara *et al.* (1979, 1980) and Horsthemke & Lefever (1984), and applied to population genetics by Matsuda & Ishii (1981). They considered a continuous dynamical system perturbed by a stochastic process (the "environment") with two possible states. The system has a stable fixed point in each of the two environmental states. Transitions between the environmental states follow an autoregressive stochastic process with an exponential autocorrelation function. When the environment fluctuates the stationary distribution of the system depends on both the intensity and the autocorrelation of the environmental process. When the autocorrelation time of the environment is long (i.e. the environmental noise is red) relative to the time scale of approach to equilibrium, the stationary distribution is concentrated at the two equilibria, and the dynamics are characterized by abrupt transitions between the alternative equilibria. When the autocorrelation time of the environment is short (i.e. white noise) the stationary distribution is unimodal, and the system fluctuates around a point intermediate between the two equilibria, without ever converging to either.

Our analysis differs from this model; rather than imposing stochastic variation on a deterministic model, we consider a stochastic model for two competing species in a variable environment. We extend the approach of Caswell & Cohen (1991*a, b*; Barradas & Cohen, 1994) to include variation with different spectral properties, from "red" through "white" to "blue". We shall consider specifically coexistence and the diversity maintained by environ-

mental disturbance in the face of competitive exclusion.

In the next section we describe our metapopulation model and its output, and our model for environmental variation. We then analyze numerically two specific cases. In one, the environmental variation affects the disturbance rate; in the other, the identity of the competitive dominant. We shall describe the results in terms of the local species diversity, the regional diversity, and the patterns of recurrence time.

2. A Patch-Occupancy Metapopulation Model

Our approach to metapopulation modelling is to specify the rates of local, within-patch processes, to transform those rates into rates of transition among local patch states, and then to infer from those rates the dynamics of a regional distribution of patch states (Caswell & Cohen, 1991*a, b*). Consider an effectively infinite set of effectively identical patches, inhabited by n species, S_1, \dots, S_n . We define the state of a patch by the presence and absence of the species (hence the name *patch-occupancy* models); there are 2^n possible patch states, X_1, X_2, \dots, X_{2^n} . We assume that the state of the metapopulation as a whole is given by a vector \mathbf{x} whose entries x_i give the proportion of patches in state X_i . This is equivalent to assuming that the system is well-mixed, so that each patch interacts equally with all others; the spatial arrangement of patches has no effect. The state of a patch changes as a result of within-patch interactions, disturbance, and colonization from other patches. Because colonization rates depend on the abundance of the colonizing species (measured by the fraction of patches occupied by each species), the resulting dynamics are given by a nonlinear Markov chain

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

The (column-stochastic) transition matrix $\mathbf{A}_{\mathbf{x}(t)}$ is calculated from the timescales of disturbance, colonization, and interspecific interaction (Caswell & Cohen, 1991*a, b*; see below for an example). Where no confusion seems likely to result, we will suppress the subscript on \mathbf{A} .

Since (1) is a nonlinear map, it is in principle capable of a variety of dynamics, including stable fixed points, oscillations, quasiperiodic orbits, and chaos. Analytical results on these models are difficult to obtain. Our extensive numerical analyses have revealed only convergence to unique, globally stable equilibria, and Barradas & Cohen (1994) have proven this result for a model which differs only slightly from the one we describe below. These equilibria depend on parameter values, but appear to be independent of initial

conditions $x(0)$ as long as all elements of $x(0)$ are positive.

Convergence of the metapopulation to a stable equilibrium probability distribution \hat{x} (satisfying $\hat{x} = A\hat{x}$) does not imply that any individual patch attains equilibrium. Indeed, one of the advantages of formulating the model as a Markov chain is that one can examine the temporal variability at the patch level while the landscape is at equilibrium (Caswell & Cohen, 1991b).

Similar patch occupancy models have been used to describe metapopulation dynamics by, e.g. Cohen (1970), Levins (1970), Slatkin (1974), Caswell (1978), Crowley (1979), Hastings (1978), Hanski (1983); see the collection of papers in Gilpin & Hanski (1991). They share several important assumptions. First, by ignoring within-patch population dynamics, they implicitly assume that the timescale of those dynamics is faster than the other timescales in the population. Second, the use of x as a state variable ignores the spatial arrangement of the patches. These models consider *only* two spatial scales—that of the local, within-patch population and that of the regional metapopulation. Comparison of the competition model we will consider here with a corresponding cellular automaton model, which does include explicit spatial pattern, shows that the patch-occupancy model is an excellent approximation to the cellular

automaton unless the disturbance process introduces spatial scales intermediate between the single patch and the regional metapopulation (Caswell & Etter, 1993; Etter & Caswell, 1994; Caswell and Etter, data in preparation).

2.1. A MODEL FOR INTERSPECIFIC COMPETITION

We consider two species, S_1 and S_2 , and define patch states as follows, where 0 indicates absence and 1 indicates presence:

S_2	S_1	State
0	0	X_1
0	1	X_2
1	0	X_3
1	1	X_4

We suppose that S_1 is the winning species, and eventually excludes S_2 from any patch in which they co-occur. The transition probabilities a_{rs} , from state X_r to state X_s , are calculated from the timescales of competitive exclusion, dispersal, and disturbance. In general, the rate of a process is given by the inverse of the timescale on which it occurs; a long timescale implies a slow rate, and vice versa.

We assume that disturbance follows a Poisson process, with a timescale (mean time between

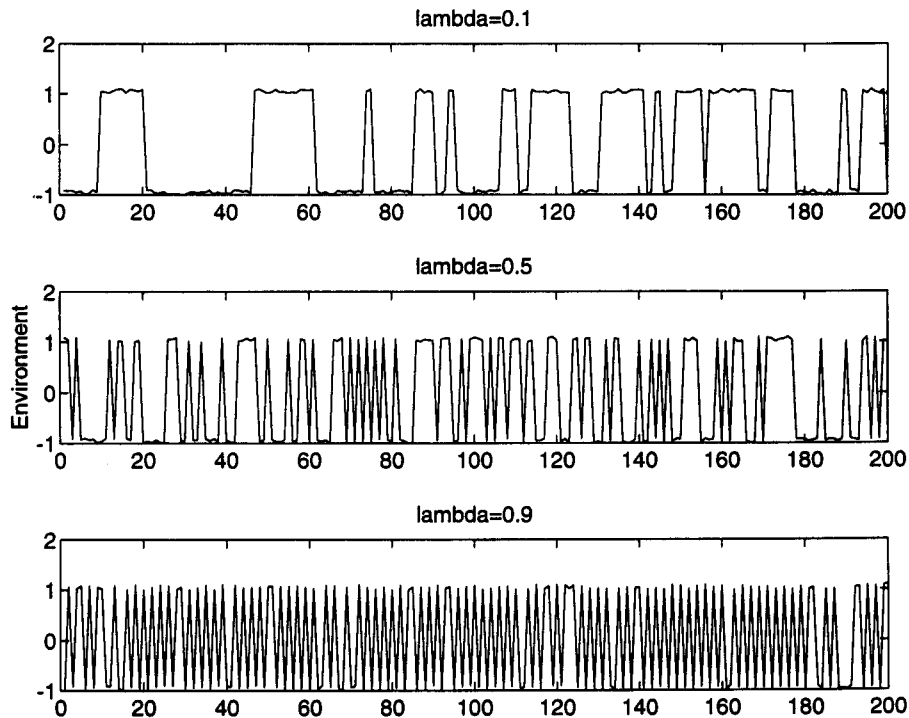


FIG. 1. Trajectories of the environmental state of a single patch as a function of the environmental spectrum, for red ($\lambda = 0.1$), white ($\lambda = 0.5$) and blue ($\lambda = 0.9$) spectra. Parameter values: $d_1 = d_2 = 0.1$, $p_c = 0.01$, $p_d = 0.5$. A small amount of random noise has been added to the values to make the graphs more easily visible.

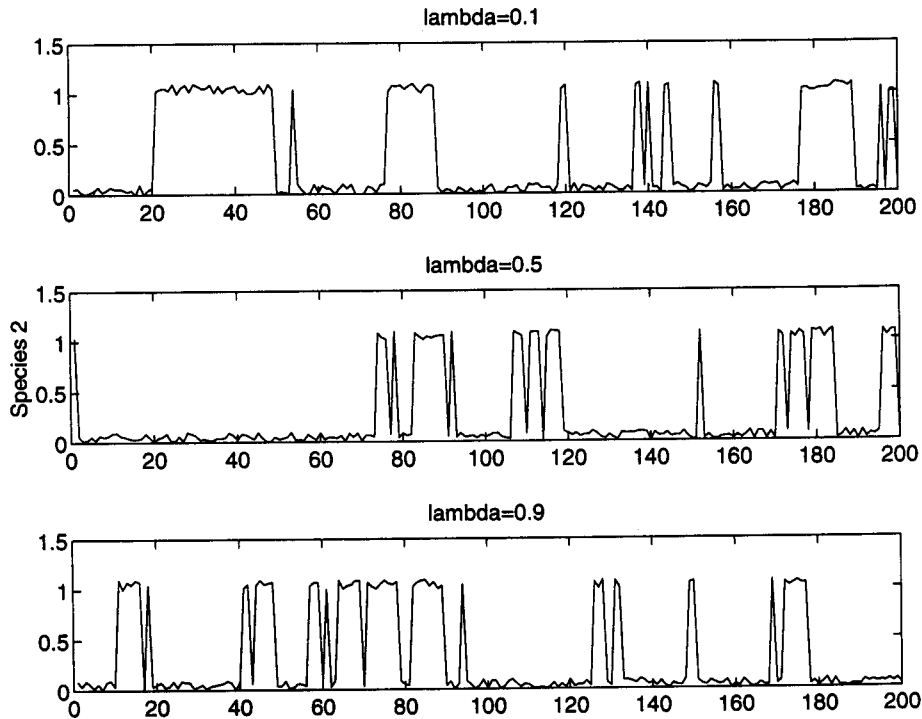


FIG. 2. Trajectories of a single patch showing the presence or absence of the inferior competitor (S_2) as a function of the environmental spectrum, for red ($\lambda = 0.1$), white ($\lambda = 0.5$) and blue ($\lambda = 0.9$) spectra. The trajectories were obtained as stochastic realizations using the transition matrix A_x evaluated at the equilibrium state frequency. In all three plots, $d_1 = d_2 = 2$, $p_c = 0.1$, and $p_d = 0.1$. A small amount of random noise has been added to the values to make the graphs more easily visible.

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

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

The rate of competitive exclusion is specified in terms of 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 , then the time required for exclusion (t_c) will follow a zero-truncated geometric distribution, with

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

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

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

Finally, we assume that colonization follows a Poisson process. The mean number of colonists of species i , $i = 1, \dots, N$, arriving in a vacant patch in $(t, t + 1]$ is proportional to the frequency of

occurrence of species i , i.e. the fraction of all patches in which species i is present. 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 ; thus $f_1 = x_2 + x_4$ and $f_2 = x_3 + x_4$. Then the conditional probability of at least one colonist arriving in a patch, given that the patch is vacant, is

$$C_i(x) = 1 - e^{-df_i} \tag{5}$$

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) which contains the winning species. Modifications of this assumption yield models of various successional mechanisms (Caswell & Cohen, 1991b).

The transition matrix A_x , which determines the dynamics in (1) is

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

where the C_i are given by (5).

2.2. MODEL OUTPUT

From the equilibrium probability distribution $\hat{\mathbf{x}}$, obtained by numerical iteration of (1) using (6), we calculate two types of output: spatial averages of patch properties (e.g. mean number of species per patch) and temporal averages of patch transitions (e.g. mean time required to go from one state to another). In biological terms, these indices of community structure include

1. The frequency (f_i) of occurrence of each species.
2. The local or alpha diversity, measured by the expected number of species per patch. In the two-species case, $\alpha = x_2 + x_3 + 2x_4$.
3. Between-patch, or beta diversity, which measures the change in species composition that would be observed along a transect or gradient across the landscape. Since there are no actual gradients on our landscape, beta diversity

can be simply measured by the entropy of the vector $\hat{\mathbf{x}}$:

$$\beta = -\sum_i x_i \log x_i. \quad (7)$$

Beta diversity is at a minimum when all patches contain the same set of species; it is maximized when all different patch types are equally abundant. We also calculate a biological beta diversity by excluding empty patches:

$$\beta_b = -\sum_{s=2}^{2^n} \left(\frac{x_s}{\sum_{j=2}^{2^n} x_j} \log \frac{x_s}{\sum_{j=2}^{2^n} x_j} \right) \quad (8)$$

Because β and β_b are highly correlated we report only the results for β_b here.

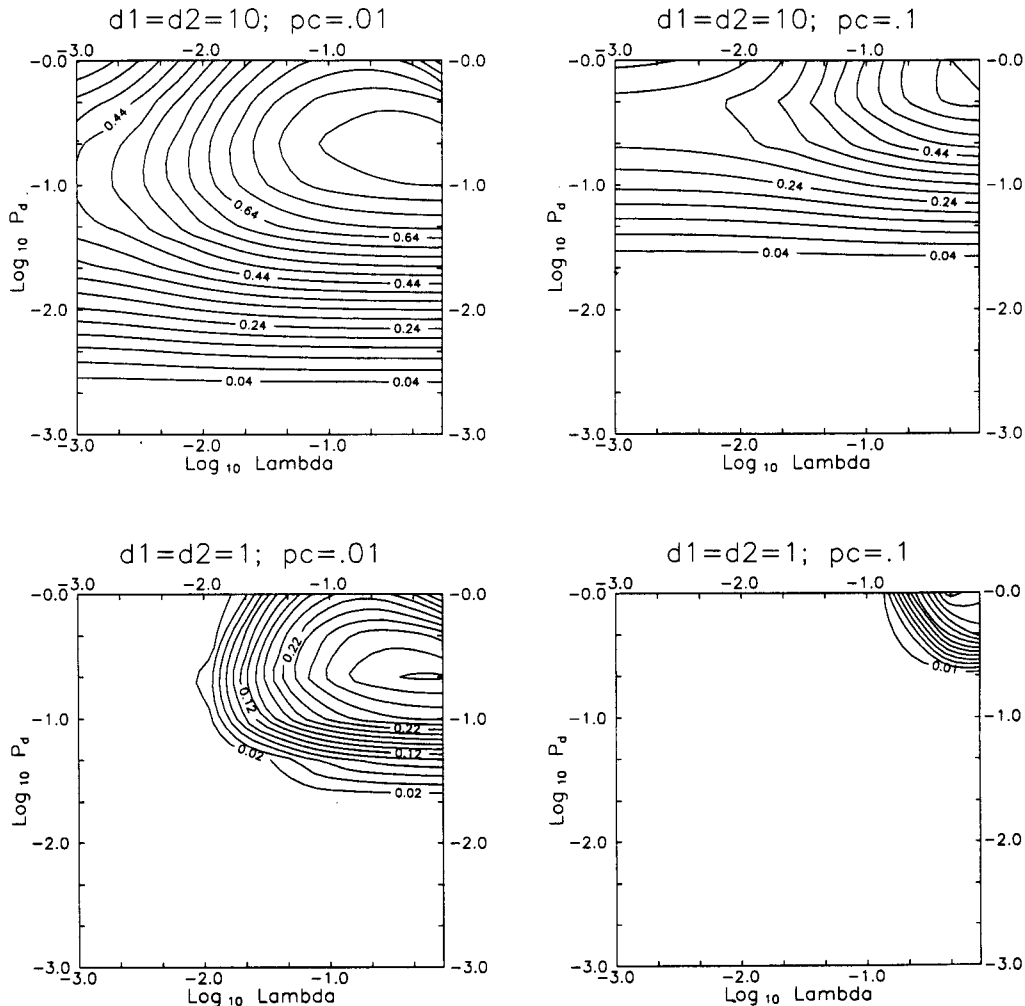


FIG. 3. The equilibrium frequency f_2 of the losing competitor as a function of dispersal rate (d_i), competitive exclusion rate (p_c), and the frequency (p_d) and spectrum (λ) of the environmental disturbance process. The two environmental states differ in their rates of disturbance.

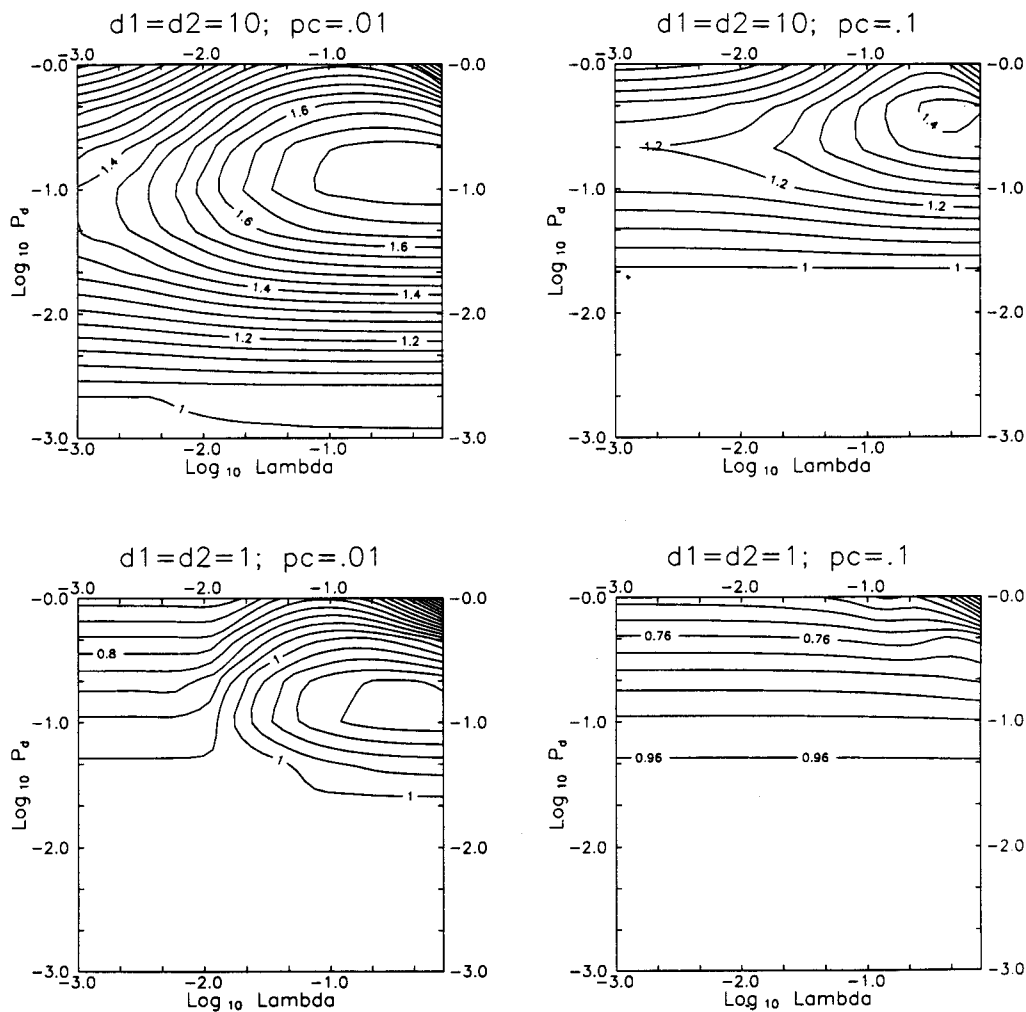


FIG. 4. Contours of alpha diversity as a function of disturbance frequency and λ . The two environmental states differ in their rates of disturbance.

4. The *recurrence times* for states and sets of states, which give some insight into the within-patch dynamics implied by the transition matrix A_s at equilibrium. The recurrence time of state X_s is the mean first passage time from X_s to X_s , and is given by

$$m_{ss} = \frac{1}{\hat{x}_s} \quad (9)$$

(Iosifescu, 1980). However, because the mean recurrence time is affected by the probability of staying in the same state from t to $t+1$, in which event the recurrence time is 1, we will use instead the mean *Smoluchowski recurrence time* $E(\theta_s)$, defined as the mean time elapsing between leaving state X_s and the next return to state X_s . It is given by

$$E(\theta_s) = \frac{1 - \hat{x}_s}{\hat{x}_s(1 - a_{ss})} \quad (10)$$

(Iosifescu, 1980: 135). $E(\theta_s)$ can be interpreted in terms of community development within patches of the metapopulation. For example, $E(\theta_1)$ gives the mean time between colonization of a patch and the next disturbance, which is the mean time available for interspecific interaction between disturbances. 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 is particularly useful for sets of states defined by the presence or absence of a species; the recurrence time for such a set of states gives the mean time elapsing between the local extinction of a species and its

next reappearance. Let ξ denote the set of states under consideration. Then

$$E(\theta_{\xi}) = \frac{1 - \sum_{s \in \xi} \hat{x}_s}{\sum_{s \in \xi} \hat{x}_s \sum_{r \notin \xi} a_{rs}} \quad (11)$$

(Iosifescu, 1980).

2.3. AUTOCORRELATED STOCHASTIC ENVIRONMENTS

We turn to a simple model of environmental variability (possibly due to disturbance, for example) which yields a spectrum that can be adjusted from red through white to blue. Consider an environment that at any time is in one of two states, characterized by real numbers z_1 and z_2 . The transitions between states are

governed by a homogeneous Markov chain with transition matrix (from columns to rows)

$$A = \begin{pmatrix} 1 - \lambda & \lambda \\ \lambda & 1 - \lambda \end{pmatrix} \quad (12)$$

where $0 < \lambda < 1$. We suppose that the environmental process is stationary, so that at time $t = 0$, $P(z(0) = z_1) = P(z(0) = z_2) = 1/2$, from which it follows that $P(z(t) = z_1) = P(z(t) = z_2) = 1/2$ for all t .

The mean and variance of $z(t)$ are easily calculated:

$$E(z(t)) = \frac{1}{2}(z_1 + z_2) \quad (13)$$

$$V(z(t)) = E(z^2(t)) - \frac{1}{4}(z_1 + z_2)^2. \quad (14)$$

To determine the spectral properties of this environment, we need the autocovariance function

$$\gamma_{zz}(k) = \text{Cov}(z(0), z(k)) \quad (15)$$

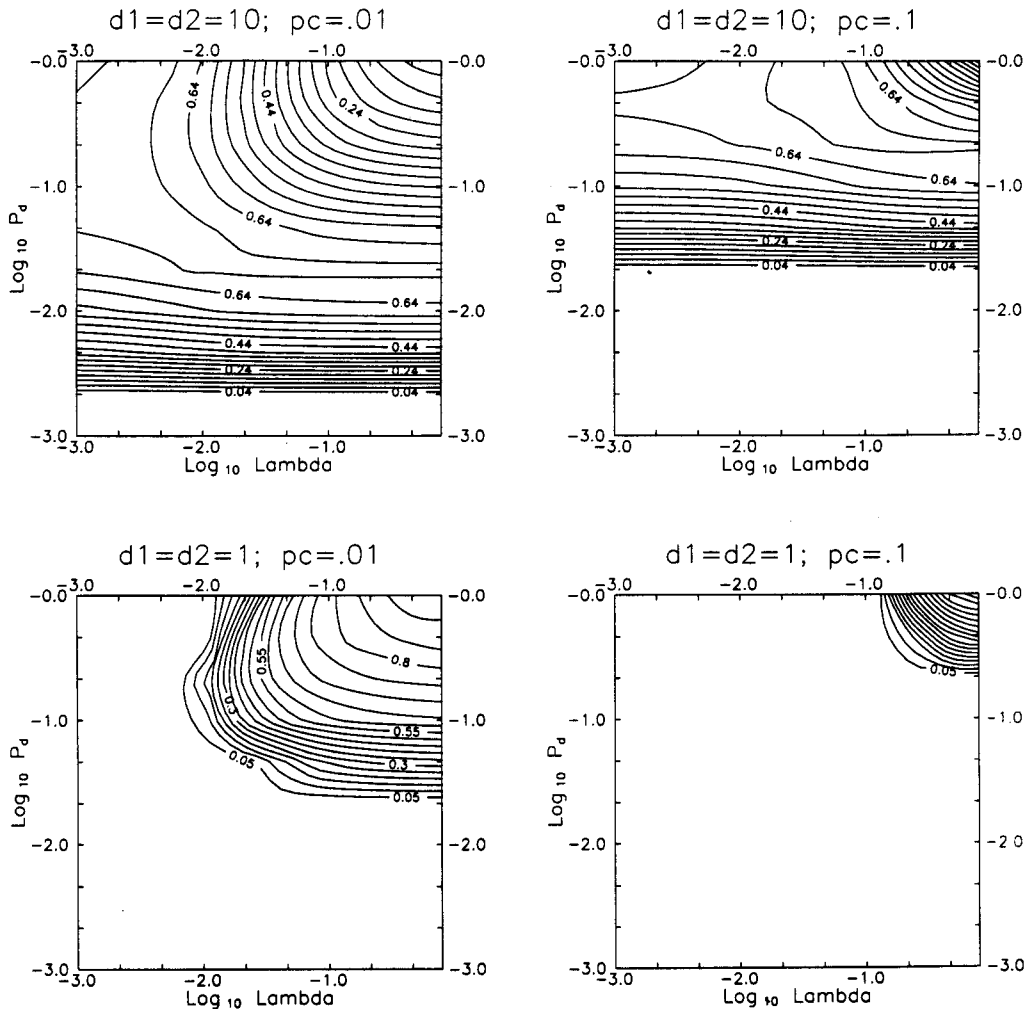


FIG. 5. Contours of biotic beta diversity β_b as a function of disturbance frequency and λ . The two environmental states differ in their rates of disturbance.

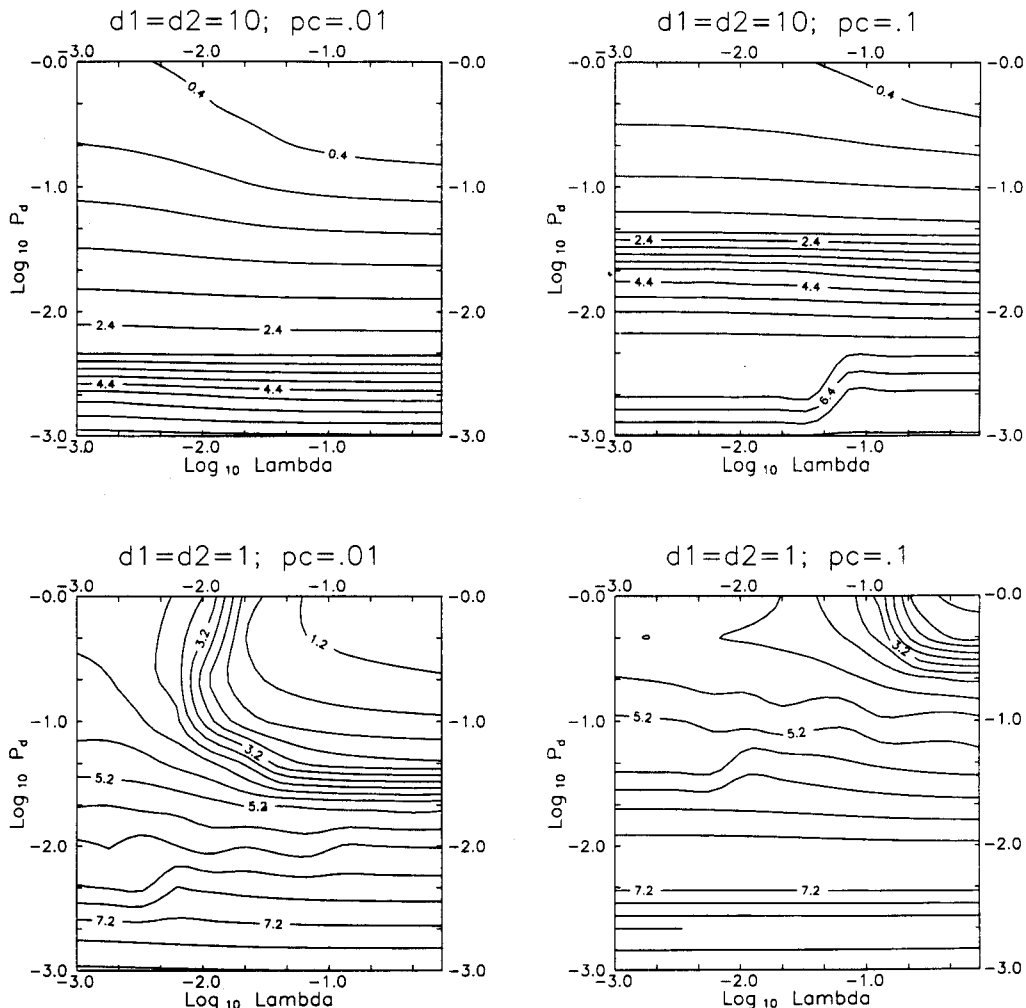


FIG. 6. Contours of the logarithm (base 10) of the Smoluchowski recurrence time for the set of states in which S_2 is present, as a function of disturbance frequency and λ . The two environmental states differ in their rates of disturbance.

Let $p_{ij}(t)$ denote the t -step transition probability $P(z(t) = i | z(0) = j)$. For any time $t > 0$,

$$E(z(0)z(t)) = \frac{1}{2}(z_1 z_2 (p_{12}(t) + p_{21}(t)) + z_1^2 p_{11}(t) + z_2^2 p_{22}(t)) \quad (16)$$

The probabilities $p_{ij}(t)$ are given by the corresponding entries of the matrix A' . From Iosifescu (1980: 55-56), we have

$$A' = \begin{pmatrix} \pi_1 & \pi_1 \\ \pi_2 & \pi_2 \end{pmatrix} + (1 - 2\lambda) \begin{pmatrix} \pi_2 & -\pi_1 \\ -\pi_2 & \pi_1 \end{pmatrix} \quad (17)$$

where the stationary distribution is $(\pi_1, \pi_2) = (1/2, 1/2)$.

Without loss of generality, we scale the environment so that $z_1 = 1$ and $z_2 = -1$. Then we have

$$E(z(0)z(t)) = (1 - 2\lambda)^t, \quad (18)$$

from which it follows that the autocovariance function is

$$\gamma_{zz}(t) = (1 - 2\lambda)^t. \quad (19)$$

This is the autocovariance function of a discrete first-order autoregressive process (e.g. Jenkins & Watts, 1968: 228). The spectral density function (given by the Fourier transform of the autocorrelation function) is

$$\Gamma(f) = \frac{1}{1 + \mu^2 - 2\mu \cos(2\pi f)}, \quad (20)$$

where $\mu = (1 - 2\lambda)$. For $0 < \lambda < 1/2$, the spectrum is dominated by low frequencies (i.e. is 'red'), while for $1/2 < \lambda < 1$ the spectrum is dominated by high

frequencies (i.e. is 'blue'). The case $\lambda = 1/2$ corresponds to white noise.

To couple this environmental model with our metapopulation model, we define two matrices \mathbf{B}_1 and \mathbf{B}_2 , corresponding to environments z_1 and z_2 . These matrices contain all the appropriate disturbance, dispersal, and interaction terms for patches in the appropriate environment. The transitions between environments are incorporated by producing a new enlarged transition matrix \mathbf{A}_x given by

$$\mathbf{A}_x = \begin{pmatrix} (1-\lambda)\mathbf{B}_1 & \lambda\mathbf{B}_2 \\ \lambda\mathbf{B}_1 & (1-\lambda)\mathbf{B}_2 \end{pmatrix}. \quad (21)$$

The state vector is now enlarged to include the proportions of patches in the various states in environment z_1 in the top half, and the proportions of patches in various states in environment z_2 in the bottom half. The matrix (21) is written assuming that change of state within an environment precedes the change from one environment to the other. If the two processes occur in the other order, the diagonal blocks would be interchanged.

3. Two Models

We applied the two-state Markovian environment to the competition model (6). The resulting model

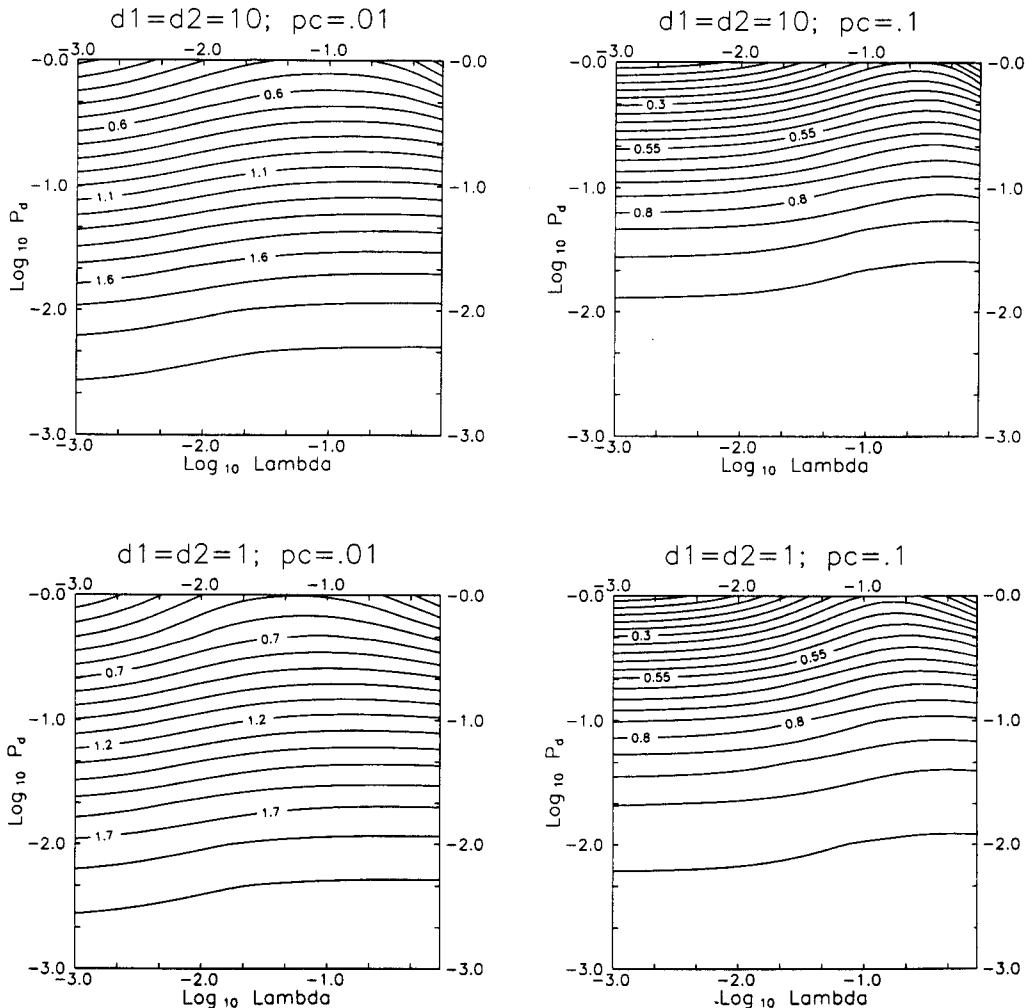


FIG. 7. Contours of the logarithm (base 10) of the Smoluchowski recurrence time for the set of states in which S_2 is absent, as a function of disturbance frequency and λ . The two environmental states differ in their rates of disturbance.

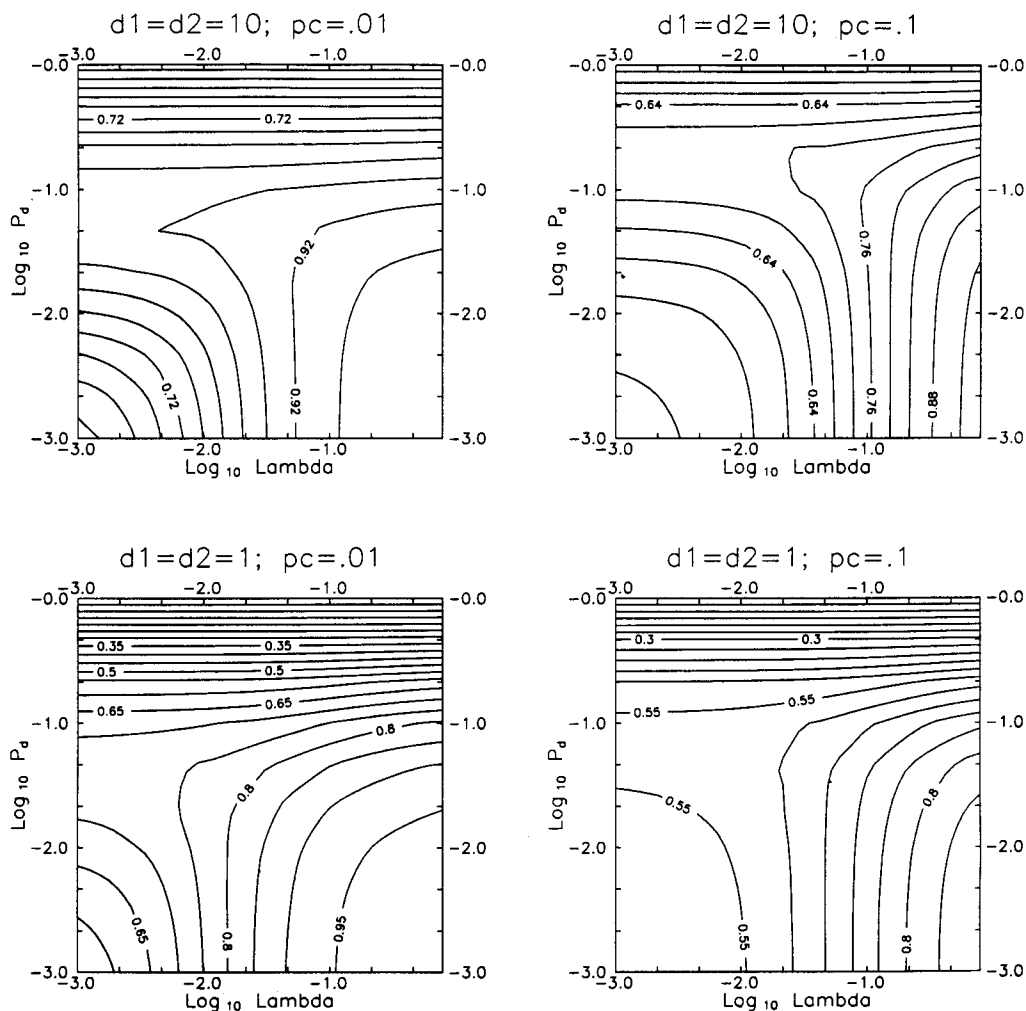


FIG. 8. Contours of the equilibrium frequency f_2 of S_2 as a function of disturbance frequency and λ . The two environmental states differ in the identity of the winning species.

contains eight states, in which patches are classified by species occupancy and the environmental state.

Env.	S_2	S_1	X
-1	0	0	1
-1	0	1	2
-1	1	0	3
-1	1	1	4
1	0	0	5
1	0	1	6
1	1	0	7
1	1	1	8

We assume that each species generates colonizing propagules at a rate independent of its environmental state. Thus the species frequencies which appear in the colonization coefficients C_i are

$$f_1 = x_2 + x_4 + x_6 + x_8$$

$$f_2 = x_3 + x_4 + x_7 + x_8.$$

This framework for environmental variation can encompass a variety of processes, depending on which parameters of the model differ between environments. We shall consider two models here. In the first, the two environments differ in the frequency of disturbance, while in the second they differ in the identity of the winning competitor.

3.1. ENVIRONMENTS DIFFERING IN DISTURBANCE RATE

Environmental variability enters the model (6) only through the independently distributed disturbance process, measured by p_d . It is not difficult to show that the spectrum of this process corresponds to white noise, with equal variance at all frequencies.

We suppose that the environment is characterized by two states, one "calm" and the other "turbulent" with differing values of p_d :

Environment	Disturbance Probability
calm (z_1)	0
turbulent (z_2)	p_d

A patch in the calm environment proceeds inexorably towards its local equilibrium: exclusion of S_2 by S_1 . A patch in the turbulent environment is occasionally returned to the empty state, in which both species can colonize. In a red environment ($\lambda < 0.5$), a patch tends to spend long periods in one or the other environment, whereas in a blue environment ($\lambda > 0.5$) a patch tends to alternate rapidly from one environment to the other.

Since the environmental process characterized by (12) has a stationary distribution $(\pi_1, \pi_2) = (1/2, 1/2)$, independent of λ , the effective disturbance frequency

in this model is $p_d/2$. We can vary the autocorrelation, and thus the spectrum, of the disturbance process, while keeping the mean frequency fixed.

Figure 1 shows a single realization of the environmental state of a single patch, for red, white and blue spectra. The effect of λ on the autocorrelation of the environmental fluctuations is evident from the figure. The translation of this environmental sequence into biological variables depends on the parameters, however. Figure 2 shows the results for the presence or absence of S_2 for this same realization. The results on recurrence time below quantify the differences in temporal scale of these fluctuations.

It was clear from our simulations that changing from red to white noise had major effects on the system, but further increases in λ towards blue noise had little effect. This is because, in our model, the mean residence time in one environmental state is λ^{-1} . As λ increases, this time decreases; once the mean residence time is

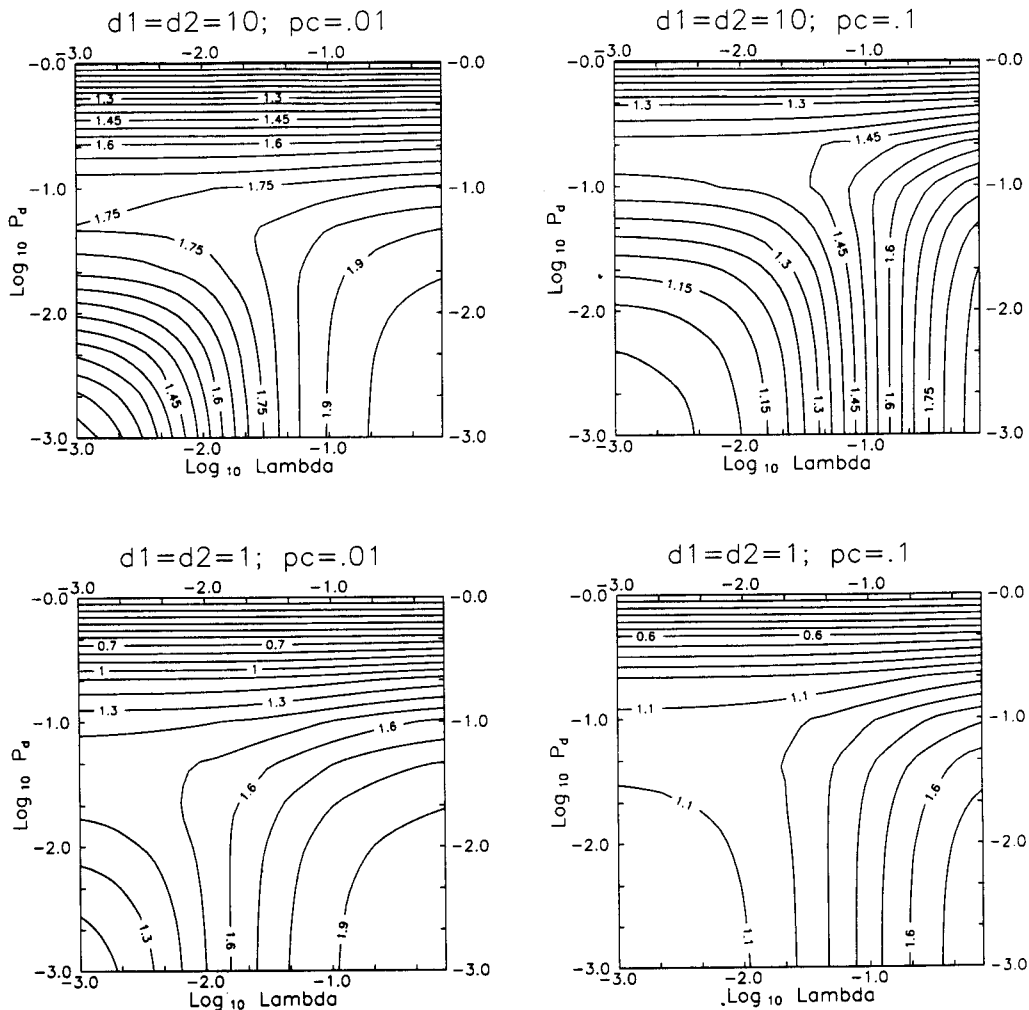


FIG. 9. Contours of alpha diversity as a function of disturbance frequency and λ . The two environmental states differ in the identity of the winning species.

Biotic beta diversity β_b increases with both p_d and λ , reaching its maximum at high disturbance rates and white (or even blue) environmental variability (Fig. 5).

To examine Steele & Henderson's (1984) hypothesis on the effects of red noise on state transitions, we computed the Smoluchowski recurrence times for two sets of states: those in which S_2 is present (which we call ξ_2) and for the set of states in which S_2 is absent ($\neg\xi_2$). The recurrence time for ξ_2 gives the mean time between extinction of S_2 and its next colonization. The recurrence time for $\neg\xi_2$ is the mean time between the colonization of S_2 and its next extinction; i.e. the persistence time for S_2 .

Steele and Henderson's models, forced with red noise, exhibit abrupt transitions between steady states which persist for relatively long periods of time. In our model, this pattern would be reflected in large values

for the Smoluchowski recurrence time for both ξ_2 and $\neg\xi_2$.

Recurrence times for ξ_2 increase, by many orders of magnitude, as p_d becomes small (Fig. 6). At intermediate to high disturbance frequencies, recurrence times increase as the spectrum becomes redder. Especially at low dispersal rates, a red spectrum leads to long intervals in which S_2 is absent, interrupted by occasional appearances.

The recurrence times for $\neg\xi_2$ are only weakly affected by λ (Fig. 7). The mean time between colonization of S_2 and its eventual extinction decreases as p_d increases, and is naturally longer when the competitive exclusion rate is lower. There is a very slight tendency, especially at high disturbance frequencies, for the recurrence time to decrease, rather than increase, as the environmental variability becomes redder.

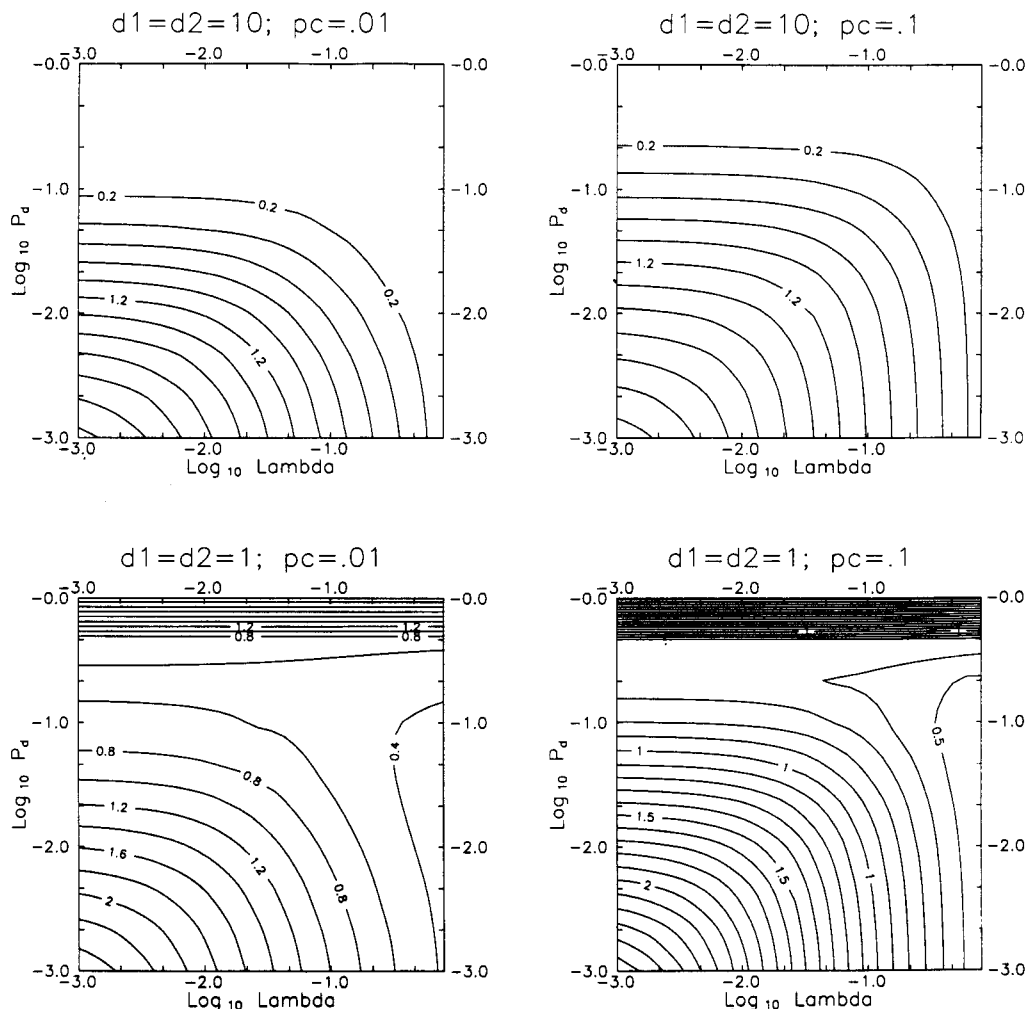


FIG. 11. Contours of the logarithm (base 10) of the Smoluchowski recurrence time for the set of states in which S_2 is present, as a function of disturbance frequency and λ . The two environmental states differ in the identity of the winning species.

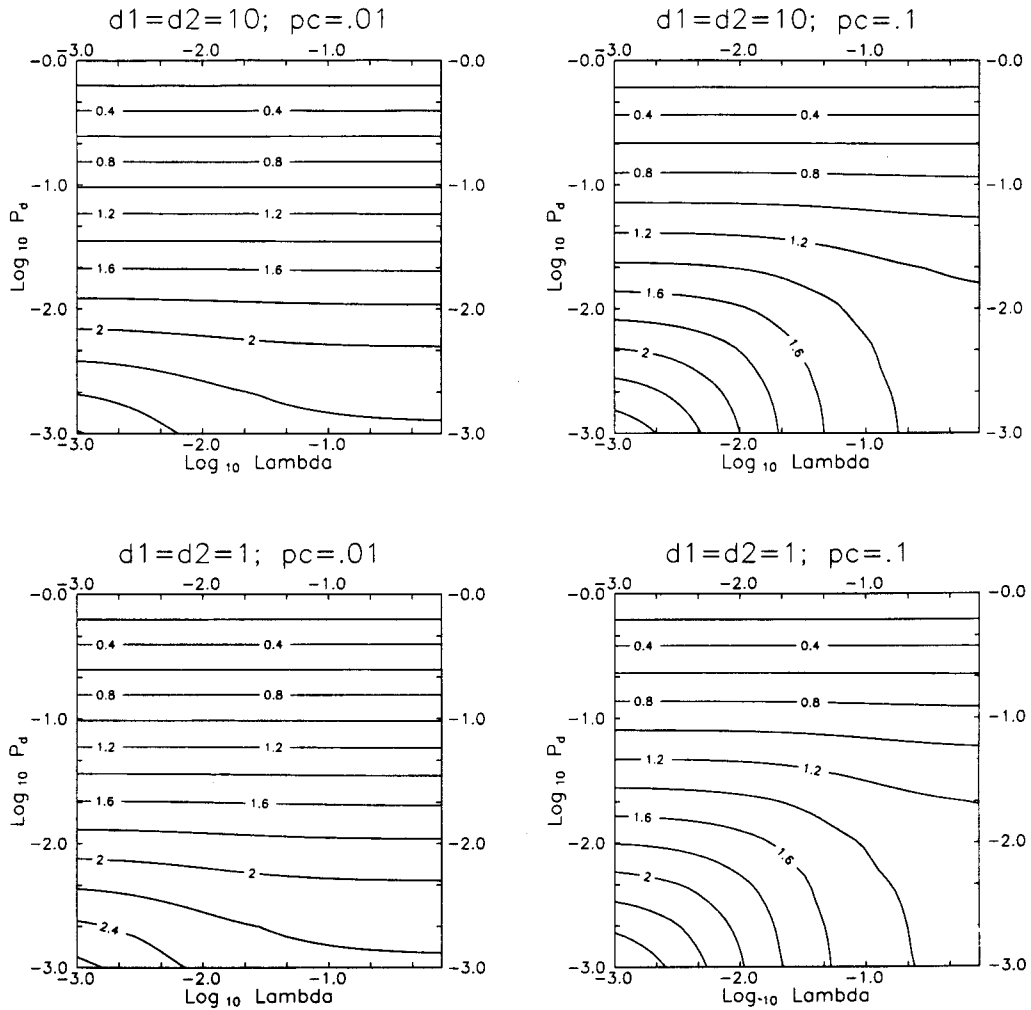


FIG. 12. Contours of the logarithm (base 10) of the Smoluchowski recurrence time for the set of states in which S_2 is absent. The two environmental states differ in the identity of the winning species.

In summary, as the spectrum of the disturbance process changes from white to red, persistence of the losing competitor becomes more difficult, and alpha and beta diversity are reduced. Within a patch, the intervals between appearances of the losing competitor become longer, and its persistence when it does appear becomes briefer.

3.2. ENVIRONMENTS DIFFERING IN COMPETITIVE DOMINANCE

As a second numerical experiment, we suppose that the winning competitor differs between the two environments. Such alternation could result from changes in the resource base or in abiotic conditions. Hutchinson (1961) suggested such changes as a mechanism for mediating coexistence in phytoplankton. For simplicity, we assume that all other parameters (d_i, p_c, p_d) are identical between environ-

ments. We consider high and low dispersal rates, ($d_1 = d_2 = 10$ and $d_1 = d_2 = 1$) and rates of competitive exclusion ($p_c = 0.1$ and $p_c = 0.01$).

The equilibrium frequency \hat{f}_2 of S_2 is shown in Fig. 8; because of the symmetry of the model, the results for \hat{f}_1 are identical.

At high disturbance frequencies, \hat{f}_2 is independent of λ . At lower disturbance frequencies, however, \hat{f}_2 is reduced as the environment becomes redder. This is because, when the environmental fluctuation is dominated by low frequencies, patches stay in one state long enough for competitive exclusion to occur, and disturbance is necessary for coexistence. As the switches in environmental state occur more rapidly, competitive exclusion has no time to occur. Alpha diversity reflects the same patterns (Fig. 9).

The results for biotic beta diversity β_b are shown in Fig. 10. At high dispersal rates, beta diversity is

maximized at low disturbance frequencies and low values of λ . Under these conditions, as p_d and λ go to zero, patches stay undisturbed in one state or the other, and spatial heterogeneity reflects a mosaic of patches at alternative equilibria. Beta diversity declines as either p_d or λ increases.

At lower dispersal rates the picture is more complicated (Fig. 10). When p_d is high, β_b is independent of λ . When p_d is low, however, there is a peak in β_b at intermediate values of λ .

The recurrence times for this model are consistent with the predictions of Steele & Henderson (1984). The results for ζ_2 and $\neg\zeta_2$ are shown in Figs 11 and 12. The recurrence times for ζ_2 increase as λ decreases and as p_d declines. The recurrence times for $\neg\zeta_2$ increase as the environment becomes redder, more so when competitive exclusion is rapid than when it is slow. Thus in this model, red noise produces a community characterized by switches between the presence and absence of a species over relatively long timescales.

In summary, variation in the identity of the competitive dominant can maintain coexistence even when disturbance is very rare. At low disturbance levels, where the switch in competitive dominant is largely responsible for coexistence, diversity is maximized at intermediate values of λ . As the environment becomes redder, the intervals between appearances of the losing competitor within a patch become longer.

4. Discussion

Variability that disturbs the approach to equilibrium is a crucial aspect of the environment for metapopulations, particularly for species that may be excluded locally by superior competitors. Our results show that the spectral properties of environmental variation have important effects. Most metapopulation models (indeed, most ecological models) describe environmental variation with white noise; we conclude that inferences drawn from such models may be sensitive to this assumption.

The color of the spectrum of a process reflects its autocorrelation pattern. The characteristic correlation time, in turn, is used as a measure of the scale of temporal variability. It is now recognized that spatial and temporal scales are an important feature of ecological processes (e.g. Haury *et al.*, 1978; Harris, 1986; Powell, 1989; Levin, 1992; Levin *et al.*, 1993; Steel & Henderson, 1994, and many others).

The effects of the spectrum depend on how it acts. Varying the intensity of the disturbance process and varying the identity of the winning competitor have different effects. Obviously, any of the parameters of

the model could have been made subject to environmental variation.

In general, a very red environmental spectrum makes the persistence of the losing competitor more difficult, reduces alpha and beta diversity, and extends the intervals between appearance of a species within a patch. However, in the model with a variable winning species, diversity may be maximized at intermediate values of λ , because at low disturbance levels the redness of the spectrum is itself responsible for maintaining coexistence.

One striking contrast between oceanic and terrestrial communities is the greater species diversity on land (Angel, 1993; May, 1994). The greater diversity of species on land may be an artifact of people living on land, rather than on the ocean floor; as more of the deep sea is sampled, the diversity of species found there may increase greatly (Grassle & Maciolek, 1992: 336). If terrestrial environments really have more species than marine environments, our models may explain why. As shown in Fig. 5, biotic beta diversity increases as the frequency of environmental disturbance increases and as the spectrum of environmental variability changes from red to white or even blue. Marine environments generally have redder spectra of environmental variability than terrestrial environments. Hence our models suggest that marine environments should have lower biotic beta diversity than terrestrial ones. This argument does not explain, however, why marine environments have about twice as many reported phyla as terrestrial.

Under some conditions, time series generated by colored noise are statistically indistinguishable from chaotic deterministic time series (Stone, 1992). Hence our results, derived for colored noise generated by environmental perturbations, may be equally relevant to perturbations derived from low-dimensional chaotic environments. This extends the relevance of our biological inferences to models in which the environment is driven chaotically.

Our simple Markovian approach to modeling the spectrum of environmental variation could be used in other theoretical analyses in population dynamics and community ecology, i.e. food web dynamics models.

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REFERENCES

- ANGEL, M. V. (1993). Biodiversity of the pelagic ocean. *Conserv. Biol.*, in press.
- BARRADAS, I. & COHEN, J. E. (1994). Disturbances allow coexistence of competing species. *J. math. Biol.* **32**, 663–676.
- CASWELL, H. (1978). Predator-mediated coexistence: a nonequilibrium model. *Am. Nat.* **112**, 127–154.
- CASWELL, H. & COHEN, J. E. (1991a). Communities in patchy environments: a model of disturbance, competition, and heterogeneity. In *Ecological Heterogeneity* (Kolasa, J. & Pickett, S. T. A., eds), pp. 97–122. New York: Springer-Verlag.
- CASWELL, H. & COHEN, J. E. (1991b). Disturbance, interspecific interaction, and diversity in metapopulations. *Biol. J. Linn. Soc.* **42**, 193–218.
- CASWELL, H. & COHEN, J. E. (1993). Local and regional regulation of species-area relations: a patch-occupancy model. In: *Species Diversity in Ecological Communities* (Ricklefs, R. E. & SCHLUTER, D., eds), pp. 99–107. Chicago: University of Chicago Press.
- CASWELL, H. & ETTER, R. J. (1993). Ecological interactions in patchy environments: from patch-occupancy models to cellular automata. In: *Patch Dynamics* (Levin, S. A., Powell, T. M. & Steele, J. H., eds), pp. 93–109. New York: Springer-Verlag.
- COHEN, J. E. (1970). A Markov contingency-table model for replicated Lotka-Volterra systems near equilibrium. *Am. Nat.* **104**, 547–560.
- CROWLEY, P. H. (1979). Predator-mediated coexistence: an equilibrium interpretation. *J. Theor. Biol.* **80**, 129–144.
- ETTER, R. J. & CASWELL, H. (1994). The advantages of dispersal in a patchy environment: effects of disturbance in a cellular automaton model. In: *Reproduction, Larval Biology and Recruitment in the Deep-Sea Benthos* (Eckelbarger, K. J. & Young, C. M., eds), pp. 284–305. Columbia University Press.
- GILPIN, M. & HANSKI, I. (eds) (1991). *Metapopulation Dynamics: Empirical and Theoretical Investigations*. London: Academic Press.
- GRASSLE, J. F. & MACIOLEK, N. J. (1992). Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *Am. Nat.* **139**, 313–341.
- HANSKI, I. (1983). Coexistence of competitors in patchy environment. *Ecology* **64**, 493–500.
- HASTINGS, A. (1978). Spatial heterogeneity and the stability of predator-prey systems: predator-mediated coexistence. *Theor. Popul. Biol.* **14**, 380–395.
- HAURY, L. R., MCGOWAN, J. A. & WIEBE, P. H. (1978). Patterns and processes in the time-space scales of plankton distributions. In: *Spatial Pattern in Plankton Communities* (Steele, J. H., ed.). New York: Plenum Press.
- HARRIS, G. P. (1986). *Phytoplankton Ecology*. New York: Chapman and Hall.
- HORSTHEMKE, W. & LEFEVER, R. (1984). *Noise-induced Transitions*. New York: Springer-Verlag.
- HUTCHINSON, G. E. (1961). The paradox of the plankton. *Am. Nat.* **95**, 137–145.
- IOSIFESCU, M. (1980). *Finite Markov Processes and their Applications*. New York: Wiley.
- JENKINS, G. M. & WATTS, D. G. (1968). *Spectral Analysis and its Applications*. New York: Wiley.
- KITAHARA, K., HORSTHEMKE, W. & LEFEVER, R. (1979). Colored-noise-induced transitions: exact results for external dichotomous Markovian noise. *Phys. Lett.* **70A**, 377–380.
- KITAHARA, K., HORSTHEMKE, W., LEFEVER, R. & INABA, Y. (1980). Phase diagrams of noise induced transitions: exact results for a class of external colored noise. *Prog. Theor. Phys.* **64**, 1233–1247.
- LEVIN, S. A. (1992). The problem of pattern and scale in ecology. *Ecology* **73**, 1943–1967.
- LEVIN, S. A., POWELL, T. M. & STEELE, J. H. (1993). *Patch Dynamics*. New York: Springer-Verlag.
- MATSUDA, H. & ISHII, K. (1981). Stationary gene frequency distribution in the environment fluctuating between two distinct states. *J. math. Biol.* **11**, 119–141.
- MAY, R. M. (1994). Biological diversity: differences between land and sea. *Phil. Trans. R. Soc. Lond.* **B343**, 105–111.
- MONIN, A. S., KAMENKOVICH, V. M. & KORT, V. G. (1977). *Variability of the oceans*. New York: Wiley.
- POWELL, T. M. (1989). Physical and biological scales of variability in lakes, and the coastal ocean. In: *Perspectives in Ecological Theory* (Roughgarden, J., May, R. M. & Levin, S. A., eds), pp. 157–176. Princeton Univ. Press.
- SINCLAIR, M. (1988). *Marine Populations*. Seattle: University of Washington Press.
- STEELE, J. H. (1985). A comparison of terrestrial and marine ecological systems. *Nature* **313**, 355–358.
- STEELE, J. H. (1991). Can ecological theory cross the land-sea boundary? *J. Theor. Biol.* **153**, 425–436.
- STEELE, J. H. & HENDERSON, E. W. (1984). Modeling long-term fluctuations in fish stocks. *Science* **224**, 985–987.
- STEELE, J. H. & HENDERSON, E. W. (1994). Coupling between physical and biological scales. *Phil. Trans. R. Soc. Lond.* **B343**, 5–9.
- STONE, L. (1992). Coloured noise or low-dimensional chaos? *Proc. R. Soc. Lond.* **B250**, 77–81.