# Disturbance, interspecific interaction and diversity in metapopulations

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Metapopulation diversity patterns depend on the relations among the timescales of local biological interactions (predation, competition), the rates of dispersal among local populations and the patterns of disturbance. We investigate these relationships using a family of simple non-linear Markov chain models. We consider three models for interspecific competition; if the species are identified with early and late successional species, the models describe the facilitation, inhibition and tolerance models of ecological succession. By adding a third competing species we also compare transitive competitive hierarchies and intransitive competitive networks. Finally, we examine the effects of predation in mediating coexistence among competing prey species. In each model we find circumstances in which biotic or abiotic disturbance can increase both local and regional diversity, but those circumstances depend on the various timescales in the model in ways that are neither obvious nor trivial.

KEY WORDS:—Competition - succession - competitive hierarchies and networks - predator-mediated coexistence - patch occupancy models - Markov chains.

## CONTENTS

## INTRODUCTION

The distinction between the metapopulation and the local populations that constitute it implies that metapopulation models must include *at least* two spatial scales, and must find a way to link processes taking place at these scales. In this paper we present a simple modelling framework to do this, and use it to explore the relationships between disturbance and diversity. We will consider both biotic and abiotic disturbance, and both local and regional species diversity. The models we use can describe many different ecological situations; we will use them here to examine alternative mechanisms of succession, transitive and intransitive competitive relations and predator-mediated coexistence.

Theories of ecological diversity have traditionally been based on results about species coexistence. Because of the multiscale organization of metapopulations, coexistence at the regional level may result from mechanisms which do not apply to local populations. In particular, in metapopulations the interaction of competition and disturbance can maintain *fugitive* or *non-equilibrium* species (Hutchinson, 1951, 1953) which persist regionally even though they are excluded locally whenever they come into contact with superior competitors. Ricklefs (1987) has emphasized the importance of distinguishing regional and local processes in the determination of diversity patterns.

What proportion of the species in a community are fugitives is not easy to determine, but in some cases it may be large. Hartshorn (1980), for example, found that more than two-thirds of the canopy and sub-canopy trees in a diverse tropical lowland forest in Costa Rica require treefall gaps for regeneration, and presumably could not persist in the absence of this type of disturbance. In some rocky intertidal areas, predatory starfish are an important agent of disturbance. Exclusion of these predators resulted in the rapid loss of 50% of the sessile invertebrate species in a study in Washington (Paine, 1966) and 33% of the species in a similar study in New Zealand (Paine, 1971). These may or may not be extreme cases, but it seems unwise to assume that fugitive species are a minority.

The interaction of disturbance and competition in metapopulations also suggests that species diversity will be maximized at intermediate disturbance frequencies (Connell, 1978; Huston, 1979). If disturbance is too rare, local competition will proceed to equilibrium and fugitive species will be eliminated. If disturbance is too frequent, it will eliminate fugitive and equilibrium species alike. At intermediate frequencies, the combination of fugitive species and equilibrium species produces a maximum in species diversity. This effect has been documented in hard substrate marine benthic communities (e.g. Dayton, 1971; Osman, 1977; Connell, 1978; Sousa, 1979a; Dethier, 1984 and many others).

The common denominator among these examples is the suggestion that coexistence and diversity in metapopulations are determined by the interaction of rates operating on several scales—competition (and other interspecific interactions) within patches, dispersal among patches and disturbance operating

across a landscape of patches. To explore these relations, we examine a family of simple models in which these rates appear explicitly.

## The model

We describe our metapopulations using a patch-occupancy model formulated as a non-linear Markov chain (for more details see Caswell & Cohen, 1990). Our approach is to specify the rates of local 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.

Consider an effectively infinite set of effectively identical patches. This landscape is inhabited by $n$ species, $S_1, \ldots, S_n$. The state of a patch is defined by the presence and absence of the species; there are $2^n$ possible patch states. These states can be numbered by letting 0 denote absence and 1 denote presence, and then adding 1 to the resulting binary number. For example, if $n = 2$, the possible states are

| $S_2$ | $S_1$ | State |
| --- | --- | --- |
| 0 | 0 | 1 |
| 0 | 1 | 2 |
| 1 | 0 | 3 |
| 1 | 1 | 4 |

We assume that the state of the metapopulation as a whole is given by a vector **x** whose entries $x_i$ give the proportion of patches in state $i$, $i = 1, \ldots, 2^n$. The state of a patch changes as a result of within-patch interactions, disturbance and colonization from other patches. The transition probabilities among patch states will depend on the state of the entire metapopulation, because colonization rates depend on the abundance of the colonizing species. The resulting dynamics are given by a (non-linear) Markov chain

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

the transition matrix for which $(\mathbf{A_x})$ is obtained from hypotheses about the timescales of disturbance, colonization, and interspecific interaction (Caswell & Cohen, 1990). In the next sections, we develop the transition matrices for a variety of different ecological models.

Patch occupancy models are commonly used to describe metapopulation dynamics (e.g. Cohen, 1970; Levins, 1970; Slatkin, 1974; Caswell, 1978; Crowley, 1979; Hastings, 1978; Hanski, 1983). They make several important simplifying 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 explicitly assumes that the spatial arrangement of the patches is of no importance; this rules out strong local interactions among patches (cf. Caswell & John, 1990 for a discussion of the effect of local interactions on the choice of state variables). Put another way, these models are limited to consideration of *only* two spatial scales—that of the local, within-patch population and that of the regional metapopulation. Only the development of comparable spatially explicit

metapopulation models will reveal how important these limitations are (Caswell, unpublished). For the present, we investigate these models as an improvement over local populations which consider only a single spatial scale.

Since equation (1) is a non-linear map, it is *a priori* capable of a variety of dynamics, including stable fixed points, oscillations, quasiperiodic orbits and chaos. Analytical results on these models are difficult to obtain, but our extensive numerical analyses have revealed only convergence to unique, globally stable equilibria. In this paper, we focus our attention on these equilibria and leave the possibility of more interesting dynamics as an open problem.

Convergence of the metapopulation to a stable equilibrium probability distribution $\hat{\mathbf{x}}$ (satisfying $\hat{\mathbf{x}} = \mathbf{A}_{\hat{x}}\hat{\mathbf{x}}$) *does not* imply that any 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, 1990).

From the equilibrium probability distribution $\hat{\mathbf{x}}$ a variety of indices of community structure can be calculated. Here we will focus on

1. The frequency $(f_i)$ of occurrence of each species. In the two species case, $f_1 = x_2 + x_4$ and $f_2 = x_3 + x_4$.

2. The local or alpha diversity, given 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 $\hat{\mathbf{x}}$:

$$\beta = - \sum_i x_i \log x_i \tag{2}$$

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 biological beta diversity by excluding empty patches:

$$\beta_b = - \sum_{s=2}^{2^n} \left( \frac{x_s}{\sum_{j=2}^{2^n} x_j} \log \frac{x_s}{\sum_{j=2}^{2^n} x_j} \right) \tag{3}$$

Because $\beta$ and $\beta_b$ are highly correlated we report only the results for $\beta_b$ here.

Examination of other community properties, including association patterns, turnover rates, and species-area relations appear elsewhere (Caswell & Cohen, 1990).

## COMPETITION AND ECOLOGICAL SUCCESSION

Connell & Slatyer (1977) identified three major types of ecological succession: facilitation, inhibition and tolerance. In each type, late successional species eventually replace early successional species. The types differ, however, in the effects of interspecific interactions on colonization. In facilitation, the later species can colonize a patch only after the early species have rendered the environmental conditions suitable for them. In the inhibition model, the later species do not require the early species to facilitate their entry into an empty patch, and either species can prevent colonization by the other; thus colonization

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occurs only into newly disturbed patches. Finally, the tolerance model supposes that either early or late species can colonize an empty patch, and that the sequence of early to late species is determined by their relative abilities to tolerate the reduction in resource levels that occurs as the populations grow.

Gallagher, Jumars & Trueblood (1983) and Turner (1983a) have recently reviewed experimental evidence on successional mechanisms in marine benthic systems. Both facilitation (e.g. Osman & Haugsness, 1981; Turner, 1983a; Harris *et al.*, 1984; Gallagher *et al.*, 1983) and inhibition (e.g. Sutherland & Karlson, 1977; Sousa, 1979b) have been clearly documented. There is less evidence for tolerance (McCall, 1977), perhaps because it lies so closely in the middle of the other two mechanisms.

No formal theory corresponding to the verbal models of Connell & Slatyer (1977) seems to have been developed. Here we use models for colonization and competition of two species as metaphors for succession, with one species representing 'early' and one species 'late' successional species.

## Models for facilitation, inhibition and tolerance

We begin with a simple model for tolerance. Suppose that $S_1$ is the within-patch winner ( = late successional species) and $S_2$ the loser. The rate of competitive exclusion of $S_2$ by $S_1$ is characterized by the exclusion probability $0 \leq p_c \leq 1$. Patches are subject to a disturbance characterized by the disturbance probability $0 \leq p_d \leq 1$, which applies to each patch independently. Disturbance eliminates all species and returns the patch to the empty state.

We suppose that dispersal of propagules is random (so there are no neighbourhood effects), and that the mean number of propagules of $S_i$ arriving at a patch is directly proportional to the frequency of patches containing $S_i$. Then the probability of the arrival of at least one propagule of $S_i$ is, according to the Poisson distribution,

$$C_i = 1 - \exp(-d_i f_i) \tag{4}$$

where $d_i$ is the dispersal coefficient and $f_i$ the frequency of species $i$.

The tolerance model assumes that $S_2$ cannot colonize patches containing $S_1$, whereas $S_1$ can colonize regardless of the presence of $S_2$.

The result of these hypotheses is a transition structure shown graphically in Fig. 1. The corresponding transition matrix $\mathbf{A_x}$ is given by

$$\mathbf{A_x}^{(T)} = \begin{pmatrix} (1-C_1)(1-C_2) & p_d & p_d & p_d \\ C_1(1-C_2) & 1-p_d & 0 & (1-p_d)p_c \\ (1-C_1)C_2 & 0 & (1-C_1)(1-p_d) & 0 \\ C_1 C_2 & 0 & C_1(1-p_d) & (1-p_d)(1-p_c) \end{pmatrix} \tag{5}$$

where the $C_i$ are functions of $\mathbf{x}$ through (4).

Models for facilitation and inhibition can be constructed in a similar manner. In the facilitation model, only the early successional species $S_2$ can invade an empty patch. The later successional species $S_1$ can invade a patch occupied by $S_2$ (but not vice versa), and eventually excludes it.

In the inhibition model, an empty patch can be invaded by either or both species, but each species is able to prevent colonization by the other. Direct competitive exclusion occurs only when both species colonize a patch
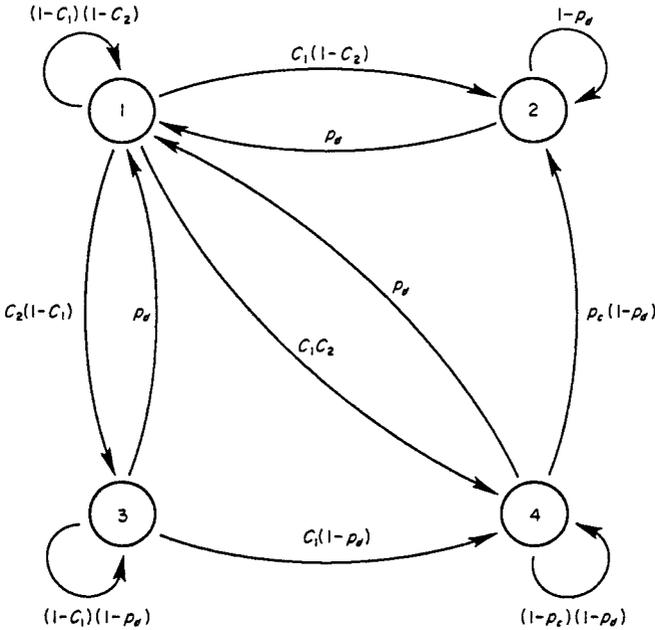
Figure 1. The transition graph for the two-species competition model (5), which also describes the tolerance model of succession. States are numbered as follows: 1, empty; 2, $S_1$ only, 3, $S_2$ only; 4, both. The late successional species $S_1$ is assumed to exclude the early successional species $S_2$. State 2, containing only $S_1$, is the successional 'climax'.

simultaneously, in which case the late successional species $S_1$ eventually excludes $S_2$. The graphs for the corresponding models of facilitation and inhibition are shown in Fig. 2. The corresponding matrices are

$$
\mathbf{A}_{\mathbf{x}}^{(F)} = \begin{pmatrix} 1-C_2 & p_d & p_d & p_d \\ 0 & 1-p_d & 0 & p_c(1-p_d) \\ C_2 & 0 & (1-C_1)(1-p_d) & 0 \\ 0 & 0 & C_1(1-p_d) & (1-p_c)(1-p_d) \end{pmatrix} \tag{6}
$$

$$
\mathbf{A}_{\mathbf{x}}^{(I)} = \begin{pmatrix} (1-C_1)(1-C_2) & p_d & p_d & p_d \\ C_1(1-C_2) & 1-p_d & 0 & p_c(1-p_d) \\ C_2(1-C_1) & 0 & 1-p_d & 0 \\ C_1C_2 & 0 & 0 & (1-p_c)(1-p_d) \end{pmatrix} \tag{7}
$$

In a numerical experiment designed to explore the parameter spaces of these models, we calculated the metapopulation equilibrium $\hat{\mathbf{x}}$ for each of the 120 combinations of parameters

$$
\begin{aligned}
d_1 &\in \{1,10\} \\
d_2 &\in \{1,10\} \\
p_c &\in \{0.01, 0.1, 1\} \\
p_d &\in \{10 \text{ values, log-uniformly spaced between } 0.001 \text{ and } 1\}
\end{aligned}
$$

Our results, extracted from this series of simulations, are shown as a series of graphs, plotting output variables as functions of disturbance frequency $p_d$, for different dispersal and competitive exclusion rates.
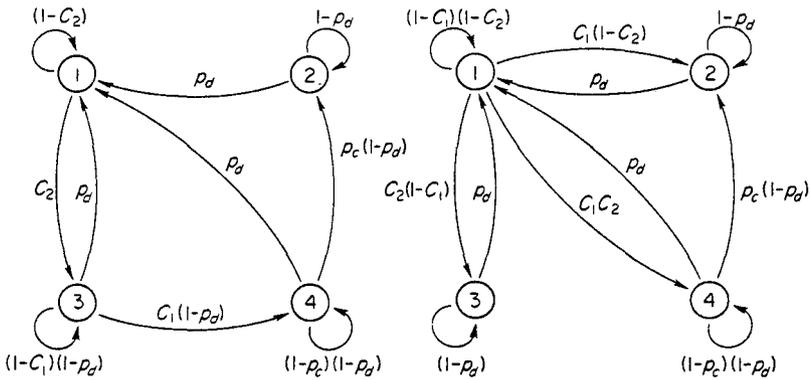
Figure 2. Transition graphs for the facilitation (left) and inhibition (right) models of succession. In each graph, $S_2$ is the early and $S_1$ the later successional species, and state 2 is the 'climax'. States are identified as in Fig. 1.

## Species frequencies

The frequency $f_1$ of the winning competitor is shown in Fig. 3. In the tolerance model, $f_1$ is independent of the losing competitor. In this model, $S_1$ persists if and only if $d_1 > p_d$ (Caswell & Cohen, unpublished). The equilibrium frequency of $S_1$ declines with increasing disturbance frequency. In the facilitation and inhibition models, there is some effect of $S_2$ on $S_1$. In both models, $f_1$ declines monotonically with $p_d$. In the facilitation model, the decline is most rapid when the dispersal rate of the early successional species is low, since this reduces the ability of $S_1$ to colonize. In the inhibition model, $f_1$ depends on both the absolute and relative dispersal rates. Given a sufficient dispersal advantage ($d_1 = 1$, $d_2 = 10$ in Fig. 3E,F), the losing competitor is capable of excluding the winning competitor; i.e. $f_1 \approx 0$.

The frequency $f_2$ of the losing competitor is shown in Fig. 4. In the tolerance and facilitation models, $S_2$ is a genuine fugitive species, and is unable to persist in the absence of disturbance. In the tolerance model, it appears that disturbance must exceed a critical frequency ($p_d \approx p_c/d_2$ in these simulations) to permit $f_2 > 0$. The frequency of $S_2$ eventually reaches a maximum at an intermediate disturbance frequency. The disturbance frequency which maximizes $f_2$ increases with increases in the rate of competitive exclusion. The facilitation model behaves similarly, except that $f_2$ is much less sensitive to variation in $d_2$ than in the tolerance model.

Note that in neither the tolerance nor the facilitation model does $S_2$ require a dispersal advantage in order to persist.

In the inhibition model, the early successional species persists only when $d_2 \geq d_1$ (Fig. 4E,F). When $S_2$ has a dispersal advantage ($d_2 > d_1$), it declines in frequency with increasing $p_d$, behaving in this regard like a competitive dominant rather than a fugitive species. When the dispersal rates are equal, $f_2$ is maximized at a disturbance frequency which increases with increasing $p_c$.

## Alpha diversity

Some combinations of competition, disturbance and dispersal result in enhanced local species diversity at intermediate disturbance frequencies (Fig. 5).
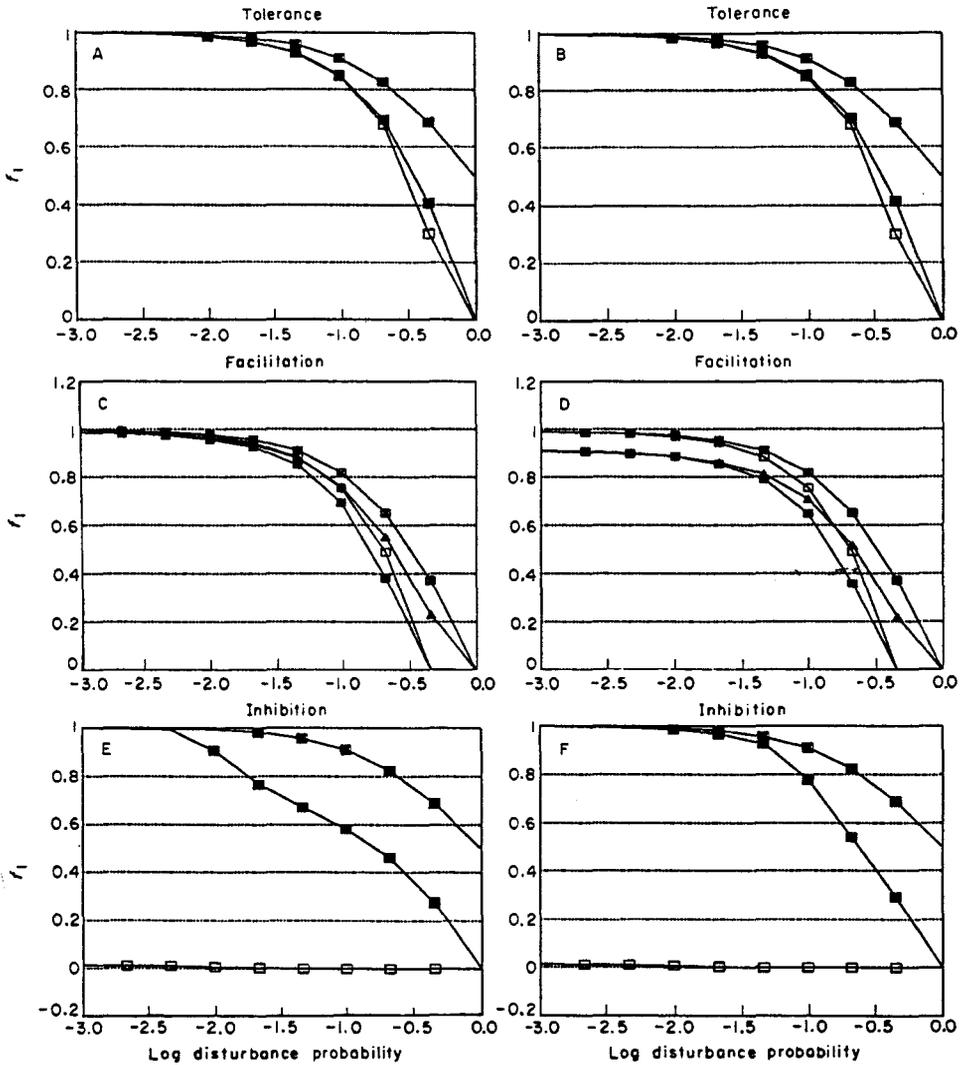
Figure 3. The equilibrium frequency $f_1$ of the winning competitor ( = late successional species) in three succession models, as functions of disturbance frequency $(p_d)$, competitive exclusion rate $(p_c)$ and species dispersal rates $(d_1, d_2)$. Left column, $p_c = 0.01$; right column $p_c = 0.1$. A,B, Tolerance. C,D, Facilitation. E,F, Inhibition. ■ 1,1; □ 1,10; ▲ 10,1; ⊠ 10,10.

In the tolerance model, diversity is enhanced by disturbance when either dispersal is rapid or competitive exclusion is slow. When competitive exclusion is slow enough, diversity is maximized when $p_d \approx 10 p_c$ (Fig. 5A). The diversity maximum disappears when dispersal rates are slow enough, and is less pronounced the more rapid the rate of competitive exclusion.

As competitive exclusion rate increases, higher disturbance frequencies and higher dispersal rates are required for diversity enhancement. If dispersal rates are high enough, no dispersal advantage on the part of the losing competitor is required for diversity enhancement.

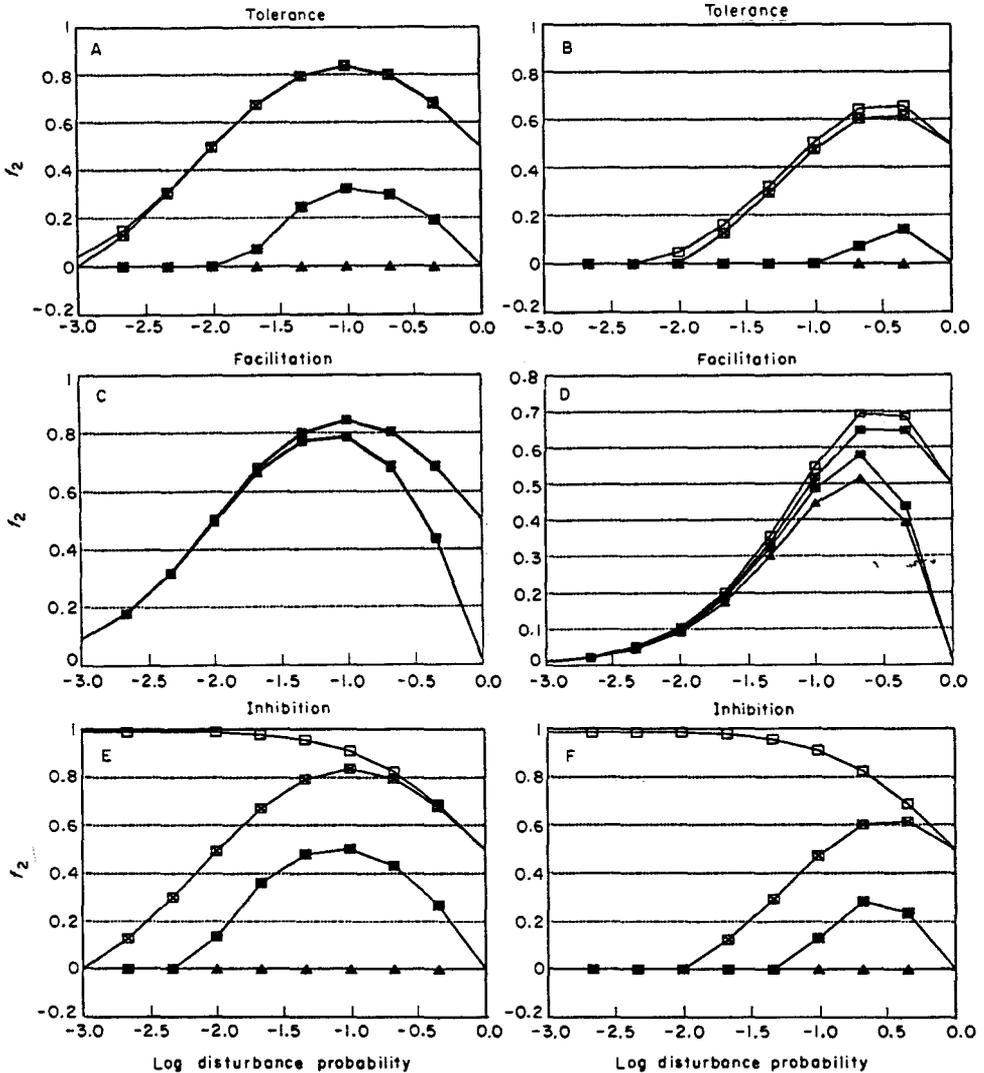Disturbance enhances alpha diversity in the facilitation model (Fig. 5C,D);

Figure 4. The equilibrium frequency $f_2$ of the losing competitor ( = early successional species) in three succession models, as functions of disturbance frequency $(p_d)$, competitive exclusion rate $(p_c)$ and species dispersal rates $(d_1, d_2)$. Left column, $p_c = 0.01$; right column $p_c = 0.1$. A,B, Tolerance. C,D, Facilitation. E,F, Inhibition. ■ 1,1; □ 1,10; ▲ 10,1; ⊠ 10,10.

the extent of the enhancement and the disturbance frequency which maximizes diversity are nearly independent of dispersal.

In the inhibition model, diversity is enhanced by disturbance only when $d_1 = d_2$. If either species has a dispersal advantage, the enhancement effect disappears; thus the alpha diversity curves for $(d_1, d_2) = (1, 10)$ and $(d_1, d_2) = (10, 1)$ coincide.

The interaction of disturbance and dispersal rates is examined in more detail in Fig. 6, which shows contours of alpha diversity as a function of $p_d$ and $d_2/d_1$, for $d_1 = 1$ and $p_c = 0.01$. A diversity maximum at intermediate disturbance frequencies can be seen for all values of $d_2/d_1$ in the facilitation model (Fig. 6B),
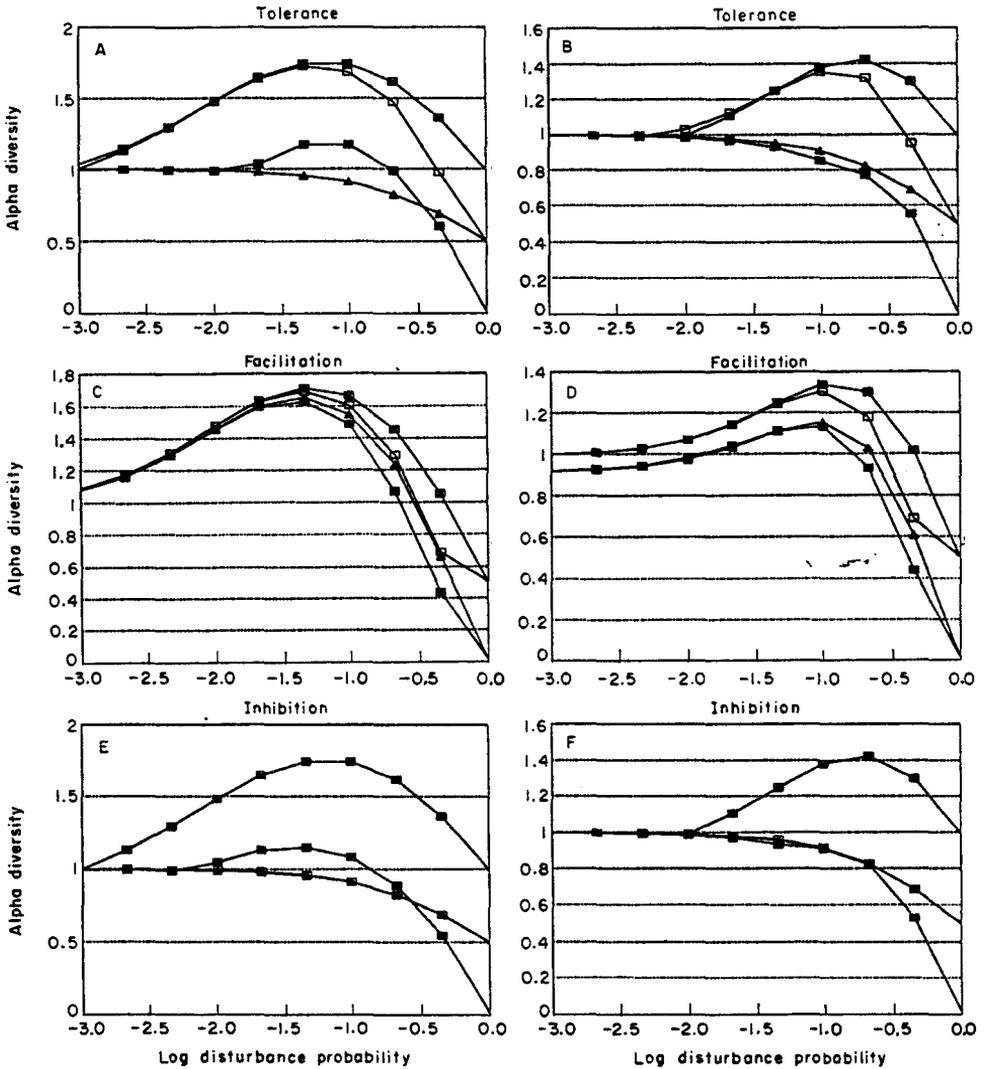
Figure 5. Mean alpha diversity in three succession models, as functions of disturbance frequency $(p_d)$, competitive exclusion rate $(p_c)$ and species dispersal rates $(d_1, d_2)$. Left column, $p_c = 0.01$; right column $p_c = 0.1$. A,B, Tolerance. C,D, Facilitation. E,F, Inhibition. ■ 1,1; □ 1,10; ▲ 10,1; ⊠ 10,10.

for $d_2/d_1 \approx 1$ in the inhibition model (Fig. 6C), and for $d_2/d_1 \geq 1$ in the tolerance model (Fig. 6A).

## Spatial heterogeneity

The interaction of disturbance and competition in producing spatial heterogeneity, measured by $\beta_b$, is shown in Fig. 7. In the tolerance model, disturbance maintains beta diversity in all cases except when the early successional species is at a dispersal disadvantage. In the other cases, $\beta_b$ increases with increasing disturbance rate, eventually reaching a maximum and declining.
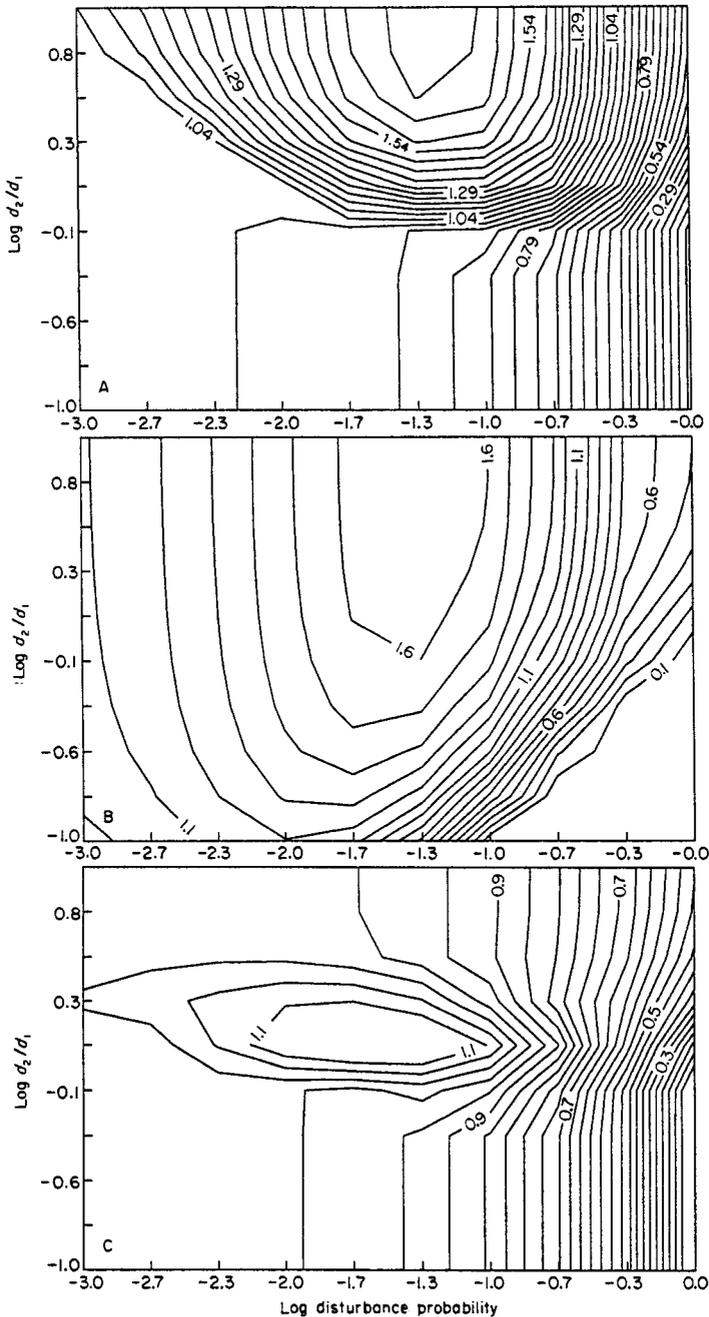
Figure 6. Contour plots of alpha diversity as a function of disturbance probability $p_d$ and the relative dispersal rates $d_2/d_1$ for the A, tolerance, B, facilitation, and C, inhibition models of succession. $d_1 = 1$ and $p_c = 0.01$ in all graphs.

Beta diversity in the facilitation model is nearly independent of dispersal rates; when the competitive exclusion rate is low (Fig. 7C) there is a suggestion of a bimodal response of $\beta_b$ to disturbance. In the inhibition model, significant beta diversity is maintained only when the two species have equal dispersal rates.
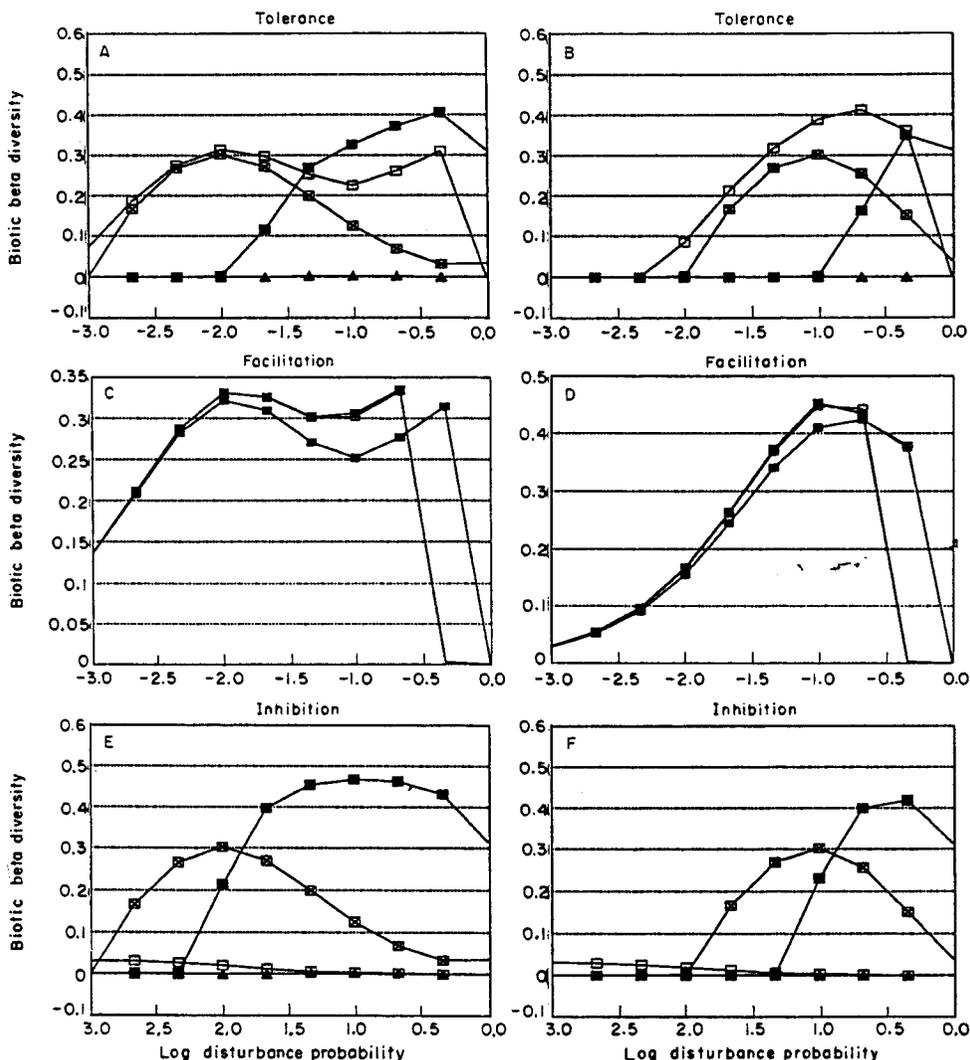
Figure 7. Biotic beta diversity in three succession models, as functions of disturbance frequency $(p_d)$, competitive exclusion rate $(p_c)$, and species dispersal rates $(d_1, d_2)$. Left column, $p_c = 0.01$; right column $p_c = 0.1$. A,B, Tolerance. C,D, Facilitation. E,F, Inhibition. ■ 1,1; □ 1,10; △ 10,1; ⊠ 10,10.

## Conclusions: The effects of successional mechanisms

The differences among the facilitation, inhibition and tolerance models have implications for coexistence, species diversity and spatial heterogeneity. These are summarized in Table 1.

### COMPETITIVE HIERARCHIES AND NETWORKS

The distinction between competitive hierarchies and competitive networks was emphasized by Jackson & Buss (1975) and Buss & Jackson (1979) in their studies of allelopathy among coral reef invertebrates. The interactions in a

TABLE 1. *Properties of tolerance, facilitation and inhibition models of succession*

| Variable | Tolerance | Facilitation | Inhibition |
|----------|-----------|--------------|------------|
| $f_1$ | independent of $S_2$ | increases with increasing $d_2$ | $> 0$ only when $d_1 \geq d_2$ |
| $f_2$ | requires $p_d > p_i/d_2$; intermediate maximum when $d_2 \geq d_1$ | intermediate maximum; weak dependence on $d_i$ | $> 0$ when $d_2 \geq d_1$; intermediate maximum when $d_1 \approx d_2$ |
| Alpha | intermediate maximum when $d_2 > d_1$ | intermediate maximum regardless of $d_i$ | intermediate maximum when $d_1 \approx d_2$ |
| Beta | $> 0$ if $d_2 \geq d_1$ | always $> 0$ | $> 0$ only when $d_1 \approx d_2$ |

competitive hierarchy are transitive, so that if $S_1$ excludes $S_2$, and $S_2$ excludes $S_3$, then $S_1$ also excludes $S_3$. In a competitive network the interactions are intransitive (e.g. in the previous example, $S_3$ excludes $S_1$). Petraitis (1979) discusses the problem of measuring the degree of intransitivity in a multispecies system. Studies in several marine habitats have produced differing opinions on the occurrence of intransitive networks (Buss & Jackson, 1979; Quinn, 1982; Sebens, 1986; Todd & Turner, 1988).

Our interest here is in the effects of intransitivity on diversity in metapopulations. Jackson & Buss (1975) suggested that competitive networks could enhance diversity. Caswell (1978) viewed this as a special case of disturbance, in which the within-patch equilibrium is disturbed not by the abiotic environment but by the arrival of another competing species. Some simulation studies (Karlson & Jackson, 1981; Karlson & Buss, 1984) have suggested that intransitive networks can enhance diversity only under low disturbance rates.

## *The model*

The simplest community capable of supporting both hierarchies and networks contains three species. We consider competing species $S_1$, $S_2$, $S_3$. Let ' $>$ ' denote 'excludes'; then the hierarcy and network models are characterized by

$$\text{hierarchy } S_1 > S_2 > S_3 \text{ and } S_1 > S_3$$
$$\text{network } S_1 > S_2 > S_3 \text{ and } S_1 < S_3$$

We shall assume (as in the tolerance model) that the presence of the winner precludes colonization by the loser. Patch states are numbered

| $S_3$ | $S_2$ | $S_1$ | State |
|-------|-------|-------|-------|
| 0 | 0 | 0 | 1 |
| 0 | 0 | 1 | 2 |
| 0 | 1 | 0 | 3 |
| 0 | 1 | 1 | 4 |
| 1 | 0 | 0 | 5 |
| 1 | 0 | 1 | 6 |
| 1 | 1 | 0 | 7 |
| 1 | 1 | 1 | 8 |

For simplicity we assume a common competitive exclusion rate $p_c$ for all three competitive interactions. We also assume that, when all three species are present in a patch, the competitive interactions among them are independent. Thus, for example, a patch in state 8 in the network model has a probability $p_c(1-p_c)^2$ of moving to each of states, 4, 6 and 7 (exclusion of one species), a probability $p_c^2(1-p_c)$ of moving to each of states 5, 3 and 2 (exclusion of two species), and a probability $p_c^3$ of moving to state 1 (exclusion of all three species).

The transition matrices for the two models are given in Tables 2 and 3.

To examine the effects of transitivity, we conducted a numerical experiment. We set the dispersal rates of all three species equal, and varied the parameters in all possible combinations of the following values:

$$d_i \in \{1, 10\} \qquad i = 1, 2, 3$$
$$p_c \in \{0.01, 0.10, 1.00\}$$
$$p_d \in \{10 \text{ values, log-uniformly spaced between } 0.001 \text{ and } 1\}$$

The results for $d_i = 1$ and $d_i = 10$ will permit us to compare low-dispersal and high-dispersal communities; within each of these types of communities, we can examine the interaction between the rate of local competitive exclusion and the probability of disturbance. The results are shown in the next series of figures.

## Species frequencies

The pattern of species frequencies in the hierarchy model (Fig. 8) is familiar from the tolerance model discussed above. The frequency $f_1$ of the winning species declines as $p_d$ increases, reaching 0 when $p_d \approx d_1$. $S_2$ and $S_3$, which both lose in competition, behave like the losing species in the tolerance model; their frequencies $f_1$ are close to zero until the product $p_d d_i > p_c$, so that the frequency of disturbance required for coexistence is directly proportional to the rate of competitive exclusion. The frequencies $f_2$ and $f_3$ are maximized at intermediate disturbance frequencies, with the maximizing values of $p_d$ proportional to the rate of competitive exclusion.

The species frequencies in the network model respond quite differently (Fig. 9). Because of the symmetry in the competitive relationships (each species excludes, and is excluded by, one other), $f_1 = f_2 = f_3$. At low dispersal rates, species frequencies decline with increasing disturbance probability. In high dispersal communities, frequencies are maximized at intermediate disturbance levels when competition is slow, and are independent of disturbance when competition is fast. Regardless of dispersal rates, species frequencies decline with increasing $p_c$.

## Alpha diversity

The response of local species diversity to disturbance for the two models is shown in Fig. 10. In the competitive hierarchy, the response is much like that of the tolerance model. Alpha diversity is maximized at an intermediate disturbance frequency when dispersal rates are high and/or competitive exclusion rates are low. The disturbance frequency which maximizes diversity is proportional to $p_c$.

In a competitive network, when dispersal rates are low, $\alpha$ declines with

TABLE 2. Transition matrix for three-species competitive network model

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | $(1-C_1)(1-C_2)(1-C_3)$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ | $p_d+(1-p_d)p_c^3$ |
| 2 | $C_1(1-C_2)(1-C_3)$ | $(1-p_d)(1-C_3)$ | 0 | $(1-p_d)p_c$ | 0 | 0 | 0 | $(1-p_d)p_c^2(1-p_c)$ |
| 3 | $(1-C_1)C_2(1-C_3)$ | 0 | $(1-p_d)(1-C_1)$ | 0 | 0 | 0 | $(1-p_d)p_c$ | $(1-p_d)p_c^2(1-p_c)$ |
| 4 | $C_1C_2(1-C_3)$ | 0 | $(1-p_d)C_1$ | $(1-p_d)(1-p_c)$ | 0 | 0 | 0 | $(1-p_d)p_c(1-p_c)^2$ |
| 5 | $(1-C_1)(1-C_2)C_3$ | 0 | 0 | 0 | $(1-p_d)(1-C_2)$ | $(1-p_d)p_c$ | 0 | $(1-p_d)p_c^2(1-p_c)$ |
| 6 | $C_1(1-C_2)C_3$ | $(1-p_d)C_3$ | 0 | 0 | 0 | $(1-p_d)(1-p_c)$ | 0 | $(1-p_d)p_c(1-p_c)^2$ |
| 7 | $(1-C_1)C_2C_3$ | 0 | 0 | 0 | $(1-p_d)C_2$ | 0 | $(1-p_d)(1-p_c)$ | $(1-p_d)p_c(1-p_c)^2$ |
| 8 | $C_1C_2C_3$ | 0 | 0 | 0 | 0 | 0 | 0 | $(1-p_d)(1-p_c)^3$ |

TABLE 3. Transition matrix for three-species competitive hierarchy model

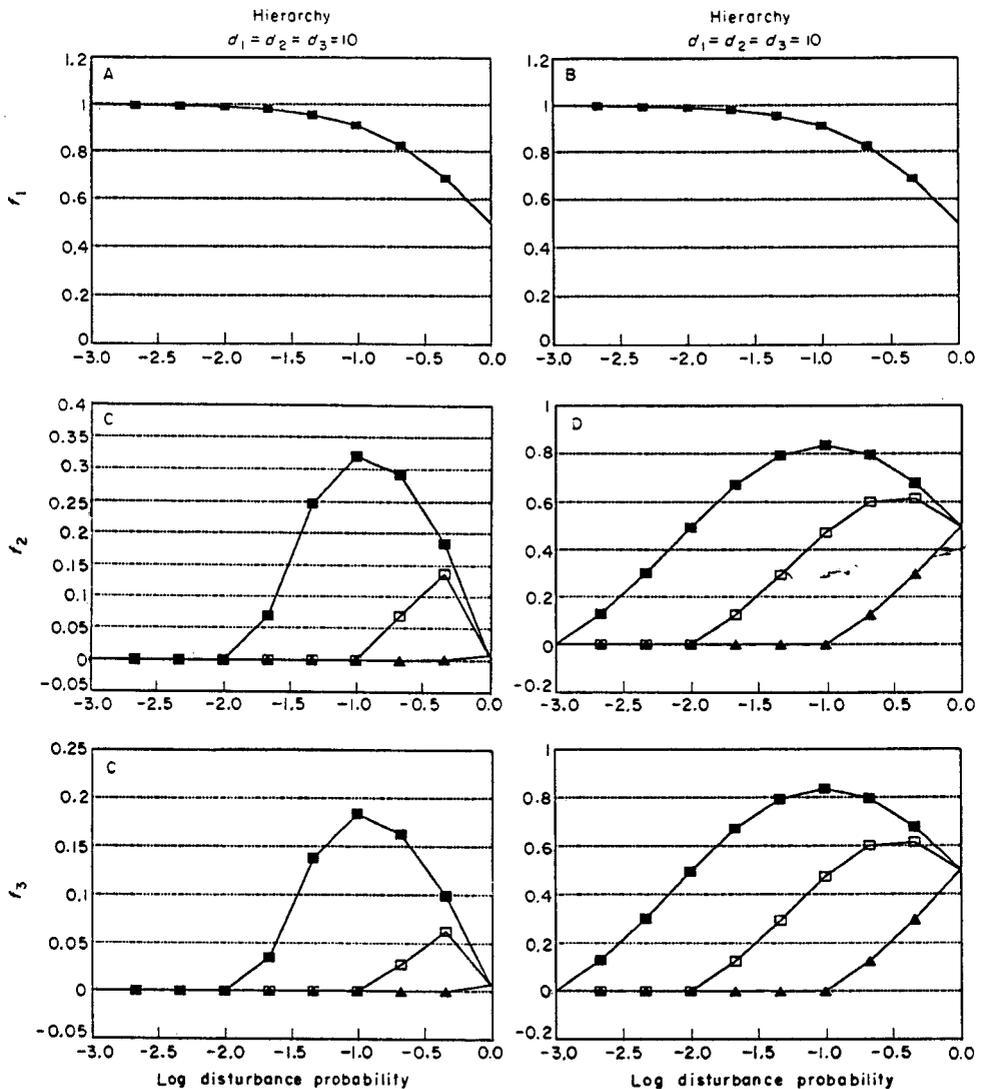| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | $(1-C_1)(1-C_2)(1-C_3)$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ | $p_d$ |
| 2 | $C_1(1-C_2)(1-C_3)$ | $(1-p_d)$ | 0 | $(1-p_d)p_c$ | 0 | $(1-p_d)p_c$ | 0 | $(1-p_d)p_c^2$ |
| 3 | $(1-C_1)C_2(1-C_3)$ | 0 | $(1-p_d)(1-C_1)$ | 0 | 0 | 0 | $(1-p_d)(1-C_1)p_c$ | 0 |
| 4 | $C_1C_2(1-C_3)$ | 0 | $(1-p_d)C_1$ | $(1-p_d)(1-p_c)$ | 0 | 0 | $(1-p_d)C_1p_c$ | $(1-p_d)p_c(1-p_c)$ |
| 5 | $(1-C_1)(1-C_2)C_3$ | 0 | 0 | 0 | $(1-p_d)(1-C_1)(1-C_2)$ | 0 | 0 | 0 |
| 6 | $C_1(1-C_2)C_3$ | 0 | 0 | 0 | $(1-p_d)C_1(1-C_2)$ | $(1-p_d)(1-p_c)$ | 0 | $(1-p_d)p_c(1-p_c)$ |
| 7 | $(1-C_1)C_2C_3$ | 0 | 0 | 0 | $(1-p_d)(1-C_1)C_2$ | 0 | $(1-p_d)(1-C_1)(1-p_c)$ | 0 |
| 8 | $C_1C_2C_3$ | 0 | 0 | 0 | $(1-p_d)C_1C_2$ | 0 | $(1-p_d)C_1(1-p_c)$ | $(1-p_d)(1-p_c)^2$ |

Figure 8. Equilibrium frequencies $f_1$, $f_2$ and $f_3$ of the three species in the competitive hierarchy model, for competitive exclusion probabilities of $p_c = 0.01$ (■), $p_c = 0.10$ (□) and $p_c = 1.00$ (▲).

increasing $p_d$. In high dispersal communities, $\alpha$ is maximized at intermediate disturbance rates for very slow competition.

Alpha diversity is much higher at low disturbance rates in networks than in hierarchies. This supports the conjecture that intransitive competition might act like a form of disturbance (Caswell, 1978) and agrees with the simulation results of Karlson & Buss (1984).

## Spatial heterogeneity

Spatial heterogeneity also differs between hierarchies and networks (Fig. 11). In a competitive hierarchy, disturbance is required to maintain any spatial heterogeneity. $\beta_b$ begins to increase when $p_d$ exceeds $p_c/d_i$ (the point at which the
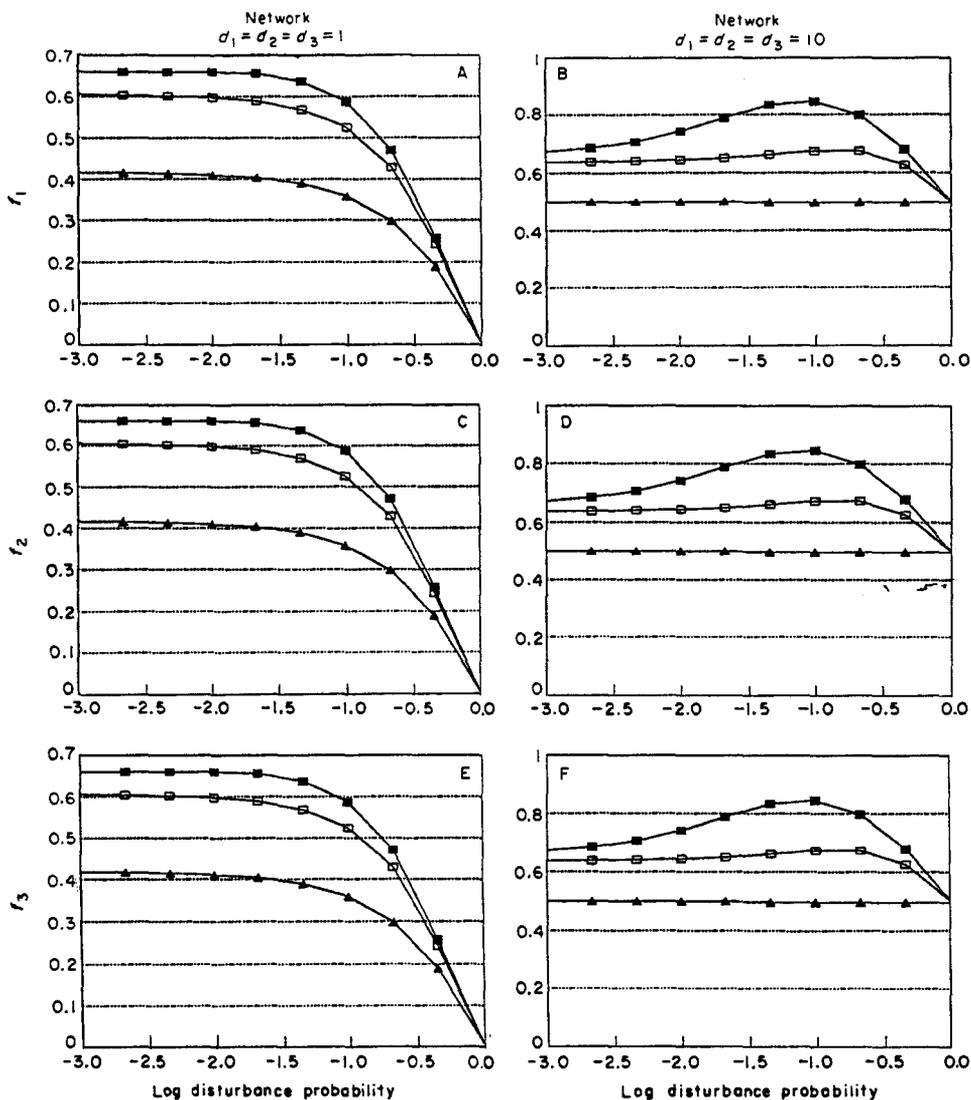
Figure 9. Equilibrium frequencies $f_1$, $f_2$ and $f_3$ of the three species in the competitive network model, for competitive exclusion probabilities of $p_c = 0.01$ (■), $p_c = 0.10$ (□) and $p_c = 1.00$ (▲).

losing species $S_2$ and $S_3$ begin to persist at appreciable frequencies; cf. Fig. 8). It increases to a maximum at an intermediate disturbance frequency, and finally declines again at high disturbance frequencies.

In contrast, competitive networks maintain spatial heterogeneity, equivalent to the maximum attained by competitive hierarchies, even at low disturbance rates. As $p_d$ increases, $\beta_b$ may increase slightly, and eventually declines.

## Conclusions: the effects of intransitivity

Transitive and intransitive competitive communities behave very differently. At any given disturbance rate, intransitive competitive networks maintain
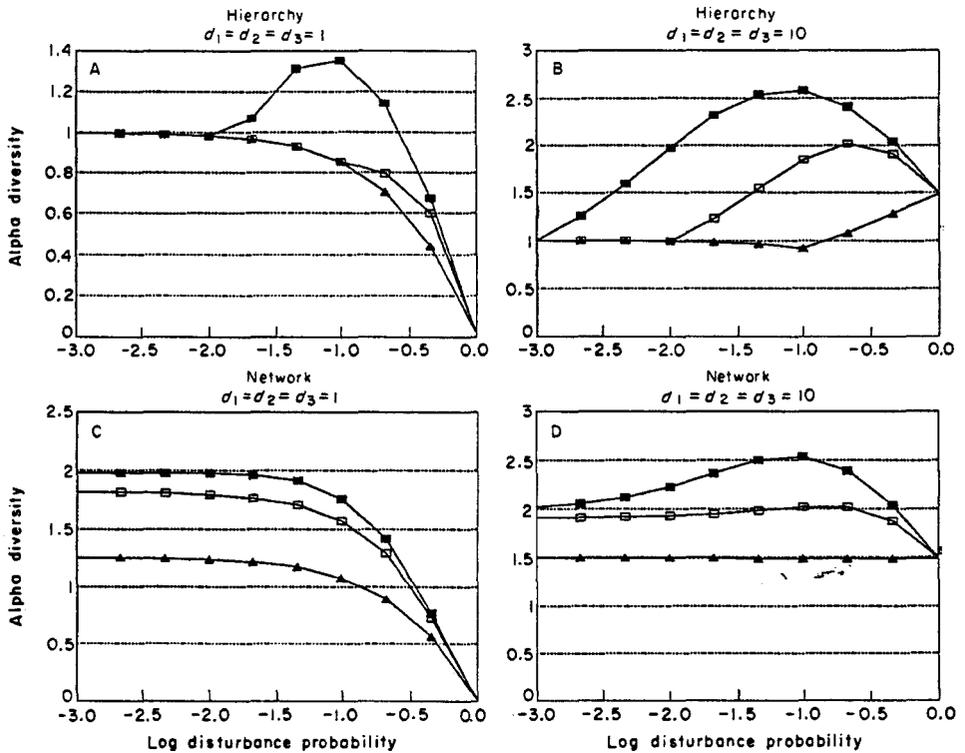
Figure 10. Alpha diversity in competitive hierarchies and networks as a function of disturbance probability, for competitive exclusion probabilities $p_c = 0.01$ (■), $p_c = 0.10$ (□) and $p_c = 1.00$ (▲).

higher values of both alpha and beta diversity than do competitive hierarchies. Most of the properties of competitive networks are less sensitive to disturbance than the corresponding properties of competitive hierarchies.

## PREDATOR-MEDIATED COEXISTENCE

Predator-mediated coexistence refers to coexistence, under the impact of predation, of two or more competing species not all of which could persist in the absence of the predator. Although studies of predator-mediated coexistence date back to the last century, focus on it as an important determinant of community structure dates from Paine's (1966) experimental work on rocky intertidal invertebrates and Harper's (1969) review of experiments on terrestrial plant communities. Janzen (1970) and Connell (1971) independently proposed a special case as a possible mechanism for maintaining high diversity in tropical forests.

There is little doubt that predation has important impacts on prey populations and communities. Sih *et al.* (1985) statistically analysed published results of field experiments in which predators were manipulated. The vast majority of these studies reported significant effects of predation on prey abundance and diversity. Almost 30% of the published comparisons found significant increases in prey species diversity, and 25% found significant increases in prey population size.
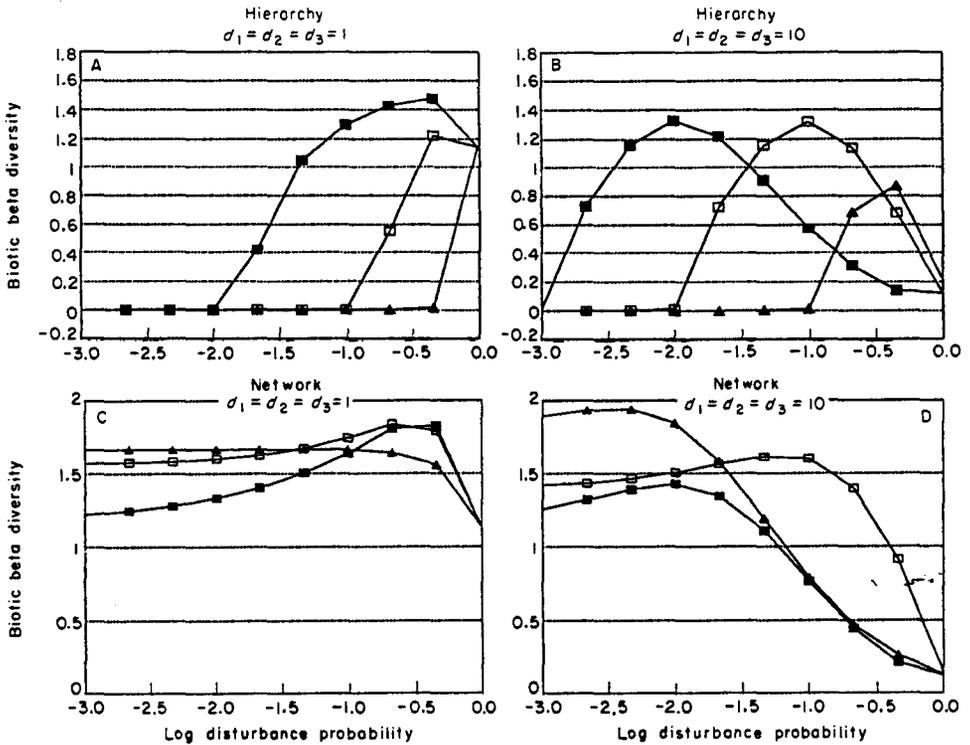
Figure 11. Biotic beta diversity $\beta_b$ in competitive hierarchies and networks as a function of disturbance probability $p_d$, for competitive exclusion probabilities $p_c = 0.01$ (■), $p_c = 0.10$ (□) and $p_c = 1.00$ (▲).

This result is at least somewhat habitat specific. Peterson (1979) reviewed the results of predator exclusion experiments in marine soft-sediment benthic communities. He found that these manipulations did not reduce the prey species diversity. In fact, they often increased prey diversity, although Peterson notes that this may be a cage effect. He proposes several possible explanations for this pattern, which is strikingly different from that seen in the intertidal studies. Perhaps the soft-sediment studies failed to allow sufficient time for competitive exclusion to occur. Perhaps interference competition was less important. Perhaps the interaction between adults and settling larvae dominated the community dynamics. Or, perhaps the developmental plasticity exhibited by many invertebrates means that exploitation competition will affect mainly growth, rather than mortality; if so, exclusion should be extremely slow.

Early theoretical attempts to model predator-mediated coexistence are reviewed by Caswell (1978). Those studies tended to focus on finding conditions under which a three-species system (two competitors and a predator) possesses a stable equilibrium while the corresponding two-species system does not. That approach is appropriate only if natural systems are usually at stable equilibria. In metapopulations this may not be true, because continual disturbance by predators of the approach to local equilibrium might greatly extend the persistence of competitors which could not maintain themselves in a local equilibrium.

## The model

We consider a model for three species: two competing prey and one predator. We label the species

$$S_1 = \text{winning competitor}$$
$$S_2 = \text{losing competitor}$$
$$S_3 = \text{predator}$$

and use the same numbering of states as in the competitive network model. We assume that competition between $S_1$ and $S_2$ follows the tolerance model. Predation leads to the elimination of the prey at a rate defined by an elimination probability $p_e$. We assume that predation, competition, and disturbance act independently within a patch. Thus a patch in state 8 (all three species present) goes to state 6 ($S_1$ and $S_3$) and probability $p_c(1-p_e)(1-p_d)$, to state 5 ($S_3$ alone) with probability $p_e(1-p_d)$, and to state 1 (an empty patch) with probability $p_d$; it remains in state 8 with probability $(1-p_c)(1-p_d)(1-p_e)$. This predator displays no preference for either prey species. Thus coexistence of prey cannot be the result of preferential predation on the winning competitor.

The losing competitor cannot invade a patch that contains the winning competitor, regardless of the presence or absence of the predator. The predator is permitted to colonize only patches containing at least one prey species. After eliminating the prey in a patch, the predator becomes extinct, even if one or both prey species should colonize the patch. These rules lead to the transition matrix shown in Table 4.

Coexistence of $S_1$ and $S_2$ in this model is genuinely predator-mediated. Suppose there is no disturbance to mediate coexistence, so that $p_d = 0$, and that the predator is absent so that $C_3 = 0$. Examination of the transition matrix of Table 4 shows that state 2 (the winning competitor alone) is an absorbing state; no matter what the initial state, the community will eventually collapse to a monoculture of the winning competitor.

Following the approach of previous sections, we conducted a series of numerical experiments, varying the parameters and examining the resulting patterns of community structure. Preliminary investigation of the model suggested that the predatory elimination rate $p_e$ sets the time scale in this model. By analogy with our studies of disturbance effects, we examine the response of the community to changes in $p_e$, varying the parameters as follows:

$$d_i \in \{1, 10\} \qquad i = 1, 2, 3$$
$$p_c \in \{0.01, 0.10, 1.00\}$$
$$p_e \in \{10 \text{ values, log-uniformly spaced between } 0.001 \text{ and } 1\}$$

## Species frequencies

Species frequencies are shown in Fig. 12. The frequency $f_1$ of the winning competitor declines with increasing $p_e$, and is independent of $p_c$. The frequency $f_2$ of the losing competitor demonstrates clear predator-mediated coexistence, since $f_2 = 0$ in the absence of predation and disturbance. $S_2$ is maintained when $p_e$ rises above a critical value ($\approx p_c/d_i$, although that is specific to this set of parameter values, where all the dispersal rates are equal), and is maximized at intermediate

TABLE 4. Transition matrix for the predator-mediated coexistence model

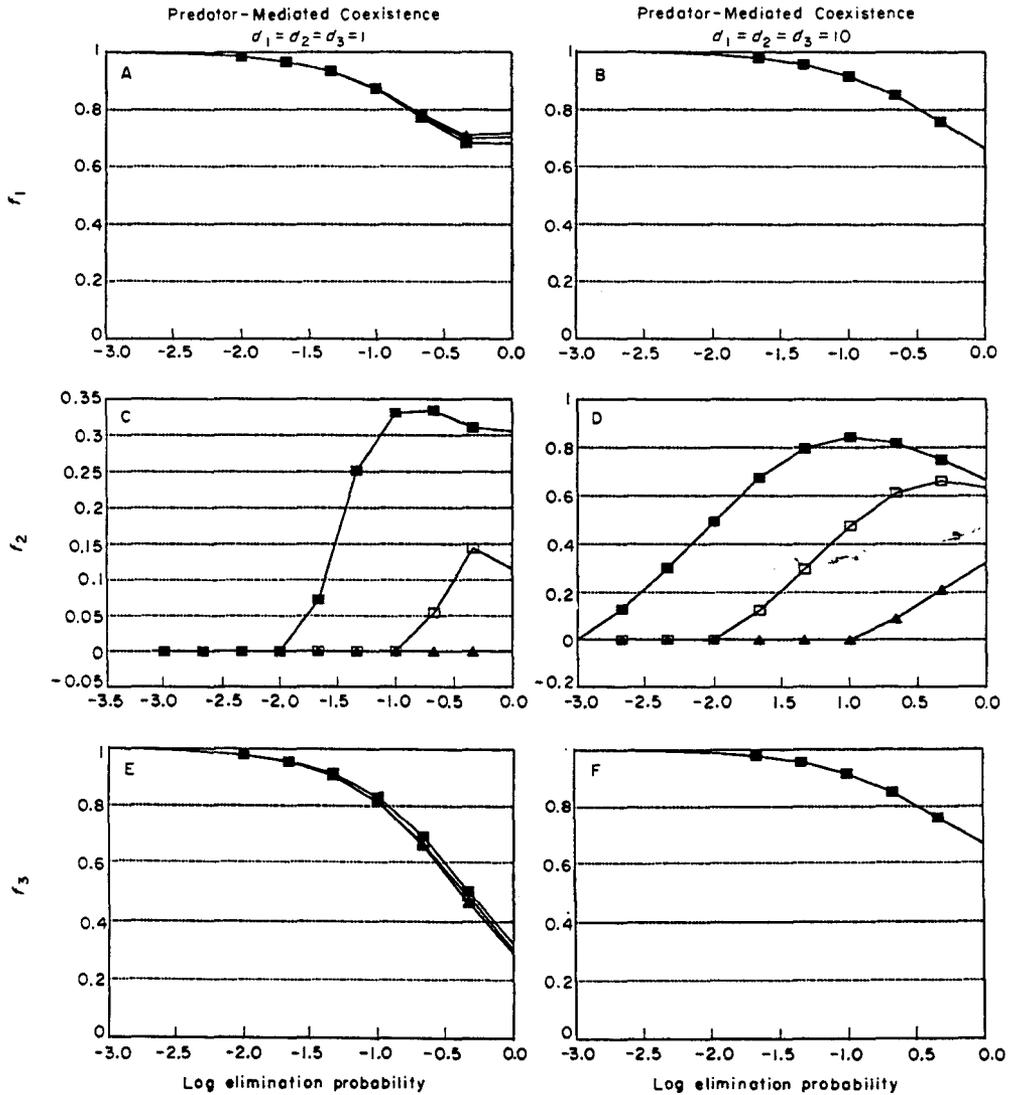| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---|---|---|---|---|---|---|---|---|
| 1 | $(1-C_1)(1-C_2)$ | $p_d$ | $p_d$ | $p_d$ | $p_d+(1-p_d)(1-C_1)(1-C_2)$ | $p_d$ | $p_d$ | $p_d$ |
| 2 | $C_1(1-C_2)$ | $(1-p_d)(1-C_3)$ | 0 | $(1-p_d)(1-C_3)p_c$ | $(1-p_d)C_1(1-C_2)$ | 0 | 0 | 0 |
| 3 | $(1-C_1)C_2$ | 0 | $(1-p_d)(1-C_1)(1-C_3)$ | 0 | $(1-p_d)(1-C_1)C_2$ | 0 | 0 | 0 |
| 4 | $C_1C_2$ | 0 | $(1-p_d)C_1(1-C_3)$ | $(1-p_d)(1-C_3)(1-p_c)$ | $(1-p_d)C_1C_2$ | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0 | 0 | $(1-p_d)p_c$ | $(1-p_d)p_c$ | $(1-p_d)p_c$ |
| 6 | 0 | $(1-p_d)C_3$ | 0 | $(1-p_d)C_3p_c$ | 0 | $(1-p_d)(1-p_c)$ | 0 | $(1-p_d)(1-p_c)p_c$ |
| 7 | 0 | 0 | $(1-p_d)(1-C_1)C_3$ | 0 | 0 | 0 | $(1-p_d)(1-C_1)(1-p_c)$ | 0 |
| 8 | 0 | 0 | $(1-p_d)C_1C_3$ | $(1-p_d)C_3(1-p_c)$ | 0 | 0 | $(1-p_d)C_1(1-p_c)$ | $(1-p_d)(1-p_c)(1-p_c)$ |

Figure 12. Species frequencies $f_i$ as a function of the predatory elimination probability $p_e$ and the competitive exclusion probability $p_c$, for low dispersal $(d_1 = d_2 = d_3 = 1)$ and high dispersal $(d_1 = d_2 = d_3 = 10)$ communities. ■, $p_c = 0.01$; □, $p_c = 0.1$; ▲, $p_c = 1$.

values of $p_c$. Thus, the maintenance of the losing competitor by predation is easiest when competition is slow and dispersal is rapid.

The frequency $f_3$ of the predator declines with increases in $p_e$, which is to be expected since $p_e$ determines the local extinction rate of the predator. It is independent of $p_c$.

### Alpha and beta diversity

Results for alpha and beta diversity are shown in Fig. 13. When competition is slow and dispersal rapid, the overall alpha diversity of this three-species
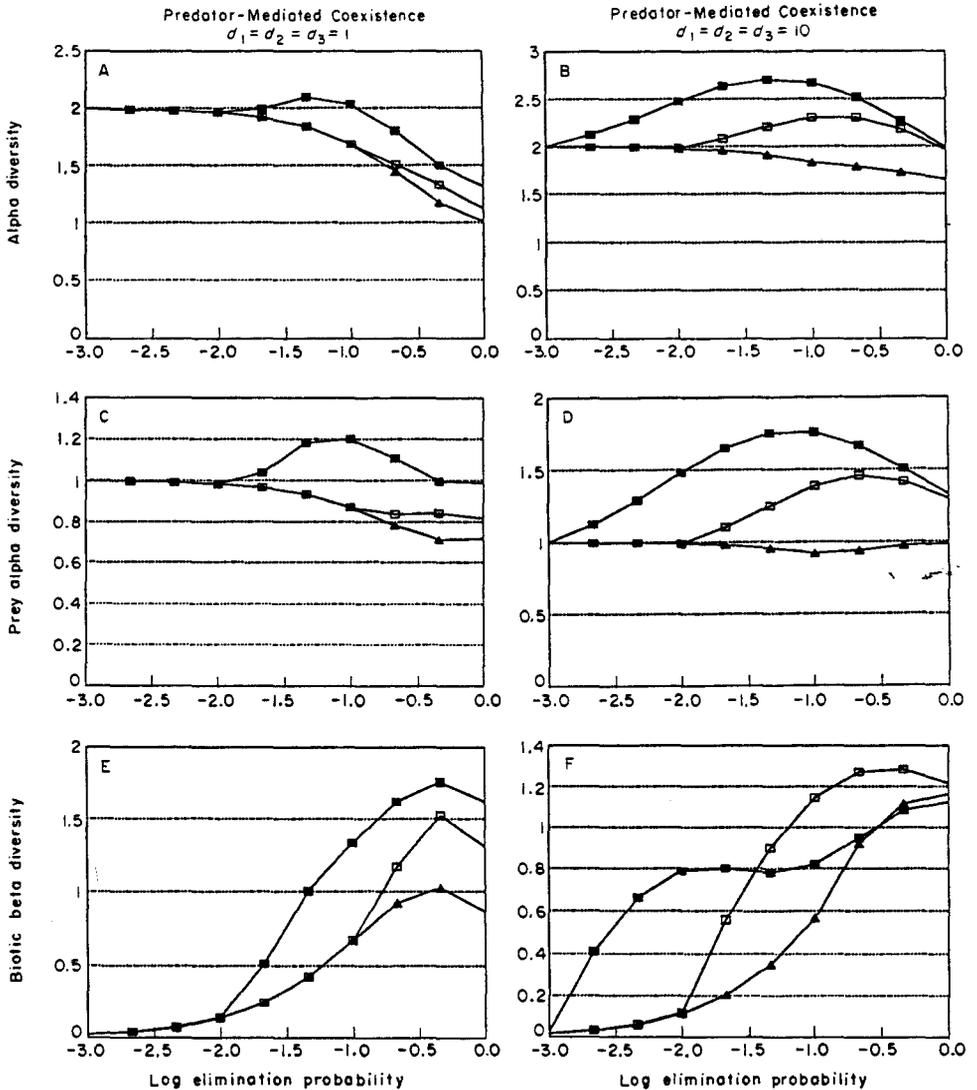
Figure 13. Diversity as a function of predatory elimination probability $p_c$ and competitive exclusion probability $p_c$, for different dispersal rates. A, B, Alpha diversity. C,D, Alpha diversity among the competing prey. E. F, Biotic beta diversity. ■, $p_c = 0.01$; □, $p_c = 0.1$; ▲ $p_c = 1$.

community is maximized at intermediate rates of predation. (Fig. 13A, B). The extent of the maximum is greater the slower the rate of competitive exclusion. In Fig. 13C, D we plot the alpha diversity among the prey species; this value can be directly compared with the results for two-species competition with disturbance. When competition is slow, prey diversity is maximized at intermediate predation rates. The maximum $\alpha$ is higher in high-dispersal than low-dispersal communities.

Predation is also capable of maintaining spatial heterogeneity. Figure 13E, F shows the biotic beta diversity $\beta_b$ for low and high dispersal communities. In the absence of predation, the community is spatially uniform, and $\beta_b$ increases with

$p_c$. The rate of elimination required to maintain significant heterogeneity increased with $p_c$.

These results show predation functioning in much the same way as physical disturbance. The rate of predatory elimination within a patch is a crucial parameter; the relation between this timescale and the timescale for competitive exclusion determines the diversity, spatial heterogeneity, and temporal variation in the community. It is of interest to consider the interaction of predation and disturbance; we will present results of such a comparison elsewhere.

## CONCLUSIONS

The results in this paper make it clear that the diversity of metapopulations reflects the interaction of at least three different scales: interactions within patches, dispersal between patches and disturbance. As our models enlarge from two to three species, and from competition alone to the interaction of competition and predation, the complexity of possible patterns increases. Any attempt to understand diversity without considering all three scales is likely to give, at best, only partial insight. Moreover, without quantitative models such as we propose here, it seems impossible to try to relate the processes at work and to demonstrate the truly surprising variety of effects produced by the interactions of these processes. The unaided intuition seems inadequate to the task.

As an example of the interaction of different scales, consider the debate over the maintenance of diversity in the deep sea (Grassle, 1989), where diversity is extremely high and disturbance rates apparently very low. It is tempting to argue that the low disturbance rate implies that the diversity must be maintained by equilibrium mechanisms rather than by disturbance. But rates of colonization (Grassle & Morse-Porteous, 1987), and of growth and metabolism (Turekian et al., 1975; Jannasch & Wirsen, 1977), are also lower. If the low growth rates translate into reduced rates of competitive exclusion, then it becomes impossible to interpret the lower rate of disturbance, since a low disturbance rate in a community with slow competition may have the same effects as a higher disturbance rate in a community with more rapid competition.

## ACKNOWLEDGEMENTS

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# Metapopulation Dynamics: Empirical and Theoretical Investigations

Edited by Michael Gilpin and
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ACADEMIC PRESS