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Disturbance, Coexistence, History, and Competition for Space

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A simple model to elucidate the effect of disturbance on a large number of competitors that compete for space and exhibit a competitive hierarchy is developed. Conditions are derived that determine presence of species, and diversity is calculated as a function of percentage cover. The model is compared to data from coral reefs collected by J. W. Porter (1974, *Science 186*, 543-545). Using parameter values in the model that allow a fit to Porter's data, the response of an individual species to changes in disturbance becomes quite complex, depending on the position (odd or even) of the species in the competitive hierarchy. For these same parameter values, the system is *interactive*: the existence of a particular species may effect the presence of another. Different parameter values would lead to a *noninteractive* system.

1. INTRODUCTION

Disturbance has often been suggested as an important structuring force in systems of competitors. In particular, it has been suggested that intermediate levels of disturbance should lead to the highest diversity in systems where space is limiting, such as the intertidal, or some terrestrial plant communities (e.g., Paine (1966, 1977), Harper (1969), Lubchenco (1978), see also references in Hastings (1978)). Although some results are in Yodzis (1978), this suggestion has not been carefully analyzed theoretically particularly in cases with many competitors. In this paper, I will develop and analyze a class of simple models based on the form of competition in space-limited systems. These models will be used to analyze the relationship between diversity and disturbance level. Data from corals studied by Porter (1972, 1974) will be used to examine the predictions of the models.

I am treating the question of how many species from a current collection will be present at a particular disturbance level. This is *not* a question of species packing, which must necessarily be a question on an evolutionary time scale, not the ecological time scale treated here.

Similar questions have been treated in a theoretical context, notably by Levin and Paine (1974), Horn (1975), and Yodzis (1978). However, these studies were

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interested in questions different from the ones considered here. Levin and Paine (1974) take a different approach by concentrating on the important role of patch structure. Horn's (1975) models consider what happens in situations without disturbance or in a linear model with disturbance. Yodzis (1978) studies the effect of considering explicit Lotka–Volterra dynamics in patches. This interesting approach allows detailed conclusions, but the added complexity makes it more difficult to consider the role of extinctions within some but not all patches, over an ecological time scale. Within this framework Yodzis suggested that intermediate levels of disturbance should lead to greater diversity.

The model in this paper isolates the phenomenon of disturbance leading to coexistence. By phrasing the model in terms of biologically meaningful and measurable parameters, additional predictions emerge.

2. Model Development

Since space is assumed limiting in the deterministic model treated here, the environment will be described as consisting of a large number of discrete identical patches, and the variables will be the frequency of patches in a particular state (cf. Levins and Culver, 1971; Levin and Paine, 1974; Levin, 1976; Hastings, 1977). I will assume that competition is sufficiently rapid (or, equivalently, patches are sufficiently small) so that, as an approximation, no patch will ever be occupied by more than a single species. Hence, in a model of n species, the variables in the system are x_i, $i = 1, n$; where x_i is the fraction of patches occupied by species i. Note that occupancy includes only those patches from which propagules are actually being sent out.

The form of competition assumed is that which arises from "overtopping" (Porter, 1974; Connell, 1973, 1978). This leads to a competitive hierachy (Horn, 1975), where if $j > i$, species i will always outcompete species j. An example of a system where this holds is corals in the eastern Pacific off Panama, as studied by by Porter (1972, 1974) and Maguire and Porter (1977).

All patches are assumed equally accessible from any given patch. Propagules of any species will approach the patches randomly, but only those landing on empty patches, or patches occupied by species lower on the competitive hierarchy, have a chance of succeeding. This is how competition is modeled. The probability of success of a propagule will be assumed not to be influenced by whether the "patch" it lands on is empty, or occupied by a species lower on the competitive hierarchy. (Note that residency in the model means the resident is currently of reproductive size or age.) Priority effects of this nature will be dealt with in a future paper.

The rate at which a species successfully colonizes appropriate patches will depend on its local growth rate, dispersal ability, and colonizing ability. For each species, these features will all be subsumed in a single function, $D_i(x_i)$, which will be the rate at which appropriate patches are settled. The functions $D_i(x_i)$ will satisfy the following two conditions:

$$D_i(0) = 0, \tag{1}$$

which says that an absent species sends out no propagules, and

$$\frac{dD_i}{dx_i} > 0, \tag{2}$$

which says that the rate at which appropriate patches are colonized increases as the area occupied by a species increases. A third condition will be assumed that says that the per capita colonization rate decreases (or does not increase) as the area occupied by a species increases. This takes into account a saturation effect, or any searching ability larvae may have. Thus, assume

$$\frac{d^2D_i}{dx_i^2} \leqslant 0. \tag{3}$$

Disturbance in this paper will be modeled as a force that occurs randomly through time and affects all species equally. Disturbance will be treated as a deterministic feature to model forces such as wave action, or predation by a predator that has an alternate food source so its feeding *rate* remains constant. Patches currently occupied are assumed to return to the empty state at a rate $e(t)$.

Using the assumptions above, one obtains n equations, each describing the rate of change of patch occupancy for one species. Each equation has three terms, one for the colonization of patches, one for loss due to competition (missing from the equation for the top competitor), and one for loss due to disturbance. Thus the n equations take the form:

$$\frac{dx_i}{dt} = D_i(x_i)\left(1 - \sum_{j=1}^{i} x_j\right) - \sum_{j=1}^{i-1} D_j(x_j)\, x_i - e(t)\, x_i\,, \qquad i = 1, n. \tag{4}$$

The analysis will begin with this model. More complex forms will be treated elsewhere, simplifications will be considered below. Note that in analyzing the model, attention will be restricted to the region

$$x_i \geqslant 0, \quad i = 1, n; \qquad \sum_{i=1}^{n} x_i \leqslant 1 \tag{5}$$

since the variables are frequencies.

One of the important factors in determining the behavior of the model is the functions $D_i(x_i)$. More detailed information will be the outcome of more experimentation.

3. Model Solution

Before "solving" the model, I will assume that over the time scale of interest, the disturbance rate, $e(t)$, can be viewed as a constant, e.

The first step in the analysis is a study of the dynamics of (4), which is in the Appendix. The primary result is that the system always has a *unique* equilibrium. point which is approached by any system in which all species are initially present.

The most interesting biological question then becomes: at this equilibrium, which depends on the disturbance level, what species are present, and what are their population levels? To answer this question, it is necessary to be more specific about the functional forms in (1). Hence, I will now make a simplifying assumption. Choose a specific form for the colonization function $D_i(x)$, namely,

$$D_i(x) = d_i x. \tag{6}$$

This form is in a certain sense a base form. Deviations from it would represent searching behavior or other behavioral aspects. Note that when this form is assumed, the model becomes one of Lotka–Volterra form, although the meaning assigned to the coefficients differs. In fact the parameter d_i could be determined by measuring the colonization rate and the area currently occupied by species i.

Now, the result that the model has a unique, feasible, globally stable (from positive initial conditions with all species present) equilibrium point will be used to examine the outcome of the model. This result says that there will be a series of algebraic conditions that determine the asymptotic behavior.

The best competitor, species 1, will be present if and only if

$$d_1 > e. \tag{7}$$

If species 1 is not present criterion (7) should then be applied to species 2, and successively until it is satisfied. If species 1 is present, species 2 will be present if and only if

$$d_2 > (d_1)^2/e. \tag{8}$$

The corresponding condition for species 3, if 1 and 2 are present, is

$$d_3 > e\frac{d_2^2}{d_1}. \tag{9}$$

Similar conditions apply for species lower in the competitive hierarchy. Since, in the model, ***to survive, a poorer competitor must be a better colonizer,***

$$i > j \qquad \text{implies} \qquad d_1 > d_j \tag{10}$$

will always be assumed. (Note that an alternative advantage for poorer competitors would be resistance to disturbance (cf. Hastings, 1978)).

A definition is useful for interpreting conditions (7)–(9) and those that follow. Note that the system would behave differently if the top competitor had been eliminated for some reason. However, in the range of e where 1 is present, it is reasonable to ask whether the presence of species 2 affects the presence of species 3. If whenever the disturbance level, e, allows species 2 to enter, species 3 can also enter, then the presence of species 2 will not affect species 3. Formally, this means that (7) and (8) imply (9). Such a system will be called *noninteractive.* Note that *noninteractive* does not refer to no interaction or competition, but that in the model one species is not eliminated by another. Extension of this definition to systems of more than three species, or more general models, is natural. A system that fails to satisfy these conditions will be called *interactive.*

If the disturbance rate varies with time, but is at a fixed level long enough for species not present at equilibrium to be eliminated, history will play a much more important role in *interactive systems* (see Fig. 1). Assume there are two levels of e, z_a at which species 1 and 3 are present, and e_b at which 1 and 2 are present, but not 3. If the system is first at e_a, then at e_b, then back at e_a, species 3 will be present since it will be present at e_b if 2 had already been eliminated. On the other hand, if the system is first at e_b, then at e_a, only species 1 will be present since 3 would have been eliminated. Such interactions involving history are possible in *noninteractive systems* only if the dominant competitor is involved, in contrast to the situation just described for an *interactive* system.

There is a corresponding important difference between *interactive* and *noninterative systems* in number of species as a function of disturbance rate. In *noninteractive systems* the number of species present first increases monotonically

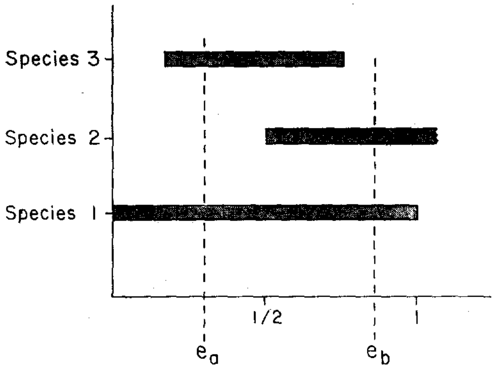

FIG. 1. The role of history in an *interactive*, three-species, competitive system with colonization rates, $d_i = i$, $i = 1. 3$. The graph indicates which species would be present if all were initially present. At disturbance rate e_a, species 2 is eliminated; at rate e_b, species 3 is eliminated if and only if 2 is present. Hence, the order in which rates e_a and e_b are experienced may influence present species competition.

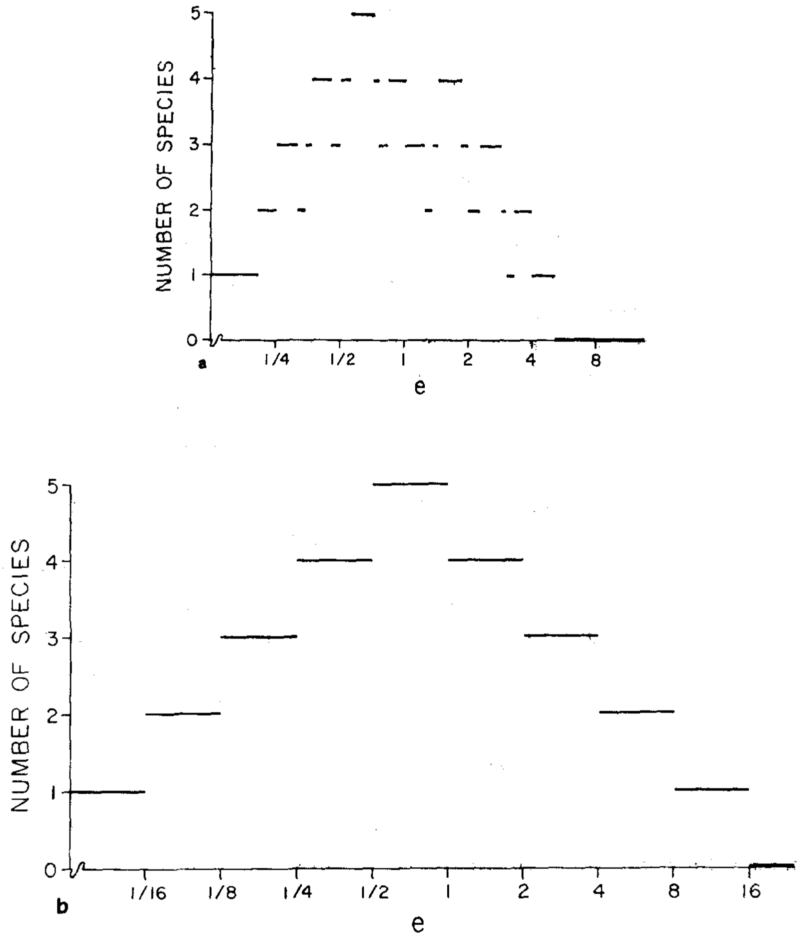

FIG. 2. Number of species present in two, five-species competitive systems as a function of the disturbance rate e. (a) An *interactive* system with colonization rates $d_i = i$, $i = 1,5$. (b) A *noninteractive* system with $d_i = 2^{(i-1)}$, $i = 1,5$.

as a function of the disturbance rate e, until all species are present, and then decreases monotonically (Fig. 2). Thus there is a single intermediate level of disturbance yielding the maximum number of species. In contrast, in *interactive systems*, although the greatest number is at an intermediate level of disturbance, the number of species is not a monotonic function of e, and there may be several peaks. These differences appear in a different fashion when the diversity measure H' is used, as discussed below.

For the simple model (1), *if the ratio* d_i/d_{i-1} *is a nondecreasing function of* i, the system is noninteractive. The borderline case where this ratio is constant is included since then the system behaves like a *noninteractive* one. Hence, if the dispersal parameters d_i are evenly spaced on an arithmetic scale, the system is *interactive*, whereas if the d_i are evenly spaced on a logarithmic scale the system is *noninteractive* (Fig. 2).

4. An Example from Coral Reefs

I will now compare the outcome of the model to data collected from coral reefs (Porter, 1972, 1974) on the Pacific side of the Isthmus of Panama. Although there has been controversy concerning some of Porter's (1972, 1974) conclusions (e.g., Glynn, 1976), the questions center on the importance of different biotic factors, particularly the role of *Acanthaster planci*, and in no way affect my use of Porter's data below. Note that although there are two major forms of competition in these corals, overtopping and chemical "warfare," in this area there is a competitive hierarchy (Porter, 1972, 1974; Lang, 1973). Also, although the data collected by Porter are from many sites, the amount of dispersal between the sites is relatively small relative to settlement from local populations (Porter, personal communication), so each site can be treated as a separate outcome of the model. One factor liliting dispersal is the posited relatively short time thata coral larvae may spend in the ocean before settling if laboratory estimates, of a maximum of a few days with most settling occurring faster, apply (Connell, 1973). Porter (1974, personal communication) reported values of H' versus percentage cover, where

$$H' = -\sum p_i \log_2 p_i ,$$

where p_i is the fraction of the total biomass that is species i. At the sites he examined, the competitive dominant was the most common species, and there

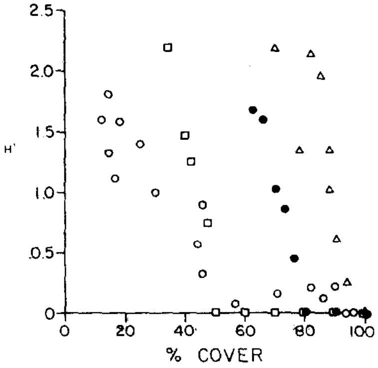

FIG. 3. Plot of diversity measure H' versus percentage cover. Data from coral reefs in Pacific off Panama, ○ (Porter, 1974). The model in the text is used three times: $d_i = 2^{i-1}$, $i = 1, 5$, △; $d_i = i$, $i = 1, 5$, ●; $d_i = 1, 1.25, 1.5, 1.75, 2$, $i = 1, 5$, □.

were five or six important species in the system. Therefore, to compare the model outcome with Porter's data, three cases are presented in Fig. 3, where H' is plotted against percentage cover. In all cases five-species models were treated. In case 1, the nonintereactive model with colonization rates proportional to $d_i = 2^{i-1}$ is considered. Disturbance rates of 0 to 0.7 are used (in intervals of 0.1), so only cases where the competitive dominant was most important were treated. The same disturbance rates are used for the interactive model with $d_i = i$. For a third case, also interactive, with $D_i = 1, 1.25, 1.5, 1.75, 2$, the disturbance rates of 0.8 and 0.9 are also used. This third case gives a very close fit to the data, duplicating the "*L*" shape. (The "*L*" shape also shows up in the second case.)

Even though it may not be surprising that with many parameters a fit to the data can be achieved, it is impressive that, with the interactive model, the "*L*" shape always appears. It is that part of the fit to the data that is striking. Note that deviations of the model from the data at very low percentage cover may be due to the importance of *Acanthaster* at these sites (a factor not included). Also, at very high percentage cover, although the model predicts $H' = 0$, the fact that the data shows H' only near zero is kot surprising, since there may not have been time for all subdominant species to be eliminated.

5. Conclusions

Thus the simple model is able to mimic the behavior of the natural system quite well. Also, since it is the interactive model that "fits" the data, the model makes an interesting prediction: although the valve of H' may respond in a fairly predictable fashion as a function of disturbance rate, there is no simple response of individual species abundance or presence to changes in the disturbance rate. This response is not dependent on any complicated interactions among species, but merely depends on the form of competition and on the colonization rates.

However, it should be noted that there is a way to characterize the response of abundance of a particular species to changes in disturbance. If, among those species *present* at a given disturbance level, e, the competitive dooinant is called species 1, the next best competitor species 2, etc., then increasing e decreases the abundance of odd-numbered species and increases the abundance of even-numbered species. Note, however, species that are very poor competitors may change from "odd" to "even" (or vice versa) quite often as e is varied.

That a simple model like the one employed here can provide such a good fit to coral reef data may be surprising, particularly since Lotka–Volterra forms are used. Yet it is important to note that only a very special, restricted Lotka–Volterra model is considered. Changes in the form of recruitment that will change the model away from the Lotka–Volterra type, as well as stochastic versions, will be considered in future papers.

Another surprising feature of the present model is how well it works given that the details of immigration are not included, as in the simulation model of Maguire and Porter (1977). A general treatment of why this may be true will appear elsewhere.

What is important about the model considered here is its portrayal of how the "intermediate level of disturbance yielding highest diversity" hypothesis works. It has been noted many times that the hypothesis holds true only for a very restricted set of parameters in Lotka–Volterra models. Yet, if one restricts attention to a class of Lotka–Volterra models that can be derived, with biologically meaningful parameters, from considering space-limited systems, it is easy to demonstrate how the "intermediate level of disturbance" hypothesis works.

APPENDIX

Here the global stability result for the model (4), with $e(t) \equiv e$, will be sketched. The proof relies on the observation that the equation for x_i' depends only on x_j with j running from 1 to i, so each equation can be integrating successively. The first step will be the following lemma.

LEMMA. *The system* (4) *has a unique equilibrium* $(\hat{x}_1, \hat{x}_2, \hat{x}_3, \ldots, \hat{x}_n)$ *in the region* (5) *with the following properties. Either* $\hat{x}_i > 0$ *or* $\hat{x}_i = 0$ *and there is no equilibrium with* $x_j = \hat{x}_j$, $j = 1$ *to* $i - 1$, *and with* $\hat{x}_i > 0$. *In addition, if* $x_i \neq \hat{x}_i$

$$(x_i - \hat{x}_i) f_i(\hat{x}_1, \hat{x}_2, \ldots, \hat{x}_{i-1}, x_i) < 0. \tag{A1}$$

Proof. Since $f_i(\hat{x}_1, x_2, \ldots, \hat{x}_{i-1}, 1 - \sum_{j=0}^{i-1} x_j) < 0$, the lemma will follow if the function

$$g_i \equiv f_i / x_i \tag{A2}$$

is strictly decreasing for $x_i > 0$. First,

$$\frac{\partial g_i}{\partial x_i} = \left[\frac{\left(\dfrac{dD_i}{dx_i} \right) x_i - D_i}{(x_i)^2} \right] \left(1 - \sum_{j=1}^{i} x_i \right) - D_i / x_i . \tag{A3}$$

Hence if

$$h_i \equiv \left(\frac{dD_i}{dx_i} \right) x_i - D_i \leqslant 0, \tag{A4}$$

the lemma will be true, since

$$\mathrm{o} - \sum_{j=1}^{i} x_j \geqslant 0. \tag{A5}$$

But $h_i(0) = 0$ and

$$\frac{dh_i}{dx_i} = \frac{d^2 D_i}{dx_i^{\,2}} x_i \leqslant 0, \tag{A6}$$

where the last inequality follows from (3). Equation (A6) now implies (A4), so the lemma follows.

The global stability result is:

THEOREM. *The system* (4) *has a unique equilibrium that is approached by all trajectories with initial conditions in* (5) *and all species initially positive.*

Proof. First note that the interior of the region (5) is invariant in finite time. Then, for any ϵ_1, by picking t_1 large enough, $| x_1(t) - \hat{x}_1 | < \epsilon_1$ for all $t > t_1$. Then, by making ϵ_1 small enough, for any δ_2, once $t > t_1$, the equation

$$f_2(x_1(t), x_2) = 0 \tag{A7}$$

will have a unique (t-dependent) solution, $\tilde{x}_2$, with $| \hat{x}_2 - \tilde{x}_2 | < \delta_2$. Now pick an ϵ_2. By taking $t_2 > t_1$ large enough, one can make $| x_2(t) - \tilde{x}_2 |$ arbitrarily small, so

$$| x_2(t) - \hat{x}_2 | < | x_2(t) - \tilde{x}_2 | + | \tilde{x}_2 - \hat{x}_2 | < \epsilon_2 . \tag{A8}$$

Clearly, this approach can be extended to more than two species.

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