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COMPETITION DURING COLONIZATION VS COMPETITION AFTER COLONIZATION IN DISTURBED ENVIRONMENTS: A METAPOPULATION APPROACH

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How two species interact during and after colonization influences which of them will be present in each stage of succession. In the tolerance model of ecological succession in a patchy environment, empty patches can be colonized by any species, but the ability to tolerate reduced resource levels determines which species will exclude the other. Here, we analyze a meta-population model of the possible roles of competition in colonization and succession, using non-linear Markov chains as a mathematical framework. Different kinds of competition affect the final equilibrium abundances of the species involved in qualitatively different ways. An explicit criterion is given to determine which interactions have stronger effects on the final equilibrium levels of the weaker species. Precise conditions are stated for the co-existence of both species. Both species are more likely to co-exist in the presence of an intermediate disturbance frequency. © 1996 Society for Mathematical Biology

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1. Introduction. In the study of mechanisms of ecological succession, Connell and Slatyer (1977) recognized three major types: inhibition, facilitation and tolerance. These types differ in the effect of inter-specific interactions during and after colonization. In the facilitation model, the later species can colonize a patch only after previous occupation by early species provides the environmental conditions suitable for them. In the inhibition model, the later species do not require the presence of early species to allow them to colonize an empty patch, but once a species (early or late) occupies a patch, it prevents others from colonizing. Finally, in the tolerance model, empty patches can be colonized by early or late species, and the ability to tolerate reduced resource levels determines which of them will exclude the other. Caswell and Cohen (1991a,b) developed non-linear Markov chain models for these three mechanisms, and examined the effects of disturbance on co-existence and diversity. Here, we focus on inter-specific interactions during and after colonization in a generalization of the tolerance model of Caswell and Cohen (1991b) and Barradas and Cohen (1994).

The way two species interact during and after colonization will influence which of them will be present in each successional stage. While modeling this interaction, differences in local and regional processes have to be considered (Ricklefs, 1987; Connell, 1978; Dayton and Hessler, 1972; Huston, 1979; Slatkin, 1974). Meta-population models can be used to study processes taking place at various spatial scales (Caswell and Cohen, 1991a,b; Caswell and Etter, 1993; Etter and Caswell, 1993; Barradas and Cohen, 1994) and the relative role played by competition at different stages. For instance, species in a patchy environment affected by disturbances can compete against each other to colonize empty patches or to prevail after colonization. During colonization, one species may be able to interfere with, or even impede, colonization by a second one whenever they meet or, alternatively, only if the first one colonizes before the second one arrives. The efficiency of the two modes of interference need not be the same. Interference from the first species during colonization by the second one could be more efficient if the first one is already settled before the second one arrives.

The present work shows that different kinds of competition have qualitatively different effects on the final equilibrium level of the species involved. We give an explicit criterion to determine which interactions have stronger effects on the final equilibrium levels of the weaker species, and we give precise conditions for the co-existence of both species. We show that both species are more likely to co-exist under an intermediate disturbance frequency.

2. The Model. Consider a patchy landscape consisting of an infinite number of identical patches, which can be occupied by individuals of two species E_1 and E_2 , with E_1 the competitive dominant (the "late successional" species). Each patch can be in one of the states numbered 0, 1, 2 or 3, according to the species that are present in it. The states of the patches are defined as follows: 0 if the patch is empty, 1 if only E_1 is present in the patch, 2 if only E_2 is present in the patch, and 3 if both species are present in it (see the table below).

Species 1	Species 2	State
Absent	Absent	0
Present	Absent	1
Absent	Present	2
Present	Present	3

The state of the landscape is described by a vector y in R^4 , whose entries y_i are the proportion of patches in state i . Changes in these proportions result from changes in the states of the patches, which result from colonization, disturbances and within-patch interactions, according to the following rules:

- (a) Colonization occurs at random, without neighborhood effects.
- (b) The mean number of propagules of species E_i arriving at a patch is directly proportional to the fraction of patches containing E_i . Therefore, the probability of colonization by at least one propagule of species E_i is given, according to the Poisson distribution, by

$$C_i = 1 - \exp(-d_i f_i), \quad (2.1)$$

where $d_i \geq 0$ is the dispersal coefficient of species i , and $f_i(t)$ is its frequency, i.e. $f_1(t) = y_1(t) + y_3(t)$, and $f_2(t) = y_2(t) + y_3(t)$.

- (c) An established population of species E_1 causes colonization by species E_2 to fail with a probability per unit of time of p_s , $0 \leq p_s \leq 1$. If both species reach the patch simultaneously, species E_1 causes colonization by species E_2 to fail with probability per unit of time of p_r , $0 \leq p_r \leq 1$.
- (d) Disturbances occur with a probability p_d , $0 \leq p_d < 1$, which is constant and independent in all patches.
- (e) Any occupied patch affected by a disturbance becomes empty, i.e. it returns to the state 0.
- (f) If both disturbance and colonization occur in the interval $(t, t + 1]$, the disturbance causes colonization to fail.

- (g) In competition between established populations within a patch, species E_1 eliminates species E_2 with a probability per unit of time of p_c , $0 \leq p_c \leq 1$.

The dynamics of the system is then described by the non-linear Markov chain,

$$\mathbf{y}(t+1) = \mathbf{A}_y \mathbf{y}(t). \quad (2.2)$$

The transition matrix \mathbf{A}_y can be written as

$$\mathbf{A}_y = \begin{pmatrix} 1 - \overline{p_d}(C_1 + C_2 - C_1 C_2) & p_d & p_d & p_d \\ \overline{p_d} C_1 (1 - \overline{p_r} C_2) & \overline{p_d} (1 - \overline{p_s} C_2) & 0 & \overline{p_d} p_c \\ \overline{p_d} (1 - C_1) C_2 & 0 & \overline{p_d} (1 - C_1) & 0 \\ \overline{p_d} C_1 \overline{p_r} C_2 & \overline{p_d} \overline{p_s} C_2 & \overline{p_d} C_1 & \overline{p_d} p_c \end{pmatrix}, \quad (2.3)$$

where the C_i are given by (2.1) and we have used the convention that, for any parameter x , $\bar{x} = 1 - x$. Each entry of this matrix describes the probability that a patch changes from one state to another. For example, $\overline{p_d} p_c$ (second row, fourth column) describes the probability that a patch changes from being occupied by both species to being occupied by E_1 only.

System (2.2) includes a great variety of cases. The special case $p_r = p_s = 0$ was studied by Barradas and Cohen (1994), and corresponds to competition only after colonization. Colonization is not affected, but species E_1 eliminates species E_2 with a probability of p_c per unit of time, whenever they meet after colonization.

Individual patches in this model never reach an equilibrium (unless $p_d = 0$). Our interest focuses on the possibilities of landscape-scale equilibrium and landscape-scale co-existence, even when local co-existence is impossible. The idea that disturbance can promote co-existence, and hence species diversity, dates back to Hutchinson's (1951) concept of the "fugitive species." We want to see how the conditions for co-existence are affected by the probabilities (p_r , p_s and p_c) that describe the competitive interactions. Since these probabilities reflect the biology of the species (resource acquisition, behavioral mechanisms, etc.), we can expect that they will evolve (or co-evolve), and that the adaptive value of changes in each parameter will reflect their impact on the conditions for co-existence.

When only a single species is present, it can be shown that the occupancy level of that species approaches an equilibrium level S_i , which depends only on the rates of dispersal and disturbance. That equilibrium is the maximum of 0 and the only positive solution of

$$(1 - p_d)(1 - e^{-d_i S_i})(1 - S_i) - p_d S_i = 0. \tag{2.4}$$

When two species are present, the outcome depends on disturbance, dispersal and competition. Our main result describes all possible outcomes for fixed $p_d \in [0, 1)$ and fixed $p_c, p_r, p_s \in [0, 1]$, as a function of the dispersal rates d_1 and d_2 , as shown in Fig. 1.

For notational convenience, define the vector $\mathbf{p} = (p_d, p_c, p_r, p_s)$. The (d_1, d_2) plane is divided into four sections by two curves,

$$d_1 = \Phi_1(\mathbf{p}, d_2),$$

$$d_2 = \Phi_2(\mathbf{p}, d_1),$$

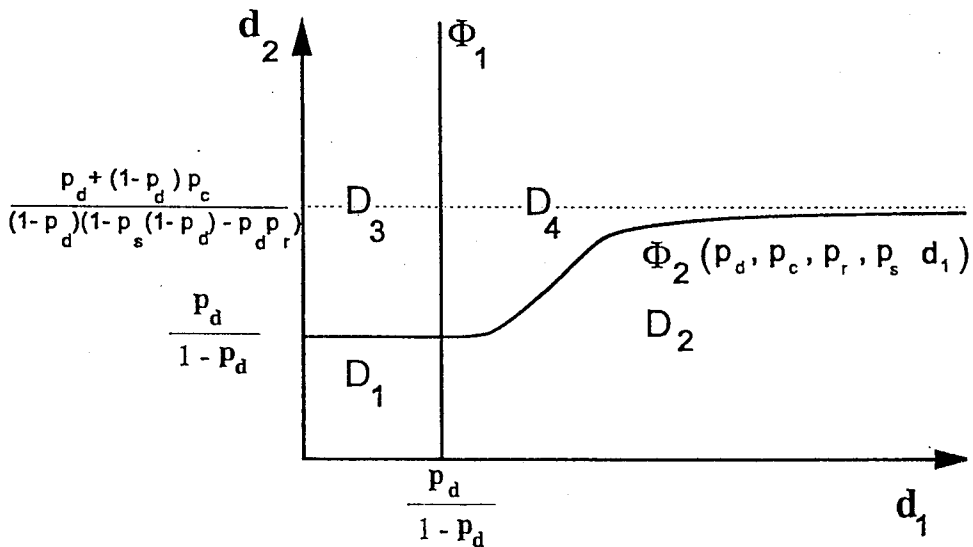


Figure 1. Regions in plane (d_1, d_2) of dispersal coefficients d_1, d_2 for species 1 and 2, respectively, where: both species go extinct (D_1), species 2 goes extinct but not species 1 (D_2), species 1 goes extinct but not species 2 (D_3) and both species co-exist (D_4). This informal description omits some unstable solutions; see Theorem 1 for exact details.

where

$$\Phi_1(\mathbf{p}, d_2) = \frac{p_d}{1 - p_d},$$

$$\Phi_2(\mathbf{p}, d_1) = \frac{p_d}{1 - p_d} \cdot \frac{p_d + (1 - p_d)p_c}{p_d \left(1 - p_s S_1 - \frac{p_d p_r S_1}{1 - p_d} \right) + (1 - S_1)(1 - S_1 - p_d)p_c}.$$
(2.5)

In this expression, S_1 is the single-species equilibrium for species E_1 , calculated from (2.4). These curves define the four regions shown in Fig. 1:

$$D_1 = \{(d_1, d_2) | 0 \leq d_1 \leq \Phi_1, 0 \leq d_2 \leq \Phi_2\},$$

$$D_2 = \{(d_1, d_2) | d_1 > \Phi_1, 0 \leq d_2 \leq \Phi_2\},$$

$$D_3 = \{(d_1, d_2) | 0 \leq d_1 \leq \Phi_1, d_2 > \Phi_2\},$$

$$D_4 = \{(d_1, d_2) | d_1 > \Phi_1, d_2 > \Phi_2\}.$$

These four regions determine the asymptotic behavior of the systems (2.2) and (2.3).

Let $\mathbf{y}(t) = (y_0(t), y_1(t), y_2(t), y_3(t))$ be the solution of (2.2) with initial condition $\mathbf{y}_0 = (y_0(0), y_1(0), y_2(0), y_3(0))$. Assume always that $p_d \in [0, 1)$ and $p_c, p_r, p_s \in [0, 1]$. If $(d_1, d_2) \in D_1$, then asymptotically neither species can persist. For every initial condition, all patches become empty. If $(d_1, d_2) \in D_2$, and if species E_1 is present in any positive fraction of patches initially, then asymptotically the only globally stable solution is $(1 - S_1, S_1, 0, 0)$, in which species E_1 has excluded species E_2 by competition. In addition, there are two unstable stationary solutions: one where all patches are empty and one with only species E_2 . If $d_2 < p_d/(1 - p_d)$, then species E_2 must be absent at equilibrium. If $(d_1, d_2) \in D_3$, then species E_2 can persist if it is initially present, but species E_1 cannot. The stationary solution with all patches empty is unstable against introduction of species E_2 . Finally, if $(d_1, d_2) \in D_4$, then (2.2) has one globally stable stationary solution, in which both species E_1 and E_2 persist and co-exist, plus three unstable stationary solutions: all patches empty, species E_1 only and species E_2 only. These properties are stated precisely in Theorem 1 of Appendix A. The rigorous proof given in Appendix A is one of the main achievements of the paper.

3. Numerical Calculation of Persistence Thresholds. In this section, we calculate numerically the regions of co-existence to see the effects of

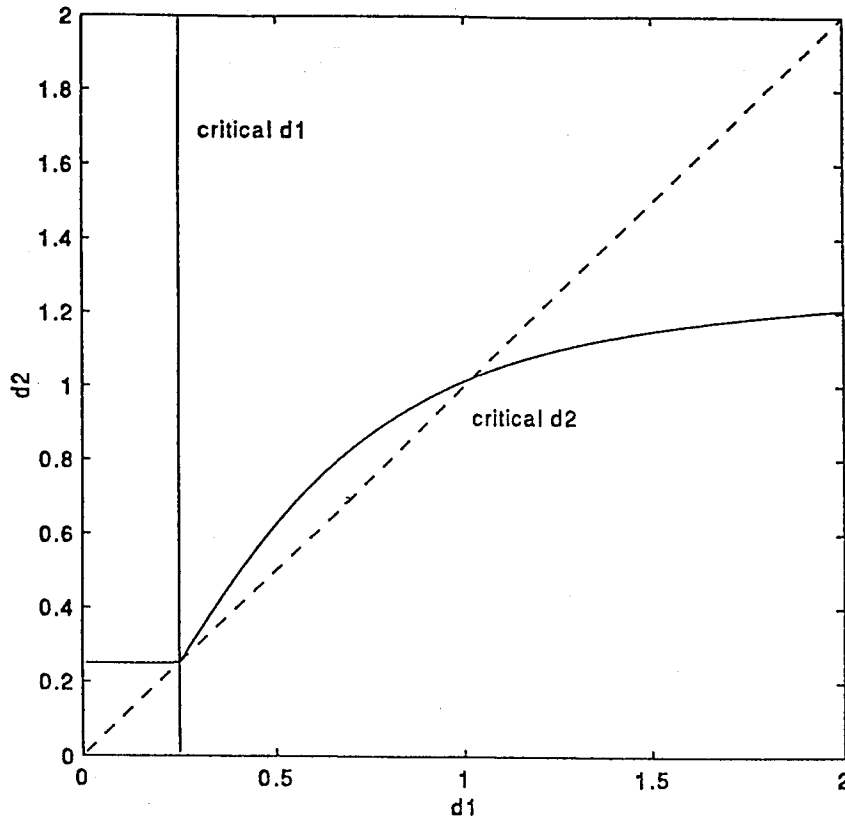


Figure 2. Numerical computation of critical values of dispersal coefficients d_1 and d_2 . Parameter values in this illustration are arbitrary: $p_d = 0.2$, $p_c = 0.9$, $p_r = 0.1$, $p_s = 0.1$. Diagonal line $d_1 = d_2$ is included to emphasize that persistence of fugitive species 2 does not always require an advantage in dispersal to compensate for its competitive inferiority.

changes in parameter values. The details of the numerical calculations are described in Appendix B. In the following section, we investigate these questions analytically and discuss the possible evolutionary implications of the results.

We calculate the persistence thresholds $\Phi_1(\mathbf{p}, d_2)$ and $\Phi_2(\mathbf{p}, d_1)$ by determining numerically the local stability of the boundary equilibria. Figure 2 shows typical numerical results for arbitrary parameter values.

The critical dispersal rate $\Phi_2(\mathbf{p}, d_1)$ for the inferior competitor depends in a complex way on p_d , p_c , p_r and p_s (Fig. 3). The top row of Fig. 3 models a low-disturbance environment ($p_d = 0.1$), the center row an intermediate-disturbance environment ($p_d = 0.5$) and the bottom row a high-disturbance environment ($p_d = 0.8$). In each-of the three columns, one of the competi-

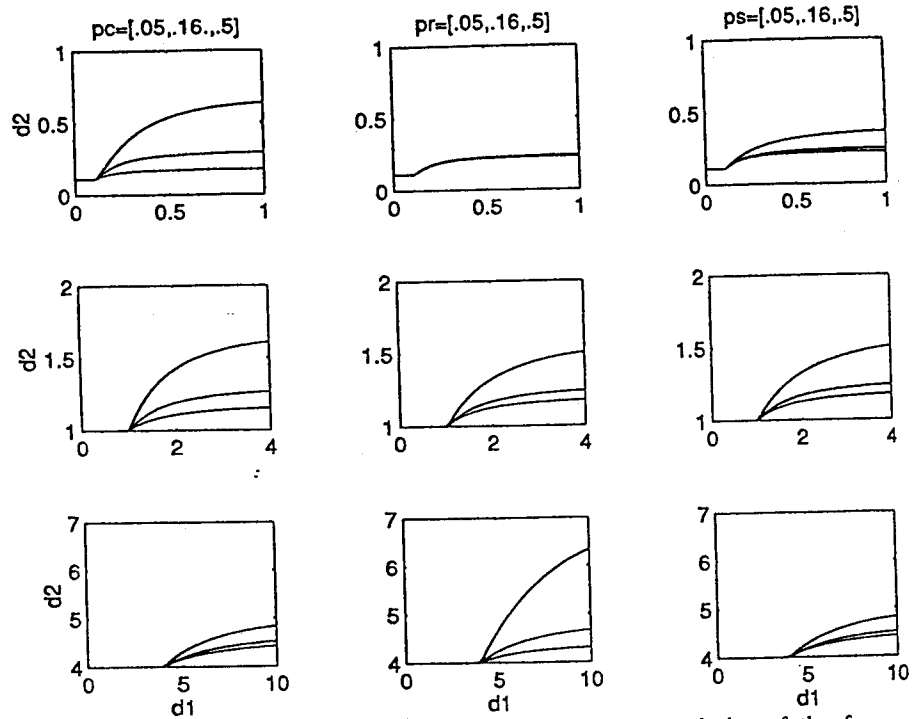


Figure 3. Effects of varying p_c , p_r and p_s on location and size of the four regions in (d_1, d_2) plane. Within each row of pictures, the value of p_d is fixed ($p_d = 0.1$ in row 1, 0.5 in row 2, 0.8 in row 3). The three curves in each plot correspond to values 0.05, 0.16 and 0.5 of parameter at top of each column. Rates other than rates being varied take the value 0.1. Graphs show that at low disturbance rates, Φ_2 is most sensitive to changes in p_c because most competition takes place after colonization. Variations of p_r , which operates only in simultaneous colonizations, have almost no effect because simultaneous colonizations are rare when disturbances are rare.

tion parameters is varied over an order of magnitude (from 0.05 to 0.5), while the others are fixed at a value of 0.1.

At low disturbance rates, $\Phi_2(p, d_1)$ is most sensitive to changes in p_c , less so to changes in p_s and almost independent of p_r . This is because, at low disturbance frequencies, simultaneous colonization, which is affected by p_r , is a rare event.

At intermediate disturbance frequencies, the critical dispersal rate is equally sensitive to all three competition parameters. At high disturbance rates, $\Phi_2(p, d_1)$ is most sensitive to p_r (which affects simultaneous colonization), and less so to p_c and p_s .

4. Comparison of Different Modes of Competition. In a meta-population like that described by (2.3), interdemetic selection would operate to reduce

local extinction rates and increase species occupancy (e.g. Gilpin, 1975). In the present model, species E_1 is unaffected by species E_2 , so the competition parameters (p_c , p_r and p_s) are selectively neutral for E_1 . The persistence of species E_2 , however, depends on these parameters, so it is of interest to see how the persistence threshold Φ_2 varies as a function of p_c , p_r and p_s .

First, we consider each form of competition acting alone. Fix p_d and d_1 . A substitution in (2.5) of the special sets of values $\{p, 0, 0\}$, $\{0, p, 0\}$ and $\{0, 0, p\}$ for p_c , p_r and p_s reveals which interaction has the greatest effect if the other two are not acting. The quantities to be compared are:

$$\Phi_2(p_d, p, 0, 0, d_1) = \frac{p_d}{1-p_d} \cdot \frac{p_d + (1-p_d)p}{p_d + (1-S_1)(1-S_1-p_d)p}, \quad (p_c = p), \tag{4.1}$$

$$\Phi_2(p_d, 0, p, 0, d_1) = \frac{p_d}{1-p_d} \cdot \frac{1}{1 - \frac{p_d p S_1}{1-p_d}}, \quad (p_r = p), \tag{4.2}$$

$$\Phi_2(p_d, 0, 0, p, d_1) = \frac{p_d}{1-p_d} \cdot \frac{1}{1-pS_1}, \quad (p_s = p). \tag{4.3}$$

The effect of p_c on the persistence threshold of species E_2 is greater than that of p_s if and only if the expression in (4.1) is bigger than the expression in (4.3), which is equivalent to

$$p_d < \frac{2 - S_1 - p}{2 - p}. \tag{4.4}$$

The right side of (4.4) is a decreasing function of p and the inequality is satisfied for $p = 0$, but not for $p = 1$. Therefore, there is a unique value $p_0 \in (0, 1]$ such that (4.4) is satisfied if and only if $p < p_0$. As d_1 increases, S_1 tends to $1 - p_d$ and therefore p_0 tends to 1. Thus, when p is small enough, the persistence threshold is more sensitive to the ability of species E_2 to persist with species E_1 than to its ability to colonize patches already occupied by E_1 .

From (4.2) and (4.3), the effect of p_r exceeds that of p_s if and only if $p_d > \frac{1}{2}$. That is, when p_d is large enough, the ability of species E_2 to colonize empty patches simultaneously with species E_1 becomes more important than the ability to colonize a patch already containing E_1 . If $p_d < \frac{1}{2}$, the effect of p_s is stronger. If $p_d = \frac{1}{2}$, changes in p_r and changes in p_s have the same effect.

Finally, the relative effects of p_c and p_r on the persistence threshold depend on the relationship between (4.1) and (4.2). The expression (4.1) is greater than (4.2) if and only if

$$2 - S_1 - p_d(3 - S_1) - pp_d(1 - p_d) > 0. \quad (4.5)$$

For small p_d , this inequality is clearly satisfied. How big p_d has to be for the effect of p_c to be greater than that of p_r depends on the values of p and d_1 . For $p_d > \frac{2}{3}$, (4.5) is never satisfied. The change of behavior occurs for some value of p_d smaller than $\frac{2}{3}$. In highly disturbed environments, E_2 is better off investing in a simultaneous colonization with E_1 than trying to persist together with it after colonization. If disturbances are not too frequent, it is more efficient for E_2 to persist with E_1 after colonization.

When all three types of competition operate, E_2 may have to choose among investing energy in reducing p_c , p_r and p_s . The relative value of these choices will depend on the sensitivity of $\Phi_2(p_d, p_c, p_r, p_s, d_1)$ to changes in p_c , p_r and p_s . Based on Fig. 3, we expect these sensitivities to reflect the turnover rates of individual patches, and thus to depend strongly on p_d . That is, when p_d is large enough, most patches will be disturbed before within-patch competition has time to operate, and p_c will be relatively unimportant. If p_d is small, colonization will be infrequent and the competitive interactions that take place during colonization (measured by p_r and p_s) will be unimportant. To make these ideas precise, we take the partial derivatives of Φ_2 with respect to p_c , p_r and p_s , and obtain

$$\frac{\partial \Phi_2}{\partial p_c} > \frac{\partial \Phi_2}{\partial p_s} \quad (4.6)$$

if and only if

$$p_d < \frac{2 - S_1 - p_c - p_s}{2 - p_r - p_c - p_s}, \quad (4.7)$$

$$\frac{\partial \Phi_2}{\partial p_r} > \frac{\partial \Phi_2}{\partial p_s} \quad (4.8)$$

if and only if

$$p_d > \frac{1}{2}. \quad (4.9)$$

Finally,

$$\frac{\partial \Phi_2}{\partial p_c} > \frac{\partial \Phi_2}{\partial p_r} \quad (4.10)$$

if and only if

$$p_d^2(p_c + p_r - p_s) - p_d(p_c + p_r - 2p_s - S_1 + 3) - p_s - S_1 + 2 > 0. \quad (4.11)$$

As in the previous comparison of the effects of p_c and p_s , condition (4.6) is likely to be satisfied (it depends on the relative values of all other parameters, but it is certainly satisfied for small values of p_c , p_r , p_s and S_1). In this case, for sufficiently large values of p_d , the system will eventually react more sensitively to changes in p_s than to changes in p_c . If equal changes in p_c and p_s have equal costs, then E_2 is better off investing energy in persisting with E_1 when both are present than in colonizing patches already occupied by E_1 .

The sensitivity of the system to changes in p_r and p_s remains unchanged with respect to the previous findings. In highly disturbed environments, the persistence threshold Φ_2 reacts more strongly to changes in p_r , whereas changes in p_s are more important if disturbances are rare. When $p_d = \frac{1}{2}$, the average inter-disturbance interval is only two time units and half of the patches are disturbed at every time step. This is quite a high rate of disturbance. It thus seems reasonable to expect that p_r will usually be less important than p_s .

Finally, for small values of p_d , the system is more sensitive to changes in p_c than to changes in p_r , but there is a threshold value for p_d (again, no greater than $\frac{2}{3}$) above which the system is more sensitive to changes in p_r .

At the extreme when disturbance is rare, p_c is more important than p_s , which is more important than p_r . The fugitive species benefits most from extending its temporary co-existence within a patch, less by improving its ability to invade an already occupied patch, and least by improving its ability to colonize simultaneously with the winning species. At the opposite extreme of frequently disturbed environments, the order of importance is reversed: rapid competitive exclusion carries little cost, and the ability to colonize (temporarily) in the presence of the winning species is most important.

There are several natural generalizations of the model analyzed here. One of them includes more than two species, with the restriction that all interactions among them can be neglected except the interaction with a leader or keystone species. Assume we have a landscape with one keystone species E_1 and $n - 1$ fugitive species. The dynamics of E_1 are not affected by any of the fugitive species. Therefore, if any other interaction among the $n - 1$ fugitive species is neglected, the generalization of the n species model is proved separately for each fugitive species by dealing in each step only with the frequency of the keystone species E_1 and the frequency of a single fugitive species.

The maximization of species diversity at intermediate levels of disturbance can be understood in the following way. According to Theorem 1, if p_d tends to 1, D_1 blows up to include the whole positive quadrant, i.e. it is likely that both species become extinct (see Fig. 4). Some kinds of pollution may act as highly frequent disturbances, and lead to biotic impoverishment.

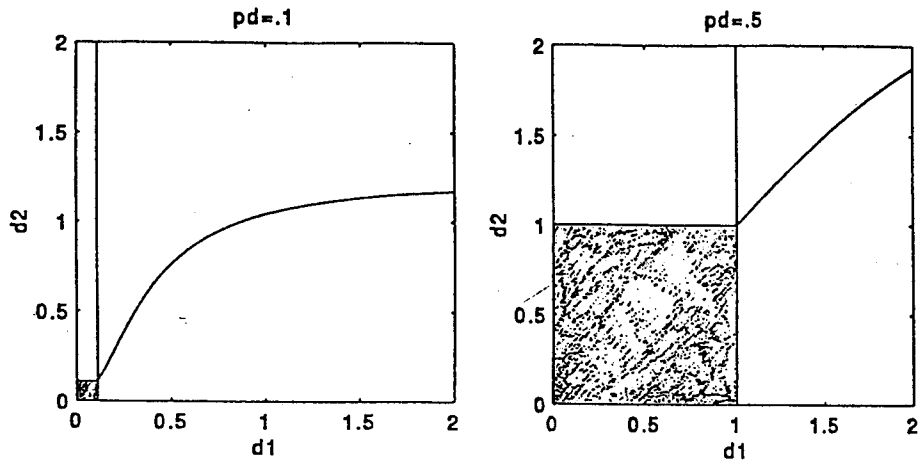


Figure 4. Example of effect of increasing disturbance probability (p_d) on size of region D_1 (shaded) in which neither species can persist. Parameter values: $p_c = p_r = p_s = 0.5$.

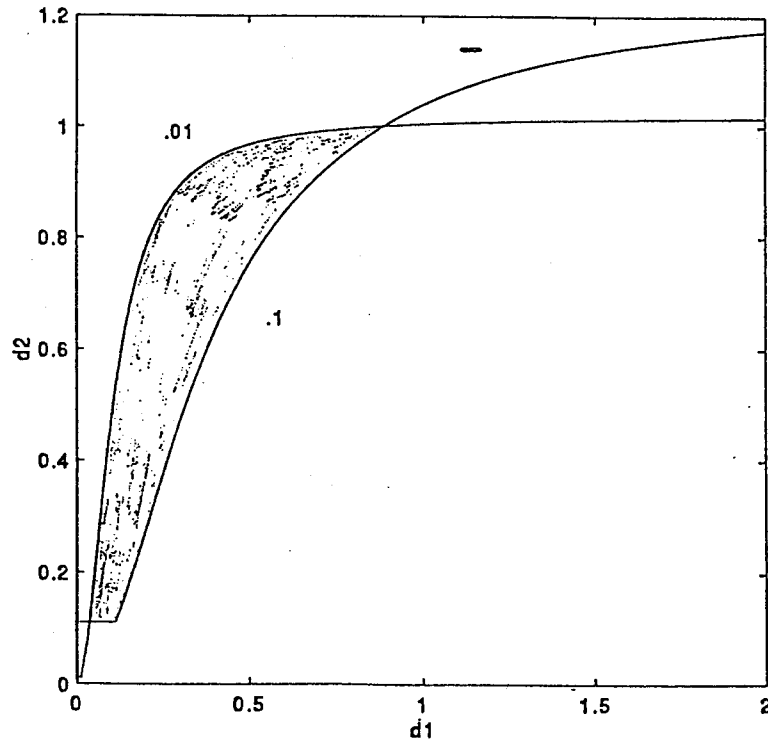


Figure 5. Example of change in critical dispersal rate $\Phi_2(p, d_1)$ with disturbance rate p_d , when disturbance is rare. Shaded area represents parameter combinations for which reduction in p_d from 0.1 to 0.01 makes persistence of fugitive species E_2 more difficult.

As D_1 increases in size, only species which spread very fast (d_1 and d_2 large) will be able to survive.

On the other hand, as p_d approaches 0, S_1 approaches 1 and $\Phi_2(\mathbf{p}, d_1) \rightarrow p_c/(1 - p_s)$. As in the models of Caswell and Cohen (1991a, b), when the winning competitor E_1 prevents colonization by the loser (i.e. when $p_s = 1$), $\Phi_2(\mathbf{p}, d_1)$ becomes infinite and species E_2 is excluded. When $p_s < 1$, species E_2 may persist when $p_d = 0$, but persistence may become more difficult because reducing disturbance may increase $\Phi_2(\mathbf{p}, d_1)$. An example is shown in Fig. 5. Since many ecosystems may contain many fugitive species, eliminating natural disturbances can cause a significant decrease in species diversity.

APPENDIX A

Theorem 1 and proof. Here we give the formal statement and proof of the theorem describing the stability of the model (2.2) and (2.3).

THEOREM 1. Let $p_d \in [0, 1]$ and $p_c, p_r, p_s \in [0, 1]$. Further, let $\mathbf{y}(t) = (y_0(t), y_1(t), y_2(t), y_3(t))$ be the solution of (2.2) with initial condition $\mathbf{y}_0 = (y_0(0), y_1(0), y_2(0), y_3(0))$.

- (a) If $(d_1, d_2) \in D_1$, then $(1, 0, 0, 0)$ is the only stationary solution of (2.2) in X and it is globally stable, i.e. $\mathbf{y}(t) \rightarrow (1, 0, 0, 0)$ as $t \rightarrow \infty$, for every initial condition in X . (Neither species can persist.)
- (b) If $(d_1, d_2) \in D_2$, then (2.2) has at most three stationary solutions in X : $(1, 0, 0, 0)$ and $(1 - S_2, 0, S_2, 0)$, which are unstable, and $(1 - S_1, S_1, 0, 0)$, which is globally stable, i.e. if $y_1(0) + y_3(0) \neq 0$, then $\mathbf{y}(t) \rightarrow (1 - S_1, S_1, 0, 0)$ as $t \rightarrow \infty$. If $d_2 < p_d/(1 - p_d)$, then $S_2 = 0$ and the first two stationary solutions coincide. (Species E_1 excludes species E_2 .)
- (c) If $(d_1, d_2) \in D_3$, then (2.2) has two stationary solutions in X : $(1, 0, 0, 0)$, which is unstable, and $(1 - S_2, 0, S_2, 0)$, which is globally stable, i.e. if $y_2(0) + y_3(0) \neq 0$ then $\mathbf{y}(t) \rightarrow (1 - S_2, 0, S_2, 0)$ as $t \rightarrow \infty$. (Species E_2 can persist, but species E_1 cannot.)
- (d) If $(d_1, d_2) \in D_4$, then (2.2) has only four stationary solutions in X : $(1, 0, 0, 0)$, $(1 - S_1, S_1, 0, 0)$ and $(1 - S_2, 0, S_2, 0)$, which are unstable, and $(1 - \hat{y}_1 - \hat{y}_2 - \hat{y}_3, \hat{y}_1, \hat{y}_2, \hat{y}_3)$, which is globally stable, i.e. if $y_2(0) + y_3(0) \neq 0$ and $y_1(0) + y_3(0) \neq 0$, then as $t \rightarrow \infty$, $\mathbf{y}(t) \rightarrow (1 - \hat{y}_1 - \hat{y}_2 - \hat{y}_3, \hat{y}_1, \hat{y}_2, \hat{y}_3)$, where $\hat{y}_1 + \hat{y}_3 = S_1$ and $\hat{y}_2 + \hat{y}_3 \leq S_2$. Moreover $\hat{y}_2 + \hat{y}_3 = S_2$ only if $p_r = p_s = p_c = 0$. (Both species can co-exist.)

Proof. Because the model operates on probability vectors, the analysis can be restricted to the set

$$X = \{(y_0, y_1, y_2, y_3) \in R^4 | y_0 + y_1 + y_2 + y_3 = 1, y_0, y_1, y_2, y_3 \geq 0\},$$

which is invariant under (2.2). Of special interest are vectors $\mathbf{y} = (y_0, y_1, y_2, y_3)$ in X which are fixed points of (2.2), that is, points in X such that

$$y_0 = [1 - (1 - p_d)(C_1 + C_2 - C_1 C_2)]y_0 + p_d y_1 + p_d y_2 + p_d y_3,$$

$$y_1 = (1 - p_d)C_1(1 - (1 - p_r)C_2)y_0 + (1 - p_d)(1 - (1 - p_s)C_2)y_1 + (1 - p_d)p_c y_3,$$

$$y_2 = (1 - p_d)(1 - C_1)C_2y_0 + (1 - p_d)(1 - C_1)y_2,$$

$$y_3 = (1 - p_d)C_1(1 - p_r)C_2y_0 + (1 - p_d)(1 - p_s)C_2y_1 + (1 - p_d)C_1y_2 + (1 - p_d)(1 - p_c)y_3,$$

or

$$(1 - p_d)(-1 + e^{-d_1(y_1+y_3)-d_2(y_2+y_3)})y_0 + p_d(y_1 + y_2 + y_3) = 0, \quad (\text{A.1})$$

$$(1 - p_d)(1 - e^{-d_1(y_1+y_3)})(1 - (1 - p_r)(1 - e^{-d_2(y_2+y_3)}))y_0 - (p_d + (1 - p_d)(1 - p_s)(1 - e^{-d_2(y_2+y_3)}))y_1 + (1 - p_d)p_c y_3 = 0, \quad (\text{A.2})$$

$$(1 - p_d)e^{-d_1(y_1+y_3)}(1 - e^{-d_2(y_2+y_3)})y_0 + ((1 - p_d)e^{-d_1(y_1+y_3)} - 1)y_2 = 0, \quad (\text{A.3})$$

$$(1 - p_d)(1 - e^{-d_1(y_1+y_3)})(1 - p_r)(1 - e^{-d_2(y_2+y_3)})y_0 + (1 - p_d)(1 - p_s) \times (1 - e^{-d_2(y_2+y_3)})y_1 + (1 - p_d)(1 - e^{-d_1(y_1+y_3)})y_2 + (p_c p_d - p_d - p_c)y_3 = 0. \quad (\text{A.4})$$

Define g_0, g_1, g_2 and $g_3: X \rightarrow \mathbb{R}$ to be the left side of (A.1), (A.2), (A.3) and (A.4), respectively. The behavior of a solution of (2.2) in X is determined only by the sign of the functions g_i . Therefore, if $g_i < 0$, the corresponding variable $y_i(t)$ decreases over time, and if $g_i > 0$, it increases in time. Finally, if $g_i = 0$, $y_i(t)$ does not change. The frequencies of E_1 and E_2 increase or decrease according to the signs of $g_1 + g_3$, and $g_2 + g_3$, respectively.

Since E_1 is not affected by E_2 , its equilibrium frequency depends only on the parameters p_d and d_1 . That is why the following lemma holds true regardless of the values of d_2, p_c, p_r and p_s .

LEMMA 1. *Let $y(t) = (y_0(t), y_1(t), y_2(t), y_3(t))$ be the solution of (2.2) with initial condition $(y_0(0), y_1(0), y_2(0), y_3(0))$.*

- (a) *If $d_1 \leq p_d/(1 - p_d)$, then $f_1(t) = y_1(t) + y_3(t)$ decreases monotonically to 0 as $t \rightarrow \infty$.*
- (b) *If $d_1 > p_d/(1 - p_d)$ and $y_1(0) + y_3(0) \neq 0$, then $f_1(t) = y_1(t) + y_3(t) \rightarrow S_1$ as $t \rightarrow \infty$.*

Lemma 1 is proved by Barradas and Cohen (1994).

E_2 is eliminated locally by E_1 , thereby reducing its equilibrium frequency. We aim to make clear this reduction of the equilibrium frequency as a function of the parameters, and to give explicit conditions for E_2 to persist. Since positive solutions are shown to be always globally stable, the conditions for their existence also describe whether E_2 is able to invade a landscape previously occupied by E_1 (see Fig. 1).

LEMMA 2. *There is a continuous function*

$$\Phi_2: [0, 1) \times [0, 1) \times [0, 1) \times [0, 1) \times [0, \infty) \rightarrow \left[\frac{p_d}{1 - p_d}, \frac{p_d + (1 - p_d)p_c}{(1 - p_d)(1 - p_s(1 - p_d) - p_d p_r)} \right)$$

such that for fixed values of p_d, p_c, p_r, p_s :

- (a) $\Phi_2(p_d, p_c, p_r, p_s, x) = p_d/(1 - p_d)$ for $x \in [0, p_d/(1 - p_d)]$.
- (b) $\Phi_2(p_d, p_c, p_r, p_s, x)$ is monotonically increasing in x for $x > p_d/(1 - p_d)$.

- (c) $\lim_{x \rightarrow \infty} \Phi_2(p_d, p_c, p_r, p_s, x) = (p_d + (1 - p_d)p_c) / ((1 - p_d)(1 - p_s(1 - p_d) - p_d p_r))$. Define $(y_0(t), y_1(t), y_2(t), y_3(t))$ to be the solution of (2.2) with initial condition $(y_0(0), y_1(0), y_2(0), y_3(0))$.
- (d) If $d_2 \leq \Phi_2(p_d, p_c, p_r, p_s, d_1)$, then $f_2(t) = y_2(t) + y_3(t) \rightarrow 0$ as $t \rightarrow \infty$.
- (e) If $d_2 > \Phi_2(p_d, p_c, p_r, p_s, d_1)$ and $y_2(0) + y_3(0) \neq 0$, then $f_2(t) = y_2(t) + y_3(t) \rightarrow \bar{S}_2$ as $t \rightarrow \infty$, with $\bar{S}_2 = \bar{S}_2(p_d, p_c, p_r, p_s, d_1) \leq S_2$. Moreover, $\bar{S}_2 = S_2$ only if $d_1 \leq p_d / (1 - p_d)$ or $p_r = p_s = p_c = 0$.

Proof. Lemma 1 guarantees that E_1 is not affected by E_2 . Therefore, E_1 will tend to the level S_1 specified by the one-species model, i.e. $f_1(t) = y_1(t) + y_3(t) \rightarrow S_1$ as $t \rightarrow \infty$. Since all functions involved are continuous, the behavior of the solution for $y_1 + y_3$ near S_1 can be understood by analyzing the case $y_1 + y_3 = S_1$. For this reason, we will concentrate first on the set

$$S = \{(y_0, y_1, y_2, y_3) \in X \mid y_1 + y_3 = S_1\}.$$

The idea of the proof is to find two curves γ and φ in S such that they intersect in at most one point with positive co-ordinates. If such a point exists, it will be shown to be a stationary solution of (2.2).

In S , the equations in system (A.1) to (A.4) may be simplified by substituting for $e^{-d_1 S_1}$ from (2.4):

$$e^{-d_1 S_1} = \frac{1 - S_1 - p_d}{(1 - p_d)(1 - S_1)}. \quad (\text{A.5})$$

Using this value in (A.3) and solving for y_3 yields a convex curve $\gamma(y_2)$, such that for any initial condition in S , $y_2(t)$ increases (with t) above γ , and decreases (with t) below it. (Figure A1 shows a special case in which $\gamma'(0) > 0$.) γ is independent of p_c , p_r and p_s . It is given by

$$y_3 = \gamma(y_2) := \frac{1}{d_2} \ln \frac{(1 - S_1 - p_d)(1 - S_1 - y_2)}{(1 - S_1)(1 - S_1 - p_d - y_2)} - y_2,$$

which is well defined for $0 \leq y_2 < 1 - S_1 - p_d$, where it is a convex function of y_2 . Since $\gamma(0) = 0$, this implies that γ is an increasing function of y_2 , whenever it takes positive values. The value of $\gamma'(0)$ will be of special interest in the later analysis. It is given by

$$\gamma'(0) = \frac{p_d}{d_2(1 - S_1)(1 - S_1 - p_d)} - 1. \quad (\text{A.6})$$

The curve φ in S mentioned above is determined by the set

$$G = \{(y_0, y_1, y_2, y_3) \in S \mid g_2(y_0, y_1, y_2, y_3) + g_3(y_0, y_1, y_2, y_3) = 0\}. \quad (\text{A.7})$$

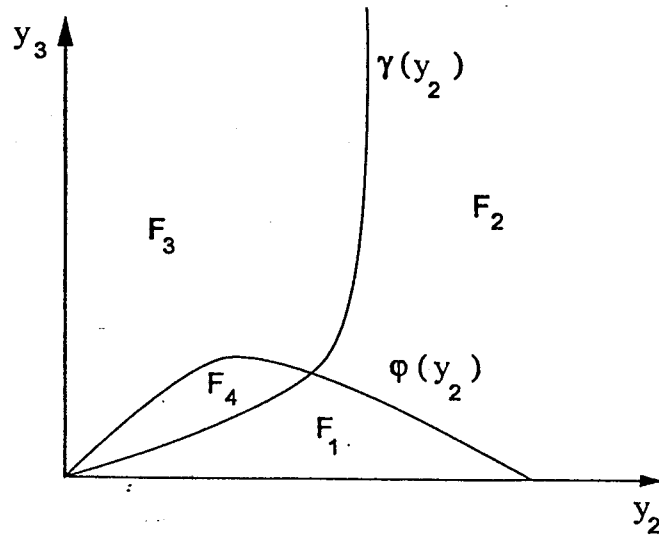


Figure A1. Curves in (y_2, y_3) plane that determine equilibril values of y_2 and y_3 by their point of intersection. y_2 is the fraction of all patches that contain species 2 but not species 1; y_3 is the fraction of all patches that contain both species.

Using the equalities $y_0 = 1 - S_1 - y_2$, and $y_1 = S_1 - y_3$, G can be written so that it does not depend on either y_0 or y_1 . A further simplification can be achieved by substituting (A.5) in (A.7). Therefore, φ consists of those points $y \in S$ whose third and fourth co-ordinates satisfy

$$\begin{aligned} (1-p_d)(1-e^{-d_2(y_2+y_3)}) \left(1-p_s S_1 - \frac{p_d p_r S_1}{1-p_d} - \left(1 - \frac{p_r p_d S_1}{(1-p_d)(1-S_1)} \right) y_2 \right. \\ \left. - (1-p_s)y_3 \right) - p_d(y_2+y_3) - p_c(1-p_d)y_3 = 0. \end{aligned} \quad (\text{A.8})$$

The definition of G also guarantees that

$$G = \{(y_0, y_1, y_2, y_3) \in S \mid y_3 = \varphi(y_2) \text{ or } y_3 = y_2 = 0\}.$$

After a substitution of the type $y_3 = k + ly_2$, with $0 \leq y_2 + y_3 \leq 1$ and k, l in R , the left side of (A.8) defines y_3 as a function of y_2 whose second derivative does not change sign. This guarantees that there are at most two values of y_2 that makes (A.8) hold true. Moreover, $\varphi' > -1$, unless $p_r = p_s = p_c = 0$, in which case φ is given by $\{(y_0, y_1, y_2, y_3) \in S \mid y_2 + y_3 = S_2\}$. This case corresponds to no interactions between species. Therefore, we will assume from now on that $\min\{p_r, p_s, p_c\} > 0$, and hence $\varphi' > -1$.

Considering special values of the variables in (A.8) ($y_2 = 0$ and $y_3 = 0$, respectively), it is clear that φ is either concave in that region or it is convex and decreasing. In either case, the convexity of γ and the fact that it is an increasing function for positive values imply that both curves intersect in a single point with positive co-ordinates, which corresponds to a non-trivial fixed point of (2.2), if and only if $\varphi(0) > 0$, or $\varphi(0) = 0$ and $\varphi'(0) > \gamma'(0)$.

For fixed p_d, p_c, p_r and p_s , we will look for conditions on d_2 as a function of d_1 such that each of the following cases is satisfied:

- Case 1. $\varphi(0) > 0$.
- Case 2. $\varphi(0) = 0$ and $\varphi'(0) > \gamma'(0)$.
- Case 3. $\varphi(0) = 0$ and $\varphi'(0) \leq \gamma'(0)$.

Case 1. For $\varphi(0)$ to be positive, we need a positive root of

$$(1 - p_d)(1 - e^{-d_2 y_3}) \left(1 - p_s S_1 - \frac{p_d p_r S_1}{1 - p_d} (1 - p_s) y_3 \right) - (p_d + p_c(1 - p_d)) y_3 = 0. \quad (\text{A.9})$$

Since the left side of (A.9) is a concave function of y_3 that takes the value 0 at 0, it has a positive root if and only if its derivative at 0 is positive, i.e. if and only if

$$d_2 > \left(\frac{p_d}{1 - p_d} + p_c \right) \frac{1}{1 - p_s S_1 - \frac{p_d p_r S_1}{1 - p_d}} = \frac{p_d + (1 - p_d) p_c}{(1 - p_d)(1 - p_s S_1) - p_d p_r S_1}. \quad (\text{A.10})$$

Case 2. Making a substitution of the form $y_3 = \alpha y_2$ in (A.8) with $\alpha > 0$, we get

$$\begin{aligned} & (1 - p_d)(1 - e^{-d_2(\alpha+1)y_2}) \\ & \times \left(1 - p_s S_1 - \frac{p_d p_r S_1}{1 - p_d} - \left(1 - \frac{p_r p_d S_1}{(1 - p_d)(1 - S_1)} + (1 - p_s) \alpha \right) y_2 \right) \\ & - \left(p_d + \frac{p_c(1 - p_d)\alpha}{\alpha + 1} \right) (\alpha + 1) y_2 = 0. \end{aligned} \quad (\text{A.11})$$

This equation will allow us to calculate $\varphi'(0)$ when $\varphi(0) = 0$. Since φ is a convex function, its derivative at 0 is given by the value of α for which (A.11) has $y_3 = y_2 = 0$ as a double zero. That is the case when the derivative at 0 of the left side as a function of y_2 is equal to 0, i.e. when

$$d_2 = \frac{p_d}{(1 - p_d)(1 - p_s S_1) - p_d p_r S_1} + \frac{\alpha p_c}{(\alpha + 1) \left(1 - p_s S_1 - \frac{p_d p_r S_1}{1 - p_d} \right)}.$$

Any value of d_2 such that

$$d_2 \in \left(\frac{p_d}{1 - p_d}, \frac{p_d + (1 - p_d) p_c}{(1 - p_d)(1 - p_s S_1) - p_d p_r S_1} \right)$$

can be written in a unique way as

$$d_2 = \frac{p_d}{(1-p_d)(1-p_s S_1) - p_d p_r S_1} + \frac{\beta p_c}{1-p_s S_1 - \frac{p_d p_r S_1}{1-p_d}}, \quad (\text{A.12})$$

with β in $(0, 1)$. For those values, the above calculations show that $\varphi'(0) = \alpha = \beta/(1-\beta)$, which, together with (A.12), yields

$$\varphi'(0) = \frac{d_2((1-p_d)(1-p_s S_1) - p_d p_r S_1) - p_d}{-d_2((1-p_d)(1-p_s S_1) - p_d p_r S_1) + p_d + (1-p_d)p_c}.$$

Combining this equality with (A.6), we finally get that $\gamma'(0) < \varphi'(0)$ transforms into

$$\frac{p_d}{d_2(1-S_1)(1-S_1-p_d)} - 1 < \frac{d_2((1-p_d)(1-p_s S_1) - p_d p_r S_1) - p_d}{-d_2((1-p_d)(1-p_s S_1) - p_d p_r S_1) + p_d + (1-p_d)p_c},$$

or

$$d_2 > \frac{p_d}{1-p_d} \cdot \frac{p_d + (1-p_d)p_c}{p_d \left(1 - p_s S_1 - \frac{p_d p_r S_1}{1-p_d} \right) + (1-S_1)(1-S_1-p_d)p_c}. \quad (\text{A.13})$$

The right side of this inequality determines the function Φ_2 used in (2.5). The case analyzed here, and Case 3 below, justify the definition of Φ_2 .

Case 3. According to the previous calculations, Case 3 occurs if and only if (A.13) fails to hold. This concludes the proof of Lemma 2. We now complete the proof of the theorem.

The definition of Φ_2 clearly satisfies conditions (a) and (b) of lemma 2. To see that it satisfies condition (c) as well, observe that for $d_1 \rightarrow \infty$, $S_1 \rightarrow 1 - p_d$, which implies

$$\varphi(p_d, p_c, p_r, p_s, d_1) \rightarrow \frac{p_d + (1-p_d)p_c}{(1-p_d)(1-p_s(1-p_d) - p_d p_r)}.$$

The continuity of Φ_2 at $d_1 = p_d/(1-p_d)$ is a consequence of the fact that as $d_1 \rightarrow p_d/(1-p_d)$, $S_1 \rightarrow 0$, which implies

$$\varphi(p_d, p_c, p_r, p_s, d_1) \rightarrow \frac{p_d}{1-p_d}.$$

For $x \leq p_d/(1-p_d)$, Lemma 1 guarantees that $S_1 = 0$.

To prove that the definition of Φ_2 satisfies the remaining conditions stated in the lemma, we will next show that γ and φ divide S into four regions (one of which becomes empty in Case 3) such that every solution of (2.2) starting in S tends to $\hat{y} = (\hat{y}_0, \hat{y}_1, \hat{y}_2, \hat{y}_3)$, the intersection of γ and φ , as $t \rightarrow \infty$.

Define the following subsets of S , as shown in Figure A1:

$$F_1 = \{(y_0, y_1, y_2, y_3) \in S \mid y_3 < \varphi(y_2), y_3 < \gamma(y_2)\},$$

$$F_2 = \{(y_0, y_1, y_2, y_3) \in S \mid y_3 > \varphi(y_2), y_3 < \gamma(y_2)\},$$

$$F_3 = \{(y_0, y_1, y_2, y_3) \in S \mid y_3 > \varphi(y_2), y_3 > \gamma(y_2)\},$$

$$F_4 = \{(y_0, y_1, y_2, y_3) \in S \mid y_3 < \varphi(y_2), y_3 > \gamma(y_2)\}.$$

Any solution of (2.2) starting in F_1, F_2, F_3 , or F_4 will eventually either tend to \hat{y} , or reach one of the curves γ or φ .

If the solution reaches γ for $y_2 > \hat{y}_2$, the fact that y_2 remains constant on γ , and $y_2 + y_3$ decreases, implies that the solution enters F_2 . If the solution reaches γ with $y_2 < \hat{y}_2$, a similar argument shows that the solution enters F_4 .

If a solution reaches φ , $y_2 + y_3$ remains constant, and the behavior of the solution depends on whether y_2 increases or decreases. Since $\varphi' > -1$, we conclude that solutions reaching φ can only enter F_2 or F_4 .

Once a solution enters F_2 or F_4 , it is clear that as $t \rightarrow \infty$, it tends to \hat{y} .

In any case, we have that as $t \rightarrow \infty$, $y_2(t) + y_3(t) \rightarrow \hat{y}_2 + \hat{y}_3$. Condition (e) in the lemma is then a consequence of Cases 1 and 2 analyzed above, whereas Case 3 proves (d).

Finally, since $\varphi' > -1$ and $y_2 = S_2$ is the only positive root of φ (when $d_2 > p_d / (1 - p_d)$), it follows that $\bar{S}_2 = \hat{y}_2 + \hat{y}_3 \leq S_2$. Here, $\bar{S}_2 = S_2$ only if $\hat{y}_3 = 0$, i.e. when $S_1 = 0$, or $p_r = p_s = p_c = 0$.

APPENDIX B

Numerical methods. Let \hat{y} denote an equilibrium, and linearize (2.2) in the neighborhood of this equilibrium (Beddington, 1974). Let

$$x(t) = y(t) - \hat{y} \tag{B.1}$$

$$x(t+1) = \left(A_{\hat{y}} + \left[\frac{\partial A}{\partial y_0} \hat{y} \dots \frac{\partial A}{\partial y_3} \hat{y} \right] \right) x(t) \tag{B.2}$$

$$\equiv Bx(t) \tag{B.3}$$

where all partial derivatives are evaluated at \hat{y} . The matrices B for both boundary equilibria are reducible: the dynamics of the states involving the invading species (i.e. of y_2 and y_3 when E_2 is invading, and of y_1 and y_3 when E_1 is invading) are independent of the other states. Thus, the success of the invasion is determined by the eigenvalues of the 2×2 submatrix of B involving the invading species.

When species E_2 is invading the boundary equilibrium $\hat{y} = (1 - S_1, S_1, 0, 0)$, the submatrix of B describing the dynamics of y_2 and y_3 is

$$\begin{pmatrix} \overline{p_d C_1} + \hat{y}_0 \overline{p_c C_1 d_2} & \hat{y}_0 \overline{p_d C_1 d_2} \\ \overline{p_d C_1} + \hat{y}_0 \overline{p_d p_r C_1 d_2} + \hat{y}_1 \overline{p_d p_s d_2} & \overline{p_d p_c} + (\hat{y}_0 C_1 + \hat{y}_1) \overline{p_d p_r d_2} \end{pmatrix}, \tag{B.4}$$

where C_1 is evaluated at \hat{y} . We solve numerically for the value of d_2 that gives a dominant eigenvalue of 1; this value of d_2 is our numerical estimate of $\Phi_2(p, d_1)$. Because the matrix is non-negative and all its entries are monotonic increasing functions of d_2 , there will be at most one such value of d_2 .

Similarly, when species E_1 is invading the equilibrium $\hat{y} = (1 - S_2, 0, S_2, 0)$, the dynamics of y_1 and y_3 are given by the submatrix

$$\begin{pmatrix} \overline{p_d}(1 - \overline{p_s}C_2) + \hat{y}_0\overline{p_d}d_1(1 - \overline{p_r}C_2) & \overline{p_d}\overline{p_c} + \hat{y}_0\overline{p_d}d_1(1 - \overline{p_r}C_2) \\ \overline{p_d}\overline{p_s}C_2 + \overline{p_d}d_1(\hat{y}_0\overline{p_r}C_2 + \hat{y}_2) & \overline{p_d}\overline{p_c} + \overline{p_d}d_1(\hat{y}_0\overline{p_r}C_2 + \hat{y}_2) \end{pmatrix}, \quad (\text{B.5})$$

where C_2 is evaluated at \hat{y} . The value of d_1 at which the dominant eigenvalue of this matrix equals one is our numerical estimate of $\Phi_1(p, d_2)$. That $\Phi_1 = p_d/(1 - p_d)$, as guaranteed by theorem 1, can be shown by substituting $d_1 = p_d/\overline{p_d}$ in the matrix and noting that both columns then sum to 1. Since the matrix is non-negative, Frobenius' theorem implies that the maximum eigenvalue is 1.

This approach can be used to investigate invasibility and persistence in other models (e.g. Caswell and Cohen, 1991a, b) for which global stability results like those proved here are not available. In such cases, invasibility of the boundary equilibria may imply co-existence, but it does not guarantee that the species co-exist at a fixed point. These issues will be explored elsewhere (Caswell and Cohen, in preparation).

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REFERENCES

- Barradas, I. and J. E. Cohen. 1994. Disturbances allow coexistence of competing species. *J. Math. Biol.* **32**, 663-676.
- Beddington, J. 1974. Age distribution and the stability of simple discrete time population models. *J. Theor. Biol.* **47**, 65-74.
- Caswell, H. and J. E. Cohen. 1991a. Communities in patchy environments: a model of disturbance, competition, and heterogeneity. In *Ecological Heterogeneity*, J. Kolasa (Ed). Berlin: Springer.
- Caswell, H. and J. E. Cohen. 1991b. Disturbance and diversity in metapopulations. *Biol. J. Linnean Soc.* **42**, 193-218.
- Caswell, H. and R. J. Etter. 1993. Ecological interactions in patchy environments: from patch-occupancy models to cellular automata. In *Patch Dynamics*, S. A. Levin *et al.* (Eds). New York: Springer Verlag.
- Connell, J. H. 1978. Diversity in tropical rain forest and coral reefs. *Science* **199**, 1302-1310.
- Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* **111**, 1119-1144.

- Dayton, P. K. and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep Sea Research* 19, 199-208.
- Etter, R. J. and H. Caswell. 1993. The advantages of dispersal in a patchy environment: effects of disturbances in a cellular automaton model. In *Reproduction, Larval Biology and Recruitment in the Deep-Sea Benthos*, K. J. Eckelbarger and C. M. Young (Eds). New York: Columbia University Press.
- Gilpin, M. E. 1975. *Group Selection in Predator-Prey Communities*. Princeton, NJ: Princeton University Press.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113, 81-101.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* 32, 571-577.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235, 167-171.
- Slatkin, M. 1974. Competition and regional coexistence. *Ecology* 55, 128-134.

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