Disturbances allow coexistence of competing species

Ignacio Barradas[1], Joel E. Cohen[2]

[1] Centro de Investigación en Matemáticas, Apdo. Postal 402, 36000 Guanajuato, Gto. México,
and Rockefeller University, 1230 York Avenue, New York, NY 10021-6399, USA
(Fax: +52-473/25749, Tel.: +52-473/27155)
[2] Rockefeller University, 1230 York Avenue, New York, NY 10021-6399, USA

Abstract. We give the first mathematically rigorous proof that disturbances allow competing species to coexist. This work provides a mathematical framework to explain the existence of fugitive species and the role played by disturbances in increasing or decreasing the biodiversity of ecosystems. We study modifications of the metapopulation model for patchy environments proposed by Caswell and Cohen (1990, 1991). For the one- and two-species models we give necessary and sufficient conditions on the parameters for the existence of a non-trivial equilibrium solution, which is shown to be always globally stable.

Key words: Disturbed competition – Coexistence – Metapopulations – Diversity – Global stability

1 Introduction

Species' coexistence, competition and diversity are important elements in the dynamics of ecosystems. Differences in local and regional processes can be very important in the determination of diversity patterns (Slatkin 1974, Houston 1979, Ricklefs 1987). A metapopulation approach makes it possible to deal properly with concepts like that of fugitive species introduced by Hutchinson (1951): fugitive species are excluded locally whenever they interact with stronger competitors, but persist on a regional scale. Metapopulation models can also account for the observation that species diversity in ecosystems seems to attain a maximum at an intermediate disturbance frequency (Dayton and Hessler 1972, Connell 1978). Many metapopulation models (or related models) that address species diversity have been proposed and analyzed (e.g., Acevedo 1981; Chesson 1985; Connell and Slatyer 1977; Grassle and Sanders 1973; Hanski 1983; Harper 1969, 1977; Hastings 1980; Horn and MacArthur 1972; Levin 1974; MacArthur and Wilson 1967; Pacala 1987; Palmer and Strathmann 1981; Shmida and Ellner 1984; Slatkin 1974).

 Caswell and Cohen (1990, 1991) proposed a family of models for metapopulations in patchy environments under perturbations. In these models, the rates of interspecific interactions and disturbance appear explicitly. Extensive numerical

simulations of these models suggest the existence of globally stable non-trivial equilibrium solutions which describe the coexistence of species. Due to the mathematical difficulty of studying such non-linear Markov chains, no analytical proof of these results has been obtained except in the case of a single species. In the present work we study modifications of the Caswell–Cohen model for one and two species and give necessary and sufficient conditions on the parameters for the existence of a non-trivial equilibrium solution, which is shown to be always globally stable. This work provides the first mathematically rigorous proof of the existence of such non-trivial solutions. It provides a mathematical framework to explain the presence of fugitive species, and to understand the role played by disturbances in increasing or decreasing the biodiversity of ecosystems.

2 The one-species model

We consider an environment consisting of an infinite number of identical patches, each of which can be either empty or occupied by the only species present in the landscape. The state of each single patch is defined by the presence or absence of the species. We will denote the two possible patch states by 0 if the species is absent, and by 1 if it is present. The state of the landscape is given by a vector y in $\mathfrak{R}^2$, whose entries, y_0 and y_1, are the fraction of patches in state 0 and 1, respectively.

The dynamics of the system is given by a non-linear Markov chain. The transition matrix $A_{y(t)}$, which depends on the state $y(t)$ at time t, models persistence and colonization from one time step to the next as these processes are affected by disturbances:

$$y(t+1) = A_{y(t)} y(t) . \tag{2.1}$$

The transition matrix A will be derived from hypotheses about the processes of persistence and colonization. Disturbances are assumed to be of one of two types, depending on whether they affect persistence or colonization. Disturbances affecting persistence are supposed to occur independently for all patches with a probability p_d, $0 \leq p_d \leq 1$, which is constant in time and equal for all patches. It is further assumed that an occupied patch affected by the disturbance becomes empty. A disturbance that affects persistence has no effect on an empty patch.

Disturbances affecting colonization are assumed to occur independently for all patches with a probability p_e, $0 \leq p_e < 1$, which is constant in time and equal for all patches. Under such disturbances colonization does not take place. A disturbance affecting colonization has no effect on an occupied patch, where colonization would be effectively invisible because the occupied patch simply remains occupied. The colonization of empty patches is assumed to be determined by a random dispersal of propagules, without neighborhood effects. The mean number of propagules reaching a patch is assumed to be directly proportional to the fraction of occupied patches, and the distribution of the number of propagules is assumed to be Poisson. Hence the probability that an empty patch is colonized by at least one propagule is given by

$$C = 1 - \exp(-d y_1) \tag{2.2}$$

where $d \geq 0$ denotes the dispersal coefficient of the species, and both y_1 and C may depend on time t. These hypotheses yield a transition matrix

$$A_y = \begin{pmatrix} 1 - C(1-p_e) & p_d \\ C(1-p_e) & 1-p_d \end{pmatrix} \tag{2.3}$$

where C is given by (2.2). The one-species model considered by Caswell and Cohen (1990, 1991) corresponds to the special case $p_e = 0$ here.

Although the analysis of system (2.1) and (2.3) in the next section is only made for $p_e < 1$, similar results are also valid for $p_e = 1$. (Of course, if $p_e = 1$, no colonization occurs, so the situation $p_e = 1$ is not of ecological interest.) The only change required is either to write all expressions so that $1 - p_e$ does not appear in the denominator, or allow $d = \infty$ and when necessary take the limit as $p_e \to 1$.

3 Analysis of the one-species model

The set

$$X = \{(y_0, y_1) \in \mathfrak{R}^2 | y_0 + y_1 = 1, \, y_0, y_1 \geq 0\} \tag{3.1}$$

is invariant under (2.1). Moreover, $y = (y_0, y_1)$ in X is a fixed point of (2.1) if and only if

$$[1 - (1 - e^{-dy_1})(1 - p_e)] y_0 + p_d y_1 = y_0 \tag{3.2}$$

and

$$(1 - e^{-dy_1})(1 - p_e) y_0 + (1 - p_d) y_1 = y_1 . \tag{3.3}$$

Because $y_0 + y_1 = 1$, (3.2) and (3.3) are equivalent. So we will analyze (3.3) in the form

$$(1 - e^{-dy_1})(1 - p_e)(1 - y_1) + (1 - p_d) y_1 - y_1 = 0 . \tag{3.4}$$

Define

$$h(y) = (1 - e^{-dy})(1 - p_e)(1 - y) - p_d y . \tag{3.5}$$

A fixed point of (2.1) corresponds to a zero of h. Moreover, $h(y_1) > 0$ implies that y_1 increases in time, i.e., $y_1(t+1) > y_1(t)$, and $h(y_1) < 0$ implies that y_1 decreases in time. Since h is a concave function of y with $h(0) = 0$ and $h(1) < 0$, (3.4) has a unique positive solution, $S(d, p_d, p_e)$, if and only if $h'(0) > 0$, i.e.,

$$d > \frac{p_d}{1 - p_e} . \tag{3.6}$$

Moreover $h(y) > 0$ for $S > y > 0$, and $h(y) < 0$ for $1 \geq y > S$. This implies that the point $(1 - S, S)$ is a global attractor for (2.1) on the subset of X where $y_1 > 0$. The same argument also shows that $(1, 0)$ is a global attractor if

$$d \leq \frac{p_d}{1 - p_e} . \tag{3.7}$$

Observe that S increases with d and decreases with p_d and p_e. For fixed p_d and p_e the highest prevalence S of the species is obtained for $d = \infty$, i.e., when y_1 is a solution of

$$(1 - p_e)(1 - y_1) - p_d y_1 = 0 , \tag{3.8}$$

which implies

$$y_1 = \frac{1 - p_e}{1 + p_d - p_e} \; . \tag{3.9}$$

Since the level of occupancy attained by the species at equilibrium depends on both p_d and p_e, it is of interest to know whether that value is more sensitive to changes in p_d or in p_e. The answer can be calculated by comparing the partial derivatives of the right side of (3.6) with respect to p_d and p_e. Thus

$$\frac{\partial}{\partial p_d}\left(\frac{p_d}{1 - p_e}\right) = \frac{1}{1 - p_e}, \qquad \frac{\partial}{\partial p_e}\left(\frac{p_d}{1 - p_e}\right) = \frac{p_e}{(1 - p_e)^2} \tag{3.10}$$

imply that

$$\frac{\partial}{\partial p_d}\left(\frac{p_d}{1 - p_e}\right) > \frac{\partial}{\partial p_e}\left(\frac{p_d}{1 - p_e}\right) \tag{3.11}$$

if and only if

$$p_d + p_e < 1 \; . \tag{3.12}$$

This means that, if disturbances are rare ($p_d + p_e < 1$), the payoff (measured by the equilibrium fraction ($t \to \infty$) of patches in which the species is present) from reducing p_d is higher than that from reducing p_e, i.e., environments affected rarely by disturbances should be expected to include species that invest more energy in persisting after colonization than in colonizing. On the other hand, if disturbances are common ($p_d + p_e > 1$), a species should increase its ability to colonize rather than to persist after colonization.

4 The two-species model

As in the one-species model, we consider an environment consisting of an infinite number of identical patches. Each patch can be occupied by individuals of two species E_1 and E_2, and can be in one of the states numbered 0, 1, 2, or 3, defined as follows; 0 if the patch is empty, 1 if it is occupied only by species one, 2 if it is occupied only by species two, and 3 if both species are present in it. In summary:

Species 1	Species 2	State
absent	absent	0
present	absent	1
absent	present	2
present	present	3

The state of the whole collection of patches is described by a vector y in $\Re^4$, whose entries y_i are the proportion of patches in state i. In the two-species model, the patches are assumed to change state as a result of colonization and disturbances, as before, and, as a new element, as a result of within-patch interactions. Within-patch interactions are assumed to consist of competition in which species one eliminates species two with a probability per unit of time of p_c, $0 \le p_c \le 1$.

Disturbances are assumed to occur independently in all patches with a constant probability, p_d, $0 \le p_d < 1$. Any occupied patch affected by a disturbance becomes empty, i.e., it returns to the state 0. Disturbances of empty patches cause colonization to fail. As in the one-species model, analogous results hold true for $p_d = 1$ after rewriting all expressions to avoid denominators that tend to zero.

In contrast to the one-species model, here the assumption that disturbances affect persistence and colonization with the same probability is made in order to keep calculations as simple as possible. Nevertheless it is worthwhile to remember that whenever a term of the form $p_d/(1 - p_d)$ appears, the numerator is related to disturbance of persistence, whereas the denominator describes the effect of the disturbance of colonization.

Colonization is assumed to occur at random, without neighborhood effects. Further, it is assumed that the mean number of propagules of species E_i arriving at a patch is directly proportional to the fraction of patches containing E_i, and the distribution of the number of propagules is assumed to be Poisson. Hence the probability that an empty patch is colonized by at least one propagule of species E_i is given by

$$C_i = 1 - \exp(-d_i f_i) \tag{4.1}$$

where d_i is the dispersal coefficient of species i, and $f_i(t)$ its frequency, i.e., $f_1(t) = y_1(t) + y_3(t)$, and $f_2(t) = y_2(t) + y_3(t)$. Under these hypotheses, the dynamics of the system is described by

$$y(t + 1) = A_y \, y(t) \tag{4.2}$$

where the transition matrix is

$$A_y =$$

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

$$\tag{4.3}$$

and the C_i are given by (4.1). The differences between this model and the two-species model of Caswell and Cohen (1990, 1991) are analyzed in the discussion below.

5 Analysis of the two-species model

The set

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

is invariant under (4.2).

A vector $y=(y_0, y_1, y_2, y_3)$ in X is a fixed point of (4.2) if and only if

$$[1-(1-p_d)(C_1+C_2-C_1C_2)]y_0+p_d y_1+p_d y_2+p_d y_3=y_0$$

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

$$(1-p_d)(1-C_1)C_2 y_0+(1-p_d)(1-C_1)y_2=y_2$$

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

or

$$(-1+e^{-d_1(y_1+y_3)-d_2(y_2+y_3)})(1-p_d)y_0+p_d(y_1+y_2+y_3)=0 \tag{5.1}$$

$$(1-e^{-d_1(y_1+y_3)})e^{-d_2(y_2+y_3)}(1-p_d)y_0-[p_d(1-e^{-d_2(y_2+y_3)})+e^{-d_2(y_2+y_3)}]y_1$$

$$+(1-p_d)p_c y_3=0 \tag{5.2}$$

$$e^{-d_1(y_1+y_3)}(1-e^{-d_2(y_2+y_3)})(1-p_d)y_0+[(1-p_d)e^{-d_1(y_1+y_3)}-1]y_2=0 \tag{5.3}$$

$$(1-e^{-d_1(y_1+y_3)})(1-e^{-d_2(y_2+y_3)})(1-p_d)y_0+(1-p_d)(1-e^{-d_2(y_2+y_3)})y_1$$

$$+(1-e^{-d_1(y_1+y_3)})(1-p_d)y_2+(p_c p_d-p_c-p_d)y_3=0 . \tag{5.4}$$

Define g_0, g_1, g_2, and $g_3: X \to \Re$ to be the left side of (5.1), (5.2), (5.3) and (5.4), respectively. The behavior of a solution of (4.2) in X is determined only by the sign of the functions g_i. So if $g_i<0$, the corresponding variable decreases over time, and if $g_i>0$, it increases in time. Finally if $g_i=0$, the corresponding variable does not change. The same can be said about g_1+g_3, and g_2+g_3, which describe the changes in frequency of species 1 and 2, respectively.

Because species one is not affected by species two, its equilibrial frequency depends only on the parameters p_d and d_1, as in the one-species model. The following lemma states this more precisely.

Lemma 1 Let $y(t)=(y_0(t), y_1(t), y_2(t), y_3(t))$ be the solution of (4.2) with initial condition $(y_0(0), y_1(0), y_2(0), y_3(0))$.

(i) If $d_1 \leq \dfrac{p_d}{1-p_d}$, then $f_1(t)=y_1(t)+y_3(t)$ decreases monotonically to 0 as $t \to \infty$.

(ii) If $d_1 > \dfrac{p_d}{1-p_d}$ and $y_1(0)+y_3(0) \neq 0$, then $f_1(t)=y_1(t)+y_3(t) \to S_1$ as $t \to \infty$,

where S_1 is the only positive solution of

$$(1-e^{-d_1 y})(1-p_d)(1-y)-p_d y=0 .$$

(Note the similarity to (3.5).)

Proof. The behavior of $y_1(t)+y_3(t)$ is determined by the sign of

$$g_1(y_0, y_1, y_2, y_3)+g_3(y_0, y_1, y_2, y_3)=(1-p_d)(1-e^{-d_1(y_1+y_3)})(y_0+y_2)-p_d(y_1+y_3)$$

$$=(1-p_d)(1-e^{-d_1(y_1+y_3)})(1-(y_1+y_3))-p_d(y_1+y_3)$$

$$=:h(y_1+y_3) .$$

As in the one-species model, h is a concave function such that $h(0)=0$ and $h(1)<0$. Therefore the existence of a point S_1 in $(0,1)$ such that $h(S_1)=0$ is equivalent to

$$(1-p_d)d-p_d=h'(0)>0 .$$

Moreover h is positive in $(0, S_1)$ and negative in $(S_1, 1]$.   □

Species two is eliminated locally by the winning species one. Consequently, for species two to persist at equilibrium, it is not always enough that $d_2>p_d/(1-p_d)$, as would be enough if species one were absent or did not compete with species two. Rather, the dispersal coefficient d_2 of species two must exceed a certain function $\Phi(d_1)$ (illustrated in Fig. 1) that may exceed $p_d/(1-p_d)$, and even so the equilibrial frequency of species two may be lower than it would be in the absence of competition from species one. All this is stated more precisely in the following lemma.
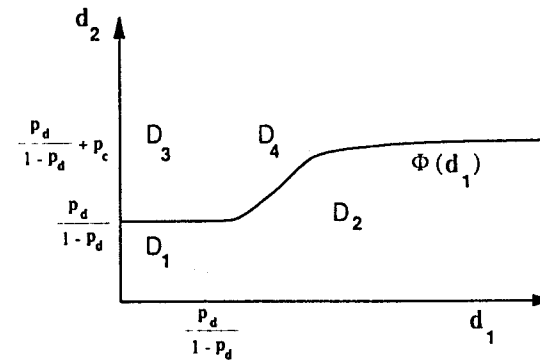

Fig. 1.

Lemma 2 There is a continuous function (illustrated in Fig. 1)

$$\Phi: [0,\infty) \to \left[\frac{p_d}{1-p_d}, \frac{p_d}{1-p_d}+p_c\right)$$

such that:

(i) $\Phi(x)=\dfrac{p_d}{1-p_d}$ for $x\in \left[0, \dfrac{p_d}{1-p_d}\right]$

(ii) $\Phi(x)$ is monotonically increasing for $x>\dfrac{p_d}{1-p_d}$

(iii) $\lim\limits_{x\to\infty} \Phi(x)=\dfrac{p_d}{1-p_d}+p_c .$

Define $(y_0(t), y_1(t), y_2(t), y_3(t))$ to be the solution of (4.2) with initial condition $(y_0(0), y_1(0), y_2(0), y_3(0))$.

(iv) If $d_2 \leq \Phi(d_1)$, then $f_2(t)=y_2(t)+y_3(t) \to 0$ as $t\to\infty$.

(v) If $d_2 > \Phi(d_1)$ and $y_2(0)+y_3(0) \neq 0$, then $f_2(t)=y_2(t)+y_3(t) \to \tilde{S}_2$, with $\tilde{S}_2=\tilde{S}_2(p_d, p_c, d_1) \leq S_2 ,$

where S_2 is the only positive solution of $(1-e^{-d_2 y})(1-p_d)(1-y)-p_d y=0$. Moreover, $\tilde{S}_2=S_2$ if and only if $d_1 \leqq \dfrac{p_d}{1-p_d}$ or $p_c=0$.
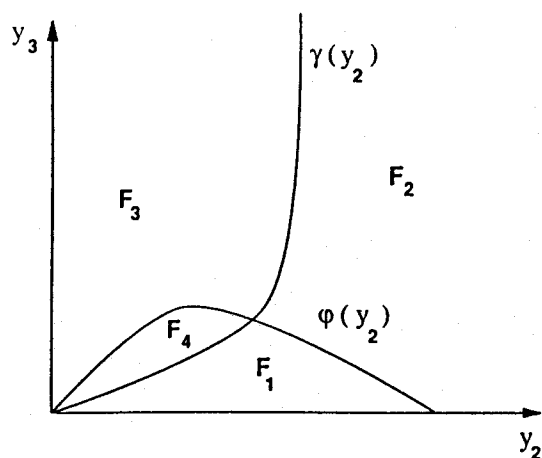

Fig. 2.

Proof. From Lemma 1, we know that $f_1(t)=y_1(t)+y_3(t)\to S_1$ as $t\to\infty$. Therefore we will concentrate first on the set

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

On this set, according to Lemma 1

$$e^{d_1 S_1}=\frac{(1-p_d)(1-S_1)}{1-S_1-p_d} . \tag{5.5}$$

The first goal is to show that there is 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. (It may help to refer to Fig. 2.) γ is obtained by substituting (5.5) in (5.3) and solving for y_3. So

$$y_3=\gamma(y_2):=\frac{1}{d_2}\ln\frac{(1-S_1-p_d)(1-S_1-y_2)}{(1-S_1)(1-S_1-p_d-y_2)}-y_2 \tag{5.6}$$

which is well defined for $0\leqq y_2<1-S_1-p_d$, where it is a convex function of y_2.

For the rest of the proof $\gamma'(0)$ will play an important role. It is given by

$$\gamma'(0)=\frac{p_d}{d_2(1-S_1)(1-S_1-p_d)}-1 . \tag{5.7}$$

Since y_2 decreases below γ, it follows that $y_2(t)\to0$ as $t\to\infty$ whenever $y_3(t)\to0$ and $\gamma'(0)>0$. Such is the case if

$$d_2\leqq\frac{p_d}{1-p_d} \quad\text{and}\quad d_1\leqq\frac{p_d}{1-p_d} ,$$

which proves (iv) for those values of d_1.

Reversing the conditions on $\gamma'(0)$ and d_2, (v) is proved for $d_1 \leqq \dfrac{p_d}{1-p_d}$ by observing that $\gamma'(0)<0$ and $y_1(t)+y_3(t)\to0$ as $t\to\infty$ imply that (5.6) transforms into the equation given in (v).

Now we turn to the case $d_2>\dfrac{p_d}{1-p_d}$.

For a non-trivial fixed point of (4.2) to exist it is necessary that γ intersects the set defined by

$$G=\{(y_0, y_1, y_2, y_3)\in S | g_2(y_0, y_1, y_2, y_3)+g_3(y_0, y_1, y_2, y_3)=0\}$$

in a point with a positive fourth coordinate.

G does not depend on either y_0 or y_1, and is given by points $y\in S$ whose third and fourth coordinates satisfy

$$(1-p_d)(1-e^{-d_2(y_2+y_3)})(1-y_2-y_3)-p_d(y_2+y_3)-p_c(1-p_d)y_3=0 \tag{5.8}$$

which defines a function $\varphi(y_2)$ such that

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

This follows from the fact that for positive y_3 the left side of (5.8) is a concave function of y_3 which is nonnegative at 0 whenever its derivative at 0 is nonnegative. After a substitution of the type $y_3=k+ly_2$, with $0\leqq y_2+y_3\leqq1, k, l$ in $\mathfrak{R}$, the left side of (5.8) defines a concave function of y_2. This guarantees that there are at most two values of y_2 that make (5.8) hold true, i.e., φ is concave in that region. The same argument also shows that $\varphi'\geqq-1$, with $\varphi'=-1$ if and only if $p_c=0$. Since for $p_c=0$ the behavior of species two is independent of species one, the proof of Lemma 1 applies to this case, too. Therefore we will assume $p_c>0$ for the rest of the proof.

Additional information on φ can be gained by analyzing special values of the variables. If $y_3=0$, the left side of (5.8) is the same as in the one-species case. Thus it is positive if and only if

$$d_2>\frac{p_d}{1-p_d} .$$

If $y_2=0$, the condition for $\varphi(0)$ to be positive is

$$d_2>\frac{p_d}{1-p_d}+p_c ,$$

and it corresponds to the condition (3.6) in the one-species case with p_d in the numerator replaced by $p_d+p_c(1-p_d)$ and p_e in the denominator replaced by p_d.

In any case $\varphi(y_2)$ is clearly bounded from above.

These observations, the convexity of γ and the concavity of φ prove that for $d_2>\dfrac{p_d}{1-p_d}+p_c, \varphi(0)>0$, and therefore the intersection of the two graphs consists of one point.

The condition for the graphs of γ and φ to intersect, when $\varphi(0)=0$, is $\gamma'(0)<\varphi'(0)$. Hence the next step is to calculate $\varphi'(0)$.

Constraining (5.8) to straight lines of the form $y_3 = \alpha y_2$, with $\alpha > 0$, and rearranging terms it becomes

$$(1-p_d)(1-e^{-d_2(\alpha+1)y_2})(1-(\alpha+1)y_2) - \left[p_d + \frac{p_c(1-p_d)\alpha}{\alpha+1} \right](\alpha+1)y_2 = 0 . \quad (5.9)$$

This equation has a unique positive solution if and only if

$$d_2(1-p_d) > p_d + \frac{p_c(1-p_d)\alpha}{\alpha+1}$$

or

$$d_2 > \frac{p_d}{1-p_d} + \frac{\alpha p_c}{\alpha+1} .$$

Due to the special form of φ, if $\varphi(0) = 0$ then $\varphi'(0)$ can be calculated by finding the value α for which (5.9) has $y_3 = y_2 = 0$ as a double zero.

Given $d_2 \in \left(\frac{p_d}{1-p_d}, \frac{p_d}{1-p_d} + p_c \right)$, d_2 can be written in a unique way as

$$d_2 = \frac{p_d}{1-p_d} + \beta p_c \qquad (5.10)$$

with β in $(0, 1)$.

For that value, the above calculations show that $\varphi'(0) = \alpha = \frac{\beta}{1-\beta}$, and after solving (5.10) for β and substituting in this equality, we get

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

Finally, the condition $\gamma'(0) < \varphi'(0)$ transforms into

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

or

$$d_2 > \frac{p_d}{1-p_d} \cdot \frac{p_d+(1-p_d)p_c}{p_d+(1-S_1)(1-S_1-p_d)p_c} =: \mu(p_d, p_c, S_1) .$$

Since S_1 is an increasing continuous function of d_1, and μ is an increasing continuous function of S_1, we define

$$\Phi(d_1) := \mu(p_d, p_c, S_1) .$$

This definition satisfies (i), (ii) and (iii) of the lemma. For $d_1 \leqq \frac{p_d}{1-p_d}$, (iv) and (v) were proved above. For $d_1 < \frac{p_d}{1-p_d}$, the definition of Φ guarantees that $d_2 \leqq \Phi(d_1)$ implies γ and φ do not intersect. This in turn implies that $y_2(t)$ decreases whenever $y_2(t) + y_3(t)$ increases, which proves $y_2(t) \to 0$ as $t \to \infty$.

The final step in the proof of the lemma will be to show that if $d_2 > \Phi(d_1)$, i.e., if γ and φ intersect, then as $t \to \infty$ every solution of (4.2) with initial condition $(y_0(0), y_1(0), y_2(0), y_3(0)) \in S$ such that $y_2(0) + y_3(0) \neq 0$ tends to $\bar{y} = (\bar{y}_1, \bar{y}_2, \bar{y}_3, \bar{y}_4)$, the intersection of γ and φ.

Define the following subsets of S, as shown in Fig. 2:

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

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

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

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

Any solution of (4.2) starting in F_3 will eventually reach either γ or φ. In the former case there is a t_1 such that $y_3(t_1) = \gamma(y_2(t_1))$. Further we can assume $y_3(t_1) > \varphi(y_2(t_1))$; otherwise $y_2(t_1) = \bar{y}_2$ and $y_3(t_1) = \bar{y}_3$. From the definitions of γ and φ we have that just after t_1, $y_2(t) + y_3(t)$ decreases and $y_2(t)$ remains constant, which implies that the solution of (4.2) enters F_2.

On the other hand, if the solution of (4.2) with initial condition in F_3 reaches φ, i.e., if $y_3(t_1) = \varphi(y_2(y_1))$, then the definitions of γ and φ and the fact that $\varphi' > -1$ imply that just after t_1, $y_2(t) + y_3(t)$ remains constant, while $y_2(t)$ increases. This implies that $y(t)$ enters F_4.

A similar argument shows that any solution of (4.2) starting in F_1 eventually enters F_4 or F_2 (or tends to $\bar{y}$).

Finally, the definitions of γ and φ imply that any solution of (4.2) starting in F_2 or F_4 remains there, and tends to $\bar{y}$.

Since $\varphi' > -1$ and $y_2 = S_2$ is the only positive root of φ $\left(\text{when } d_2 > \frac{p_d}{1-p_d} \right)$, it follows that $\tilde{S}_2 = \bar{y}_2 + \bar{y}_3 \leqq S_2$. Moreover $\tilde{S}_2 = S_2$ if and only if $\bar{y}_3 = 0$ and $d_2 > \frac{p_d}{1-p_d}$. $\qquad \square$

For fixed $p_d \in [0, 1)$, $p_c \in [0, 1]$ consider now the four regions described in Fig. 1, i.e.,

$$D_1 = \left\{ (d_1, d_2) \in \mathfrak{R}^2 \,\Big|\, 0 \leqq d_1 \leqq \frac{p_d}{1-p_d}, \, 0 \leqq d_2 \leqq \frac{p_d}{1-p_d} \right\}$$

$$D_2 = \left\{ (d_1, d_2) \in \mathfrak{R}^2 \,\Big|\, d_1 > \frac{p_d}{1-p_d}, \, 0 \leqq d_2 \leqq \Phi(d_1) \right\}$$

$$D_3 = \left\{ (d_1, d_2) \in \mathfrak{R}^2 \,\Big|\, 0 \leqq d_1 \leqq \frac{p_d}{1-p_d}, \, d_2 > \frac{p_d}{1-p_d} \right\}$$

$$D_4 = \left\{ (d_1, d_2) \in \mathfrak{R}^2 \,\Big|\, d_1 > \frac{p_d}{1-p_d}, \, d_2 > \Phi(d_1) \right\} .$$

The behavior of the solutions of (4.2) can be summarized:

Theorem 3 *Let $p_d \in [0, 1)$ and $p_c \in [0, 1]$. Further, let $y(t) = (y_0(t), y_1(t), y_2(t), y_3(t))$ be the solution of (4.2) with initial condition $y_0 = (y_0(0), y_1(0), y_2(0), y_3(0))$.*

(i) If $(d_1, d_2) \in D_1$, then $(1, 0, 0, 0)$ is the only stationary solution of (4.2) in X and it is globally stable, i.e., $y(t) \to (1, 0, 0, 0)$ as $t \to \infty$, for every initial condition in X.

(ii) *If* $(d_1, d_2) \in D_2$, *then* (4.2) *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* $y(t) \to (1 - S_1, S_1, 0, 0)$ *as* $t \to \infty$. (*If* $d_2 \leq \dfrac{p_d}{1 - p_d}$, *then* $S_2 = 0$ *and the first two stationary solutions coincide.*)

(iii) *If* $(d_1, d_2) \in D_3$, *then* (4.2) *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* $y(t) \to (1 - S_2, 0, S_2, 0)$ *as* $t \to \infty$.

(iv) *If* $(d_1, d_2) \in D_4$, *then* (4.2) *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* $(1 - \bar{y}_1 - \bar{y}_2 - \bar{y}_3, \bar{y}_1, \bar{y}_2, \bar{y}_3)$, *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* $y(t) \to (1 - \bar{y}_1 - \bar{y}_2 - \bar{y}_3, \bar{y}_1, \bar{y}_2, \bar{y}_3)$ *where* $\bar{y}_1 + \bar{y}_3 = S_1$ *and* $\bar{y}_2 + \bar{y}_3 \leq S_2$. $\bar{y}_2 + \bar{y}_3 = S_2$ *only if* $p_c = 0$.

6 Discussion

Theorem 3 gives exact conditions for the coexistence of competing species that would not be present simultaneously in undisturbed environments. It proves, for the first time we believe, that disturbances allow the coexistence of competing species, thereby increasing the species diversity of ecosystems.

Although Theorem 3 is stated for the two-species model, an important generalization of it that includes one leader or keystone species and $n - 1$ fugitive species can be proved in the same way. Lemma 1 shows that the dynamics of species one is not affected by species two. So if any other interaction among the $n - 1$ fugitive species is neglected, the generalization to the n species model can be proved separately for each fugitive species by dealing in each step only with the frequency of the keystone species and the frequency of the single species.

Theorem 3 also explains why species diversity is maximized at intermediate levels of disturbance. As can be seen from the conditions for the existence of non-trivial equilibrium points, if p_d tends to 1, D_1 blows up to include the whole positive quadrant, i.e., for p_d near 1 it is likely that both species become extinct. Pollution and overgrazing are examples of perturbations with high frequencies (values of p_d close to 1), and Theorem 3 explains how they can lead to biotic impoverishment.

On the other hand, for small values of p_d, S_1 tends to 1, i.e., almost all patches will eventually be occupied by species one. Once species one reaches a high level of occupancy, species two will have to live under almost continuous competition, being eventually eliminated whenever it meets species one. Even though species two is theoretically still able to sustain a positive level of occupancy, that level will be very small, so it is likely to become extinct due to any additional disturbance. Since the number of fugitive species in an ecosystem can be very high, eliminating natural disturbances like fire can cause a notable decrease in species diversity.

Once the winning species has reached its equilibrial level, the winner affects the loser in the same way as an abiotic disturbance of the loser's survival. So the presence of a competitor or a predator is quantitatively equivalent to a higher frequency of abiotic disturbances of survival at equilibrium.

The one-species model shows that there are two distinct kinds of disturbances, with distinct effects. One kind of disturbance, occurring with probability p_d, affects persistence; the other kind, occurring with probability p_c, interferes with colonization. The effect on the equilibrium species frequency of disturbances of persistence is strictly limited compared to the much stronger effect, proportional to $1/(1 - p_c)$, of disturbances of colonization. Future work will explore whether there are analogous results in a two-species model that allows for competition that affects colonization. (The present two-species model considers competition that affects persistence, through the parameter p_c, but does not consider competition that affects colonization.) Extensive numerical simulation of a two-species model with two kinds of competition, that affecting persistence and that affecting colonization, suggests that competition that affects colonization has a qualitatively different effect on equilibrial species frequencies from that of competition affecting persistence after colonization.

There are some important differences between the two-species model here and the one studied by Caswell and Cohen (1990, 1991). They assume disturbances do not affect empty patches, which leads to a different first column in (4.3). The first column in their model is

$$
\begin{pmatrix}
(1 - C_1)(1 - C_2) \\
C_1(1 - C_2) \\
(1 - C_1)C_2 \\
C_1 C_2
\end{pmatrix}.
$$

Further, they assume that species two is not able to colonize after species one. That assumption, which is a plausible interpretation of the meaning of competitive exclusion, but not the only plausible interpretation, makes their last entry in the second column equal to zero. Because disturbances do not affect empty patches but do affect patches occupied by any individual, regardless of the species (as is the case of disturbances induced by occupancy, such as predation or forest fires), it follows that the presence of species two reduces the probability of colonization by species one, thereby reducing species one's equilibrial frequency in the model of Caswell and Cohen. In particular, Lemma 1 does not apply to their model, and therefore the analysis of the system cannot be reduced to the study of the dynamics in a plane as in Lemma 2.

Even though a zero in the last entry of the second column of A_y makes A_y look simpler, the actual dynamics are more complex. The only way to make G and (5.8) independent of y_1 is to have $(y_0 + y_1)$ as a factor in $g_2 + g_3$, in order to replace it by $1 - y_2 - y_3$. This replacement is not possible in the Caswell–Cohen model.

References

Acevedo, M. F.: On Horn's Markovian model of forest dynamics with particular reference to tropical forest. Theor. Popul. Biol. **19**, 230–250 (1981)

Caswell, H., Cohen, J. E.: Communities in patchy environments: a model of disturbance, competition, and heterogeneity. In: Kolasa, J. (ed.) Ecological Heterogeneity. Berlin Heidelberg New York: Springer 1990

Caswell, H., Cohen, J. E.: Disturbance and diversity in metapopulations. Biol. J. Linn. Soc. 42, 193–218 (1991)

Chesson, P.: Coexistence of competitors in spatially and temporally varying environments: a look at the combined effect of different sorts of variability. Theor. Popul. Biol. 28, 263–287 (1985)

Connell, J. H.: Diversity in tropical rain forest and coral reefs. Science 199, 1302–1310 (1978).

Connell, J. H., Slatyer, R. O.: Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144 (1977)

Dayton, P. K., Hessler, R. R.: Role of biological disturbance in maintaining diversity in the deep sea. Deep-Sea Res. 19, 199–208 (1972)

Grassle, J. F., Sanders, H. L.: Life histories and the role of disturbance. Deep-Sea Res. 20, 643–659 (1973)

Hanski, I.: Coexistence of competitors in patchy environment. Ecology 64, 493–500 (1983)

Harper, J. L.: The role of predation in vegetational diversity. Brookhaven Symp. Biol. 22, 48–62 (1969)

Harper, J. L.: Population Biology of Plants. London, England: Academic Press 1977

Hastings, A.: Disturbance, coexistence, history and competition for space. Theor. Popul. Biol. 18, 363–373 (1980)

Horn, H. S., MacArthur, R. H.: Competition among fugitive species in a harlequin environment. Ecology 53, 749–752 (1972)

Huston, M.: A general hypothesis of species diversity. Am. Nat. 113, 81–101 (1979)

Hutchinson, G. E.: Copepodology for the ornithologist. Ecology 32, 571–577 (1951)

Levin, S. A.: Dispersion and population interactions. Am. Nat. 108, 207–228 (1974)

MacArthur, R. H., Wilson, E. O.: The theory of island biogeography. Princeton, NJ: Princeton University Press 1967

Pacala, S.: Neighborhood models of plant population dynamics. III. Models with heterogeneity in the physical environment. Theor. Popul. Biol. 31, 359–392 (1987)

Palmer, A. R., Strathmann, R. R.: Scale of dispersal in varying environments and its implications for life-histories of marine invertebrates. Oecologia 48, 308–318 (1981)

Ricklefs, R. E.: Community diversity: relative roles of local and regional processes. Science 235, 167–171 (1987)

Shmida, A., Ellner, S.: Coexistence of plant species with similar niches. Vegetatio 58, 29–55 (1984)

Slatkin, M.: Competition and regional coexistence. Ecology 55, 128–134 (1974)