



# Habitat Destruction and Competitive Coexistence in Spatially Explicit Models with Local Interactions

CLAUDIA NEUHAUSER

*School of Mathematics, University of Minnesota, 206 Church Street, S. E., Minneapolis, MN55455, USA*

*(Received on 5 September 1997, Accepted 16 March 1998)*

We investigate the competition–colonization trade-off in a two-species competition model in various heterogeneous environments. The competitiveness of species is hierarchically ordered and the dynamics of the model are described by spatially local interactions of individuals. The size of the local neighborhood may depend on the species. The habitat consists of inhabitable and permanently destroyed sites. It was previously observed (Nee & May, 1992; Tilman *et al.*, 1994, 1997) that destruction of habitat may aid the inferior species and cause the superior species to go extinct. These conclusions were based on an  $n$ -species model in which the spatial arrangement of destroyed sites was ignored. We examine the effects of different spatial arrangements of destroyed sites on survival and coexistence of the two species. We conclude that the spatial arrangement plays an important role and can influence the outcome qualitatively and quantitatively. The key quantity for predicting the outcome of habitat destruction on species survival is the relationship between the mean dispersal distance and the mean distance between inhabitable and destroyed sites. We contrast the hierarchical model with a version of the Lotka–Volterra model of interspecific competition and show that habitat destruction can alter the dominance relationship between species by reducing intraspecific competition.

© 1998 Academic Press

## 1. Introduction

Recently, Nee & May (1992) and Tilman *et al.* (1994, 1997) investigated the effects of habitat destruction on species abundance in a multi-species metapopulation model. In their model species were hierarchically ordered according to their competitive ability. A trade-off between dispersal and competitive ability facilitated persistence of inferior competitors in the presence of the superior competitor. Nee & May (1992) focused their investigation on the effects on equilibrium abundance when a fixed proportion of sites was randomly destroyed. They studied the case of two competing species and concluded that such habitat destruction decreases the abundance of the superior competitor and may actually increase the number of sites occupied by the inferior competitor. Tilman *et al.* (1994, 1997) generalized the two-species model to an  $n$ -species hierarchical model with the same type of habitat destruction and obtained the

rather surprising result that the different species suffer from habitat destruction in the order of their competitiveness; that is, species become extinct in order from best to poorest competitor as habitat destruction increases.

A potential shortcoming in the analysis of both Tilman *et al.* (1994) and Nee & May (1992) is that the spatial arrangement of destroyed sites was completely ignored. In this paper we will argue that the spatial arrangement of destroyed sites plays a crucial role in the outcome of competition. Specifically, the outcome of competition will depend strongly on the average number of offspring produced and the relation between dispersal distance and the distance between inhabitable sites. Furthermore, we will give an argument which will elucidate the somewhat surprising effects of habitat destruction on regional abundance of species observed in Tilman *et al.* (1994). In addition, we will discuss a version of the

Lotka–Volterra model of interspecific competition in which a different mechanism causes a change in competitiveness as habitat destruction increases.

In the theoretical papers cited above, the analysis is based on a simple extension of Levins' (1969) metapopulation model to a multi-species metapopulation model in which the habitat is divided into patches. In Tilman's formulation each patch can be occupied by at most one individual and individuals can disperse randomly among all patches. Species are ordered from best (species 1) to poorest competitor. The dynamics for species  $i$  are described by the following equation in which  $p_i$  denotes the proportion of sites that are occupied by species  $i$ .

$$\frac{dp_i}{dt} = c_i p_i (1 - D - \sum_{j=1}^i p_j) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j. \quad (1)$$

We refer to this equation as the mean-field equation. The coefficient  $c_i$  describes the colonization rate of species  $i$  and  $m_i$  describes the mortality rate of species  $i$ . A fraction  $D$  of the sites are permanently destroyed. (Destroyed sites can never be occupied). The first term on the right-hand side of (1) thus describes the colonization of inhabitable sites which are either vacant or occupied by an inferior species. The second term describes the mortality of species  $i$ . The third term describes the invasion of superior competitors into patches occupied by species  $i$ , which results in the death of species  $i$  upon invasion. Hastings (1980) studied (1) when  $D = 0$ . There,  $m_i$  was interpreted as a disturbance rate independent of  $i$ . The equilibrium densities are given by

$$\hat{p}_i = 1 - D - \frac{m_i}{c_i} - \sum_{j=1}^{i-1} \hat{p}_j \left(1 + \frac{c_j}{c_i}\right). \quad (2)$$

We restrict ourselves to either the single-species or the two-species case since all effects we wish to discuss can already be seen in these two cases. In the two-species case (2) yields

$$\begin{aligned} \hat{p}_1 &= 1 - D - \frac{m_1}{c_1} \\ \hat{p}_2 &= \frac{m_1}{c_2} - (1 - D) \frac{c_1}{c_2} - \frac{m_2}{c_2} + \frac{m_1}{c_1} \end{aligned} \quad (3)$$

Nee & May (1992) concluded from (3) that habitat destruction decreases the regional abundance of the superior competitor but increases the number of sites occupied by the inferior competitor; that is, the inferior competitor may actually gain from habitat destruction. This was also observed in Tilman *et al.* (1994) in the general  $n$ -species case. Tilman *et al.*

(1994) went further in their analysis and concluded that species become extinct in the order of their competitive ranking, from the best to the poorest competitor, as habitat destruction increases. Their 1994 analysis also showed that the effects of habitat destruction are most severe on the dominant species, namely, if a proportion  $D$  of sites is destroyed, the equilibrium density of the dominant species decreases by the same amount  $D$  compared with the equilibrium density in an environment without destroyed sites. That is, it appears as if exactly those sites were destroyed that were occupied by the dominant competitor. These conclusions are robust, holding for a large class of models (Tilman *et al.*, 1997). Spatially explicit simulations where habitat was destroyed in a checkerboard pattern, showed that there was no qualitative difference in the sense that species still went extinct in the order from best to poorest competitor as long as their monoculture equilibrium abundances in an intact habitat were ordered such that equilibrium abundance decreased from the poorest competitor to the best competitor. The spatially explicit simulations were carried out for both global and local dispersal. In the case of local dispersal, all species had the same dispersal neighborhood.

The paper is organized as follows: we introduce a spatially explicit hierarchical model with three different patterns of habitat destruction. We first discuss the single-species model, followed by the two-species model. We conclude with a discussion of the effects of habitat destruction on the competitive outcome in the two-species Lotka–Volterra model of interspecific competition. Throughout this paper, we restrict our discussion to the biologically most relevant two-dimensional case. Most results can be easily generalized to higher dimensions. All proofs are relegated to the Appendix.

## 2. The Model

We begin with introducing three heterogeneous environments which are defined on the two-dimensional integer square lattice. We designate sites as either permanently destroyed or inhabitable and consider the following three environments in which the fraction of destroyed sites is always  $D$  but the spatial arrangement of destroyed sites varies.

(I) We designate each site independently as being destroyed with probability  $D$  and inhabitable with probability  $1 - D$  [see Fig. 1(a)].

(II) We tile the square lattice into  $L \times L$  squares as shown in Fig. 1(b). Each square is independently designated as being destroyed with probability  $D$  and

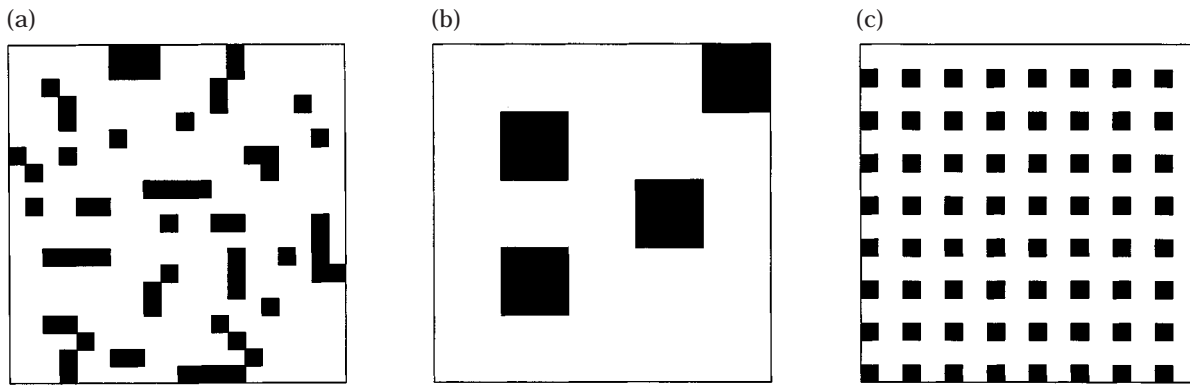


FIG. 1. Examples for the three environments. Solid black squares are destroyed sites. In each case, 16% of the environment is destroyed. See text for further explanation.

inhabitable with probability  $1 - D$ . In an inhabitable square, all sites are inhabitable; in a destroyed square, all sites are destroyed.

(III) We tile the square lattice into  $L \times L$  squares. In each square, we destroy all sites in a  $K \times K$  square whose lower left corner coincides with the lower left corner of the  $L \times L$  square. We choose  $L$  and  $K$  so that  $(K/L)^2 = D$ . See Fig. 1(c) for an illustration.

We define the two-species model as a continuous time Markov process. Each site of the two-dimensional integer square lattice is in one of the four states 0, 1, 2 or  $\Delta$ . If a site is in state 0, we say the site is vacant and inhabitable; if a site is in state 1, we say that the site is occupied by species 1, the superior competitor; if it is in state 2, we say it is occupied by species 2, the inferior competitor; the state  $\Delta$  denotes a destroyed site. Whether or not a site is destroyed will be determined at time 0 and then held fixed for the remainder of the time. Destroyed sites are never occupied. Below, when we say that an event occurs at rate  $\lambda$ , we mean that the times  $\tau_i$  between successive occurrences have an exponential distribution with parameter  $\lambda$ , that is,  $P(\tau_i \leq t) = 1 - e^{-\lambda t}$ . The dynamics are as follows:

(i) if a site is in state 1 (respectively, 2), the individual at this site gives birth to an offspring of the same type at rate  $\lambda_1$  (respectively,  $\lambda_2$ );

(ii) an offspring of type  $i$  lands on a site uniformly chosen from the set  $x + \mathcal{N}_i$  where  $\mathcal{N}_i$  is either a box of radius  $M_i$  or consists of the four nearest neighboring sites. The radius  $M_i$  is the species specific dispersal range. If the offspring is of type 1, it can colonize the chosen site if the site is inhabitable and either vacant or occupied by species 2. In the latter case, species 1 replaces species 2. If the offspring is of type 2, it can only colonize the chosen site if it is inhabitable and vacant. Invasions of destroyed sites

are always unsuccessful. Whenever a colonization attempt is unsuccessful, the invading individual dies;

(iii) if a site is either in state 1 or 2, then the site becomes vacant (i.e. it becomes a 0) at rate 1.

That is, the superior competitor gives birth at rate  $\lambda_1$  and sends its offspring to a site chosen at random from its neighborhood. Offspring of species 1 can invade vacant sites or sites occupied by the inferior competitor (species 2). The inferior competitor gives birth at rate  $\lambda_2$  and sends its offspring to a site chosen at random from its neighborhood. Offspring of the inferior competitor can only invade vacant sites. If an offspring tries to invade a destroyed site, the invasion will be unsuccessful and the offspring dies. In addition, individuals experience a density-independent death rate, which is the same for both species. (Setting the death rates equal to each other simplifies the analysis. The specific choice for the death rate, namely 1, fixes the time scale). Note that there is at most one individual present at each site. The connection with the model introduced in eqn (1) is thus  $m_1 = m_2 = 1$ ,  $c_1 = \lambda_1$  and  $c_2 = \lambda_2$ .

We choose the dispersal kernel to be uniform over the dispersal neighborhood. This is the mathematically simplest case. Biologically more realistic kernels will produce qualitatively similar results as long as the dispersal kernel has a finite maximum range. The dispersal kernels of the two species are typically chosen so that the dispersal range of the inferior competitor is at least as large as the dispersal range of the superior competitor. A large range can make the inferior competitor a better colonizer (at least in undestroyed habitats). This mechanism is referred to as the competition-colonization trade-off. Below we will see that depending on the geometry of habitat destruction this mechanism might not be a good strategy for the inferior competitor.

The model is defined on infinite space and our results are stated as equilibrium results, i.e. technically speaking, these results hold in the limit as time tends to infinity. In biological applications one is of course interested in finite space and a finite time horizon. Below we will point out when the finite system at finite times can be compared with the equilibrium of the infinite system.

The single-species model obtained by simply assuming that there is only one species present initially, is known as the basic contact process in a heterogeneous environment. The basic contact process in a homogeneous environment was introduced by Harris (1974) and has been studied extensively in both homogeneous and inhomogeneous environments (see Liggett, 1985; Durrett, 1988, 1995; or Durrett & Levin, 1994 for a list of references on the homogeneous contact process; the heterogeneous contact process was studied, e.g. in Liggett, 1991, 1992; Klein, 1994; or Madras *et al.*, 1994). The two-species process in a homogeneous environment was studied by Durrett & Swindle (1991) and Durrett & Schinazi (1993). It is a spatial analogue of the two-species competition metapopulation in Nee & May (1992).

### 2.1. THE SINGLE-SPECIES MODEL

Since the superior competitor is unaffected by the inferior competitor, the single-species model in which just the superior competitor is present suffices to illustrate the effects of different spatial patterns of habitat destruction on the abundance of the superior competitor. Furthermore, it should explain the somewhat surprising phenomenon that destroying a fixed proportion of the habitat seems to have the same effect as destroying precisely the fixed proportion of sites that are actually occupied by the species. We will therefore begin with investigating the single-species model.

In the case  $D = 0$ , Harris (1974) showed that there exists a non-trivial critical value so that if  $\lambda_1$  exceeds this critical value, the process has a positive probability of survival, whereas if  $\lambda_1$  is less than the critical value, the population dies out. [Bezuidenhout & Grimmett (1990) showed that the process dies out at the critical value]. Bramson *et al.* (1989) investigated the  $d$ -dimensional long range contact process; they showed that the critical value converges to 1 as the range goes to infinity and gave rates of convergence. Numerical results by Brower *et al.* (1978) and Grassberger & de la Torre (1979) indicate that the critical value for the nearest neighbor case in two dimensions is approximately 1.648 and in one dimension approximately 3.299.

Our first result discusses the effects of the different environments on survival in the single-species model. In order to do this, we need to define two-dimensional site percolation on the two-dimensional integer square lattice (see, e.g. Durrett, 1988). This process is a collection of independent random variables with values in  $\{0, 1\}$  that indicate whether a site in the two-dimensional integer lattice is open (1) or closed (0). A site is open with probability  $p$  and closed with probability  $1 - p$ . Let  $\mathcal{M}_q$ ,  $q = 1$  or  $2$ , be the neighborhood set of 0 such that  $\mathcal{M}_1$  is the neighborhood for the four nearest neighbors and  $\mathcal{M}_2$  is the neighborhood for the eight nearest neighbors. For two sites  $x, y$  in the two-dimensional integer square lattice, we say that  $y$  can be reached from  $x$  ( $x \rightarrow y$ ) if there is an *open path* from  $x$  to  $y$ ; that is, there is a sequence  $x_0 = x, x_1, \dots, x_n = y$  of open sites such that for each  $m \leq n$ ,  $x_{m-1} - x_m \in \mathcal{M}_q$ ,  $q = 1$  or  $2$ . We denote by  $C_0^q = \{x: 0 \rightarrow x\}$  the cluster of open sites containing 0 when the neighborhood structure is given by  $\mathcal{M}_q$ . (Note that in the definition of  $C_0^q$  we require 0 to be open). We can define the critical probability for  $q = 1$  or  $2$ ,

$$p_{c,q} = \inf\{p: P(|C_0^q| = \infty) > 0\}.$$

Above the critical value, percolation occurs, that is, there is an infinite cluster of open sites. Below the critical value, only finite clusters of open sites occur. Note that  $p_{c,1} \geq p_{c,2}$ . Numerical investigations indicate that  $p_{c,1} \approx 0.5923$  (Djordjevic *et al.*, 1982).

Let us start by considering environment I in which sites are independently designated as destroyed with probability  $D$  and inhabitable with probability  $1 - D$ . The case where  $M_1$  is very large can be approximated by the mean-field eqn (1). The equilibrium proportion of abundance of species 1 in the mean-field model is

$$\hat{p}_1 = \begin{cases} 1 - D - \frac{1}{\lambda_1} & \text{if } D \leq 1 - \frac{1}{\lambda_1} \\ 0 & \text{if } D \geq 1 - \frac{1}{\lambda_1} \end{cases} \quad (4)$$

We thus obtain the following results for the long range case whose proofs can be found in the Appendix. If  $D < 1 - 1/\lambda_1$ , there exists a non-trivial equilibrium for  $M_1$  sufficiently large, in which the density of 1's is close to  $1 - D - 1/\lambda_1$ . If  $D > 1 - 1/\lambda_1$ , species 1 dies out for  $M_1$  sufficiently large. (Note, for fixed  $\lambda_1$  we first choose  $D$  and then  $M_1$  sufficiently large). That is, the long range model in environment I behaves essentially the same as the metapopulation model considered in Nee & May (1992) and Tilman *et al.* (1994) when  $M_1$  is sufficiently large.

We will contrast the long-range behavior with the case when dispersal is only possible to the four nearest neighboring sites. As long as  $D < 1 - p_{c,1}$ , i.e. the inhabitable sites form an infinite cluster based on the neighborhood set consisting of the four nearest neighboring sites, species 1 can survive provided  $\lambda_1$  exceeds the critical value for the one-dimensional basic contact process with neighborhood set consisting of the two nearest neighbors. We denote this critical value by  $\lambda_c(1)$ . That is, the critical value  $D_c(\lambda_1) = 1 - p_{c,1}$  for  $\lambda_1 \geq \lambda_c(1)$ ; if  $D < D_c(\lambda_1)$ , the process survives, if  $D > D_c(\lambda_1)$ , the process dies out. This was shown in Bramson *et al.* (1991) (see also Kang *et al.*, 1995). We denote the critical value for the two-dimensional basic contact process with neighborhood set consisting of the four nearest neighbors by  $\lambda_c(2)$ . If  $\lambda_1$  is between the critical value for the one-dimensional and the two-dimensional basic contact process, then the critical value  $D_c(\lambda_1)$  is increasing in  $\lambda_1$ . When  $\lambda_1$  is below the critical value for the two-dimensional contact process, then the process dies out regardless of the amount of habitat destruction; that is,  $D_c(\lambda_1) = 0$  for  $\lambda_1 \leq \lambda_c(2)$ . See Fig. 2 for a sketch of the critical curves  $D_c(\lambda_1)$  in the mean-field case and nearest neighbor case. The dashed curve in Fig. 2, i.e.  $D_c(\lambda_1) = 1 - 1/\lambda_1$ , holds strictly speaking only for the mean-field case. When  $M_1$  is very large, however, the critical curve for  $D_c$  is very well approximated by the mean-field curve. The solid curve describes the basic features of the critical curve in the nearest neighbor case. Between  $\lambda_c(2)$  and  $\lambda_c(1)$ , we only know that the curve is monotonically increasing, its exact shape can be obtained by simulations (this was not done in Fig. 2).

The main difference between the nearest neighbor case and the mean-field case is that in the nearest neighbor case, the critical value for the proportion of destroyed sites does not depend on the reproduction rate of the species once the reproduction rate exceeds

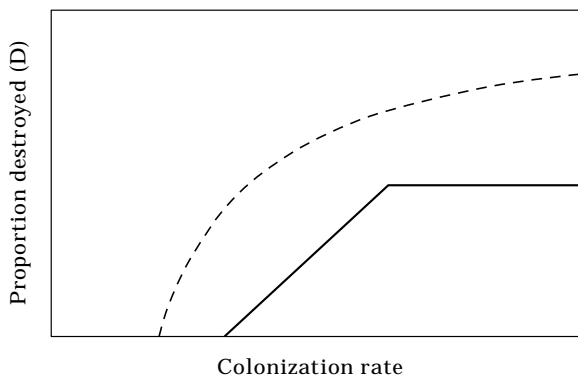


FIG. 2. Critical curves  $D_c(\lambda_1)$  for environment I in the mean-field case (dashed curve) and the nearest neighbor case (solid curve).

$\lambda_c(1)$ , whereas in the mean-field case, the critical value always depends on the reproduction rate [namely,  $D_c(\lambda_1) = 1 - 1/\lambda_1$  in mean-field]. This can be extended to any finite range as follows. For any dispersal range  $M_1$  we can find  $D_0(M_1)$  so that survival is no longer possible for all  $D \geq D_0(M_1)$ , no matter how large  $\lambda_1$  is, simply because all individuals are confined to finite clusters which are prone to stochastic extinction events. (A cluster consists of open sites that can be reached by a dispersing individual). Once a finite cluster is extinct, it cannot be recolonized. That is, contrary to the mean-field case, where a species can always compensate for habitat destruction by increasing its fecundity (or colonization rate)  $\lambda_1$ , in a spatially explicit setting, there is a critical value  $D_0(M_1)$  beyond which the species would inevitably die out, regardless of  $\lambda_1$ . Only an increase in the dispersal range  $M_1$  would enable the species to survive. This illustrates that being a “good disperser” in a spatially explicit habitat can either mean producing a large number of offspring or dispersing over long distances. It depends on the spatial structure of the habitat which strategy is more successful.

Next we consider environment II. Destruction now occurs in  $L \times L$  squares which are randomly distributed as described above. As in the previous case, we will first discuss the long range dispersal case,  $M_1 \gg 1$ , and subsequently contrast it with the nearest neighbor case. The critical curves  $D_c(\lambda_1)$  for both cases are sketched in Fig. 3(a) and 3(b), respectively.

We assume now that  $M_1 \gg 1$ . The critical value of  $\lambda_1$  for survival when  $D = 0$  is then close to 1. If in addition  $L \gg M_1$  as well, then extinction occurs if either  $\lambda_1$  is less than its critical value or if  $D > 1 - p_{c,2}$  [solid curve in Fig. 3(a)]. In the latter case, there is no infinite cluster and hence all individuals are confined to finite clusters of open patches which are again prone to stochastic extinction events as above. (The time to extinction in finite clusters might take a very long time, however). That is, when  $\lambda_1 > 1$  and  $D < 1 - p_{c,2}$ , we can find  $M_1 \gg 1$  and  $L \gg M_1$  so that survival is possible. In this case, the proportional abundance of species 1 in each undestroyed patch, which is accessible to species 1, is close to  $1 - 1/\lambda_1$ . (The proof for this case is sketched in the Appendix). The qualitative part of this argument is valid even if we assume that  $M_1$  is not necessarily much larger than 1 and  $L$  not necessarily much larger than  $M_1$ . In the following we only assume that  $M_1$  is positive and  $L$  is large enough so that most of the time the dispersers stay within the same patch. If  $L$ , the patch length, is above the minimum patch size which is required to sustain a population with high probability, then the qualitative behavior is the same as in the case

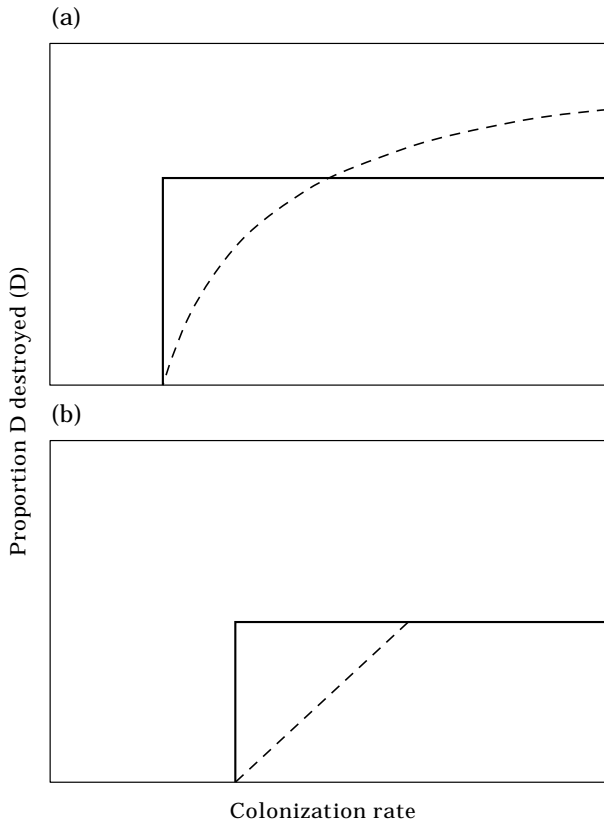


FIG. 3. Critical curves  $D_c(\lambda_1)$  for environment II (a) when  $M_1 \gg 1$  and  $L \gg M_1$  (solid curve) and  $L \ll M_1$  (dashed curve); (b) in the nearest neighbor case and  $L \gg 1$  (solid curve) and  $L = 1$  (dashed curve).

$1 \ll M_1 \ll L$ . Within undestroyed patches the system will essentially behave as if it lived in an undestroyed habitat. The density in the patch is then governed by the local dynamics. There will be quantitative differences if  $M_1$  is small. If  $D < 1 - p_{c,2}$ , survival is possible. If  $D > 1 - p_{c,2}$ , ultimate extinction will occur but the system may survive for a long time. As the patch size gets smaller, relative to the dispersal range, survival in isolated patches will be more difficult. If  $L$ , the patch length, is below the minimum patch size which is required to sustain the population with high probability, then the stochastic extinction events mentioned above become important and the time to extinction of isolated patches will be small. In this case, if  $D < 1 - p_{c,2}$ , survival is possible for  $\lambda_1$  sufficiently large; but if  $D > 1 - p_{c,2}$ , extinction will typically occur on a relatively short time-scale.

We again assume that  $M_1 \gg 1$ , but this time  $L \ll M_1$ . The process now behaves essentially the same way as in environment I when  $M_1 \gg 1$  since a dispersing individual does not see the small scale pattern of the environment but averages over a large number of  $L \times L$  squares. The critical curve  $D_c(\lambda_1)$  is therefore

approximately  $1 - 1/\lambda_1$  [dashed curve in Fig. 3(a)]. (The proof is the same as in the long range case environment I when  $M_1 \gg 1$  and is therefore omitted).

We turn now to the case when dispersal is only allowed to the four nearest neighbors. When  $L = 1$ , this is the same as the nearest neighbor case in environment I [dashed curve in Fig. 3(b)]. When  $L \gg 1$  and  $\lambda_1$  is between the critical value for the two-dimensional and the one-dimensional nearest neighbor contact process, survival is facilitated compared with the case  $L = 1$ . In fact, for  $\lambda_1 > \lambda_c(2)$  and  $D < 1 - p_{c,1}$ , survival is possible provided  $L$  is sufficiently large [solid curve in Fig. 3(b)]. In this case, a percolating cluster of  $L \times L$  squares exist; when  $L \gg 1$ , most individuals in an undestroyed block do not experience the destruction and thus behave as if they lived in an undestroyed two-dimensional habitat. Extinction in these large squares takes a long time and recolonization is possible if the square is contained in the infinite cluster of undestroyed  $L \times L$  squares. Of course, when  $\lambda_1 < \lambda_c(2)$ , the process dies already out when  $D = 0$ .

The third scenario we wish to consider is environment III. This environment illustrates the effect of corridors which have width  $L - K$ . As long as  $M_1$  is much smaller than  $L - K$ , species 1 will not experience much of a reduction in abundance. Even in the extreme case when  $L - K = 1$  and species 1 only disperses to the four nearest neighbors, survival is possible as long as  $\lambda_1$  exceeds twice the critical value for the one-dimensional basic contact process,  $\lambda_c(1)$ . In this case, the suitable habitat consists of one-dimensional corridors and therefore only two out of the four neighboring sites of an undestroyed site are undestroyed. As the dispersal range of species 1 increases relative to  $L - K$ , but remains below  $L$ , more and more offspring are lost in the destroyed patches which reduces the effective birth rate and thus makes it harder for species 1 to survive (see the Appendix for a brief sketch of the proof). As  $M_1$  increases even further, the spatial structure becomes less important since then a dispersing offspring will not experience the fine scale structure of the environment and the behavior can be approximated by the mean field model.

The corridors clearly facilitate survival when  $M_1$  is small compared with  $L - K$ . In this case, a population can tolerate rather high levels of destruction. We wish to point out, however, that for  $D$  close to 1 and  $M_1$  fixed,  $L$  needs to be rather large to ensure survival in the inhabitable corridors of the environment since the width of the corridor needs to be sufficiently large compared with the dispersal range so that most dispersing individuals will not land in the

destroyed habitat. Another way to compensate for the destruction is a sufficiently high birth rate so that even large losses due to dispersal into destroyed patches will not cause extinction.

The above discussion shows that survival/extinction depends strongly on the spatial arrangement of destroyed and undestroyed sites and on the dispersal range. When  $M_1$  is small, a population in environment I behaves fundamentally different from a population in either environment II, when  $L$  is large, or environment III, when  $L$  and  $L - K$  are large. A typical dispersing individual in environment I actually experiences a fraction  $D$  of destroyed sites, whereas in environments II or III, only individuals which live close to destroyed areas experience the heterogeneity of the environment. Most individuals in these cases simply see a homogeneous, undestroyed environment and thus behave as if they lived in a homogeneous, undestroyed environment.

To understand the paradoxical phenomenon mentioned in Tilman *et al.* (1994), we turn to the long-range, one-species model in environment I. I am indebted to Jonathan Dushoff for the following explanation which is adapted from an argument used for the effect of vaccination on disease spread. In equilibrium, the effective birth rate is equal to the death rate. The effective birth rate is the birth rate multiplied by the fraction of available sites. Since the birth rate is  $\lambda_1$  and the death rate is 1, it follows that the fraction of available sites is  $1/\lambda_1$ . This is independent of  $D$ . Thus the reduction in habitable sites (i.e. sites which are occupied or available) must come entirely from the occupied sites.

The analogous reasoning in environment II when  $D < 1 - p_{c,2}$  and  $L \gg M_1 \gg 1$ , yields a different result. The destruction of squares may render undestroyed squares inaccessible. For instance, an undestroyed square which is completely surrounded by destroyed squares cannot be accessed when  $L \gg M_1$ . We denote by  $q$  the fraction of inaccessible sites. The fraction of available sites among the accessible squares (fraction  $1 - q$ ) satisfies

$$\frac{\lambda_1(\# \text{ available sites})}{1 - q} = 1$$

Hence, the number of available sites is equal to  $(1 - q)/\lambda_1$ . The total number of sites which are not occupied, is therefore  $q + (1 - q)/\lambda_1$ . Since

$$q + \frac{1 - q}{\lambda_1} = q \left( 1 - \frac{1}{\lambda_1} \right) - D + D + \frac{1}{\lambda_1}$$

and  $D + 1/\lambda_1$  was the fraction of unoccupied sites (available or destroyed) in environment I, we can find

conditions under which species 1 will do better in environment II compared with environment I. Namely, if the number of occupied sites in environment II exceeds the number of occupied sites in environment I. This occurs when  $q(1 - 1/\lambda_1) - D < 0$ . This can happen when  $\lambda_1 < 1/(1 - p_{c,2})$  since then there will be a window of values for  $D$  where species 1 will go extinct in environment I but will still be able to survive in environment II. By continuity, there will then be smaller values of  $D$  where species 1 can survive in both environments but its density will be higher in environment II. Of course, when  $D > 1 - p_{c,2}$ , extinction ultimately occurs in environment II since individuals live on finite clusters with no possibility of migration between clusters to replenish extinct populations. In this case, species 1 will do better in environment I provided  $\lambda_1 > 1/(1 - D)$ .

To understand the effect of habitat destruction on abundance in the case of short range dispersal, we conducted a spatial simulation of the one-species model in environment I with nearest neighbor dispersal. Our simulations indicate that the proportional abundance of species 1 is a concave down function of the proportion of destroyed sites (see Fig. 4). The following argument might elucidate this observation. As  $D$  tends to 0, most destroyed sites are isolated and since the destroyed sites are randomly distributed, they effectively reduce the birth rate as in the long-range case. As the proportion of destroyed sites increases, the proportional abundance of species 1 decreases at an accelerated rate since more and more undestroyed sites become inaccessible due to destroyed sites completely surrounding them. Since the proportional abundance of species 1 is bounded

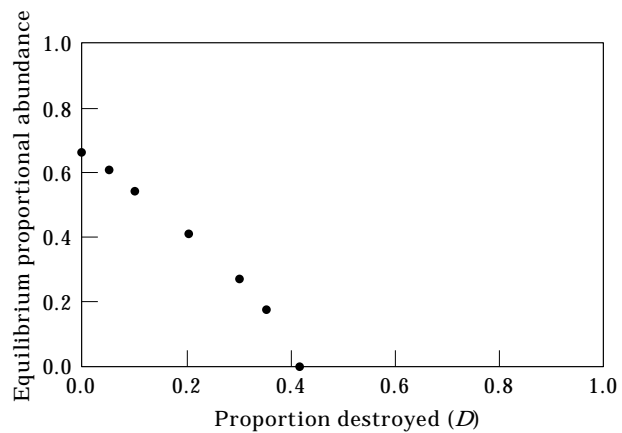


FIG. 4. Equilibrium proportional abundance of species 1 in environment I as a function of the proportion of destroyed habitat ( $D$ ) in the case of nearest neighbor dispersal.

above by the probability that the origin is contained in the infinite lattice, it follows that when  $D = 1 - p_{c,1}$ , the proportional abundance is equal to 0. In other words, the proportional abundance is a continuous function of  $D$ . (This is not clear *a priori* since the proportional abundance could jump, i.e. be discontinuous at the critical value, in which case it would be impossible to have an arbitrarily low density of species 1).

As the discussion above shows, an important quantity, which determines the behavior, is the mean distance from a randomly chosen undestroyed site to the closest destroyed site. We call this quantity the *mean free path* and denote it by  $\mu$ . If  $\mu$  is much larger than the mean dispersal range, such as in environments II and III when the block size  $L$  was large compared with  $M_1$ , then a typical undestroyed site will see a neighborhood of mostly undestroyed sites and the process on these undestroyed clusters will behave like the process when  $D = 0$ . If, however,  $\mu$  is much smaller than the dispersal range, such as in environment I, then a dispersing offspring will feel the heterogeneity of the environment quite strongly and a certain percentage of attempted births will fail just because the offspring lands on a destroyed site. Systems in which  $\mu$  and  $M_1$  are comparable, will show a mixture of the behavior in the extreme cases.

We wish to discuss the relevance of our results for biologically more realistic situations. The mean free path can be defined for any habitat. If the average dispersal distance is much larger than the mean free path, then regardless of the underlying spatial pattern of the destroyed habitat, the dispersal mechanism will average over the spatial pattern so that the mean-field description will be quite accurate.

If the average dispersal distance is much smaller than the mean free path, then most individuals do not "feel" the destruction, that is, they typically live in large (compared with their average dispersal distance) undestroyed patches. The mechanisms that made survival possible in environment II are then relevant. That is, as long as there is a sufficiently large connected set of patches, the system will likely be able to persist for a very long time even in a finite habitat. (Local stochastic extinction events are only important when the habitat patch is relatively small).

Percolation results played an important role in determining survival or extinction in the three habitats we discussed above. Percolation is a concept which is defined for infinite habitats. A finite habitat can be thought of as cutting a finite piece out of the infinite habitat implying that if percolation occurs in the infinite habitat, then in the finite habitat there is likely a connected set of undestroyed patches which

can exchange dispersers. If the connected set is large enough, then, at least for a long time, the finite system will behave like the infinite system. Even if the destruction results in isolated patches, the system might still survive for an extended period of time if the isolated patches are large enough to support a sufficiently large subpopulation which is not prone to frequent stochastic extinction events.

It is now not difficult to guess the effects of the spatial arrangement of destroyed and undestroyed sites on the behavior of competing species in the two-species model, which was introduced above.

## 2.2. THE TWO-SPECIES MODEL

The next step is to investigate the effect of habitat destruction on a community of species. As observed in Tilman (1994), since the better competitor can always displace inferior competitors, coexistence requires an interspecific trade-off between competitive ability and dispersal ability. This trade-off has been explored numerous times (see, e.g. MacArthur & Wilson, 1967; Tilman, 1982, 1990, 1994). Furthermore, Tilman (1994) showed in the hierarchical mean-field model that species need to be dissimilar enough for coexistence to occur. This limiting similarity is a well-known phenomenon in competition models (see, e.g. May, 1981; Pacala & Tilman, 1994; Hurtt & Pacala, 1995; Lehman & Tilman, 1997).

The goal in this section is to investigate the effects of the different spatial patterns of habitat destruction on the competition-colonization trade-off and on limiting similarity. We restrict ourselves to just two species since the effects of the spatial arrangement of destroyed patches we are interested in, can already be seen in this case. For a multi-species analysis in the metapopulation context and for some simulations, see Tilman *et al.* (1997).

We start with environment I. If both  $M_1$  and  $M_2$  are large, then the behavior can again be approximated by mean-field equations and we obtain the following results (an outline of the proofs will be presented in the Appendix). Fix  $D \in [0, 1)$ . If  $\lambda_1 > 1/(1 - D)$  and  $\lambda_2 > (1 - D)\lambda_1^2$ , then coexistence occurs for  $M_1$  and  $M_2$  sufficiently large. In this case, the density of 1's is close to  $1 - 1/\lambda_1 - D$  and the density of 2's is close to  $1/\lambda_1 - (1 - D)\lambda_1/\lambda_2$ . If  $\lambda_1 > 1/(1 - D)$  and  $\lambda_2 < (1 - D)\lambda_1^2$ , then the 2's die out for  $M_1$  and  $M_2$  sufficiently large when starting from a configuration with infinitely many 1's. (We first choose  $D$ , then  $\lambda_1$  and  $\lambda_2$ , and finally  $M_1$  and  $M_2$ ).

The mean field critical value for species 2 in the presence of species 1 is  $(1 - D)\lambda_1^2$ . For fixed



$\lambda_1 > 1/(1 - D)$ , the difference in the colonization rates of both species necessary for coexistence is thus

$$(1 - D)\lambda_1^2 - \lambda_1 = \lambda_1[(1 - D)\lambda_1 - 1] > 0$$

since  $\lambda_1 > 1/(1 - D)$ . That is, the colonization rate for species 2 needs to be larger than the colonization rate of species 1, an illustration of the competition–colonization trade-off. In addition, it shows that there is a limit to similarity between the two species, the colonization rate  $\lambda_2$  needs to exceed  $\lambda_1$  by a positive amount in order for coexistence to be possible. This was already observed in Tilman (1994). For fixed  $\lambda_1$ , however, this difference is a decreasing function of  $D$ . In this sense, species 2 is helped by habitat destruction.

Species 2 is helped even more when its dispersal range is much larger than the dispersal range of species 1. To investigate this case, we assume that species 1 can only disperse to the four nearest neighboring sites and  $M_2$  is large. The condition for survival of 1's changes as already observed in the single species model. Irrespective of the value of  $\lambda_1$ , 1's cannot survive once  $D$  exceeds  $1 - p_{c,1}$ . Since  $M_2$ , the dispersal range of species 2, is very large, dispersing 2's average over the fine scale structure of species 1, that is, they experience the global density of species 1 when dispersing. The spatial structure of species 1 becomes important in the competition part of the dynamics when 1's displace 2's. We observed in the single-species case that the density of 1's decreases faster than  $D$  when the dispersal range of 1's is small. Therefore, habitat destruction facilitates survival of species 2 even more when species 1 has short range dispersal.

Note, when  $D = 0$ , 2's may or may not be able to invade, depending on  $\lambda_2$ . As  $D$  increases, the proportional abundance of species 1 decreases and species 2 might be able to invade if it is not already present when  $D = 0$ . Once  $D > 1 - p_{c,1}$ , species 1 dies out. If species 2 is present, its density will decrease as  $D$  increases further until species 2 becomes extinct as well. Extinction of species 2 in the absence of species 1 is governed by the behavior of the single species model when the range of dispersal is large; i.e. when  $D > 1 - 1/\lambda_2$ , species 2 can no longer survive.

We now assume that species 1 is a global disperser and species 2 is the local disperser (i.e.  $M_1 \gg M_2$ ). Since the presence of species 1 decreases the number of sites available to species 2, species 2 might be unable to spread simply because the available sites do not percolate. This effect is enhanced by the presence of destroyed sites. This together with the results above shows that survival of species 2 is facilitated by being

the better colonizer in the sense of having a larger dispersal range compared with species 1.

Next we consider environment II. Here  $L$  denotes the length of the big patches. When both  $M_1$  and  $M_2$  are much bigger than  $L$ , the behavior of the model is the same as in environment I since individuals of both species average over the small scale heterogeneity of the environment when dispersing.

In other cases, the percolation threshold may become important. "Percolation of  $L \times L$  squares" depends on the dispersal range of the respective species. In the following, when we say that there exists an infinite cluster of  $L \times L$  squares for species  $i$ , we implicitly assume that the definition of a cluster is based on the appropriate neighborhood set. Since it will be obvious in each case what the appropriate neighborhood is, we will not explicitly mention it each time.

We assume now  $M_1 = M_2 \ll L$ . If  $D > 1 - p_{c,2}$ , undestroyed  $L \times L$  squares form only finite clusters and both species will eventually become extinct, though typically not at the same time. Depending on the cluster size of inhabitable patches, the time to extinction may be very long. The species with the lower proportional abundance when  $D = 0$  is more prone to extinction due to random fluctuations which tend to increase when the abundance gets smaller (see, e.g. Terborgh & Winter, 1980; Shaffer, 1981; Simberloff, 1984; Soule, 1986).

On the other hand, if  $M_1 = M_2 \ll L$  but  $D < 1 - p_{c,1}$ , an infinite cluster of undestroyed  $L \times L$  squares is present. Coexistence in the infinite cluster of undestroyed  $L \times L$  squares is essentially determined by the same condition as in the case  $D = 0$ . Habitat destruction, therefore, does not facilitate survival of the inferior competitor as before in environment I, that is, the difference between the colonization rates of the two species necessary for coexistence does not decrease with the amount of destroyed habitat.

We assume now that species 1 can only disperse to the four nearest neighbors and that the dispersal range  $M_2$  satisfies  $1 \ll M_2 \ll L$ . As long as  $D < 1 - p_{c,1}$ , species 1 sees an infinite cluster of undestroyed sites and can survive provided  $\lambda_1$  exceeds the critical value for the two-dimensional basic contact process and  $L$  is sufficiently large. (For fixed  $D < 1 - p_{c,1}$ , we first choose  $\lambda_1$  and then  $L$ ). In contrast to environment I, the density of 1's in patches that are contained in the infinite cluster, will typically be close to the density of species 1 when  $D = 0$ , as already observed in the single species case. Since  $M_2 \gg 1$ , species 2 now benefits from destruction by having access to undestroyed patches which are inaccessible to species

1. These are patches which are not contained in the infinite cluster for species 1 but which are contained in an infinite cluster when the neighborhood structure of species 2 is taken into account. In those patches, species 2 will be at its monoculture equilibrium abundance, whereas in patches which are contained in the infinite cluster for species 1, species 2 will be at the same abundance level if it lived in an undestroyed habitat together with species 1. Once  $D > 1 - p_{c,1}$ , species 1 only experiences finite clusters of undestroyed  $L \times L$  squares and will therefore ultimately go extinct.

Since species 2 has access to more patches than species 1, species 2 might be able to survive in the presence of species 1 even when  $\lambda_2$  is smaller than the critical value when species 1 is present and  $D = 0$ . This effect will likely occur when  $D$  is close to the critical value for species 1. The two species will then essentially be spatially segregated, species 1 will be confined to its infinite cluster, whereas species 2 will be found primarily in undestroyed patches which are only accessible to species 2.

We consider now the case when species 1 can only disperse to the four nearest neighbors but  $M_2 \gg L \ll 1$ . The behavior of species 1 is the same as in the previous case since species 1 is unaffected by species 2. When  $D < 1 - p_{c,1}$ , species 1 can survive provided  $\lambda_1$  is large enough. In this case, species 2 experiences a reduced birth rate due to attacks from species 1 and due to losses when offspring land in destroyed patches or on sites already occupied by species 1. When  $D > 1 - p_{c,1}$ , species 1 can no longer survive and the behavior of species 2 can be approximated by the mean field case; that is, species 2 survives if  $\lambda_2 > 1/(1 - D)$ . Therefore, when  $\lambda_1$  is sufficiently large, species 2 can again benefit from habitat destruction in the sense that as  $D$  increases, species 2 might be helped more by the reduction of species 1 than harmed by the reduction of habitat. (This can be seen by comparing the critical value of  $\lambda_2$  when  $D = 0$  and  $D = 1 - p_{c,1}$ ; the former will exceed the latter when  $\lambda_1$  is sufficiently large).

We briefly wish to discuss the case  $M_2 \ll M_1 \ll L$ . Since survival in environment II is largely characterized by survival in a pristine habitat plus accessibility to undestroyed patches, survival of species 2 in the case  $M_2 \ll M_1 \ll L$  will primarily depend on whether species 2 can coexist with species 1 in a pristine habitat. As already mentioned in the context of environment I, the presence of species 1 (even in the absence of habitat destruction) can make it impossible for species 2 to spread.

Lastly, we consider environment III. We begin with the case when species 1 can only disperse to the four

nearest neighboring sites and  $\lambda_1$  exceeds twice the critical value for the one-dimensional basic contact process so that species 1 is supercritical even when  $K = L - 1$ , that is, when the corridors are one-dimensional. As  $K$  increases from 0 to  $L - 1$ , species 1 experiences a reduction in abundance but not severe enough to drive it to extinction. Given  $\lambda_2$ , we can choose  $M_2$ ,  $L$  and  $K$  large so that the effective birth rate of species 2 can be made arbitrarily small and hence species 2 will eventually go extinct. The extinction of species 2 is caused by losing too many offspring which land in destroyed patches, effectively reducing its birth rate. Species 2 is now harmed by habitat destruction. It would need to increase  $\lambda_2$  to compensate for losses. When  $\lambda_1$  is between the critical values for the two-dimensional and twice the critical value of the one-dimensional basic contact process, there will be a critical value  $K_c$  such that species 1 goes extinct for  $K > K_c$  and will be able to survive for  $K < K_c$ . (Analogous results hold when  $M_1$  is much smaller than  $L$  and  $M_2$  is large). Of course, when both  $M_1$  and  $M_2$  are much larger than  $L$ , neither species sees the small scale structure and the model will behave approximately like the mean field model.

Habitat III is a case where an increase in dispersal range of species 2 is not necessarily a good strategy since species 2 might lose too many offspring due to frequent dispersal into destroyed regions. That is,  $M_2 \ll M_1$  might actually help species 2 and harm species 1 to the extent that species 1 might go extinct whereas species 2 might be able to survive in the corridors between the destroyed patches.

We summarize our findings in the two-species case. We recall the definition of the *mean free path*. This is the average distance from a randomly chosen undestroyed site to the closest destroyed site. When both dispersal ranges are much larger than the mean free path, then the mean-field equation (1) is again a good approximation in all three environments. When both dispersal ranges are much smaller than the mean free path, percolation effects become important in determining abundance and whether coexistence is possible. In particular, the process in the undestroyed patches of environments II and III are better described by the process in a homogeneous environment. This shows that the mean free path is the crucial quantity and the effects observed in Tilman *et al.* (1994) can only be expected when the mean free path is much smaller than the dispersal range of the species. In particular, whether or not the inferior competitor is helped by habitat destruction depends critically on the spatial arrangement of the destroyed patches and whether the better dispersal ability of the inferior competitor results in a higher fecundity or

dispersal over greater distances. It should also be clear now, why the inferior competitor increases in abundance initially when increasing the proportion of destroyed habitat in environment I; the inferior competitor experiences a reduced death rate since due to the lowered density of the superior competitor, fewer individuals of the superior species attempt births onto sites that are already occupied by the inferior competitor.

Finally, we wish to comment on how these results relate to biologically more realistic heterogeneous landscapes. As already pointed out in the one-species case, the relationship between the mean free path and the dispersal range governs the behavior, and, at least qualitatively, the results we obtained in the three environments hold for more general heterogeneous habitats. Namely, if both dispersal ranges are much larger than the mean free path, the mean field approach is a good approximation since long range dispersal has an averaging effect.

If both dispersal ranges are small compared with the mean free path, most dispersers will land within the same patch as their parents. If the suitable habitat forms a sufficiently large cluster, then survival and coexistence in the heterogeneous habitat will depend on whether the species can survive and coexist in a pristine habitat. This also means that stochastic extinction events will likely not play an important role.

If both dispersal ranges are of the order of magnitude of the mean free path, then percolation effects will become important. In addition, if the dispersal range is small, this will likely mean that isolated patches are relatively small so that stochastic extinction events will become important.

If one dispersal range is much smaller than the mean free path, whereas the other is much larger, then the behavior of the species with the large dispersal range is governed by mean field behavior, that is, it will average over the heterogeneities. The behavior of the other species will depend very much on whether large enough undestroyed patches are present. If this is the case, then the respective behavior in environment II will be relevant.

As mentioned in the introduction, biologically more realistic landscapes are finite and whether survival and coexistence are possible is of interest over a finite time interval. Our equilibrium results for finite systems are relevant in the case where survival and coexistence occur. As long as the habitat is large enough so that stochastic extinction events which would eliminate the entire population, are not very

likely, the finite system will track the infinite system for a very long time. In cases where the infinite system ultimately dies out, the finite system may still survive for a very long time. This will be the case in environment II when the patch size is large compared with the dispersal range. In this case, the system in large undestroyed patches will behave like the infinite system in a pristine environment until it "feels" the finiteness of the habitat. This may take a very long time which might not be relevant for biological applications.

### 3. The Effect of Habitat Destruction in the Lotka–Volterra Model of Interspecific Competition

In the hierarchical model we considered above, habitat destruction acted on the competition–colonization trade-off. In this section, we wish to investigate a different model, namely a version of the Lotka–Volterra model of interspecific competition, where the reversal in dominance is caused by a different mechanism.

The Lotka–Volterra model of interspecific competition in an undestroyed habitat is a standard theoretical model in ecology which illustrates the effects of competition between species. Species are not hierarchically ordered but rather have negative effects of various degrees on themselves and on each other. Since in the standard Lotka–Volterra model the intrinsic rate of growth of neither species affects the outcome of competition, Gause (1935) suggested that the effect of different growth rates could be investigated by simply removing individuals at a constant rate. This corresponds to adding a non-selective predator. In fact, Slobodkin (1961) showed in the theoretical model that this could reverse dominance. (For experimental evidence of this mechanism, see references in Slobodkin, 1961). We wish to demonstrate that habitat destruction can have a similar effect.

We consider a community of two perennial plant species and denote by  $u_i$  the proportion of patches occupied by species  $i$ , that is,  $u_i \geq 0$  and  $u_1 + u_2 \leq 1$ . Mortality has a density independent component at rate  $\delta_i$  for species  $i$  and a density dependent component at rate  $\beta_i(u_i + \alpha_{ij}u_j)$  for species  $i$  where  $i \neq j$ . An individual's fecundity is density dependent and is given by  $f_i(1 - u_1 - u_2)$  for species  $i$  when the habitat is undestroyed. When a fraction  $D$  of the habitat is destroyed, the fecundity is reduced to  $f_i(1 - D - u_1 - u_2)$  for species  $i$ . We consider the case when  $\alpha_{ij} = 1$ , that is the two species cannot coexist. This leads to the following model which was also

considered in Pacala & Levin (1997) in the case  $D = 0$ .

$$\begin{aligned}\frac{du_1}{dt} &= u_1[-\delta_1 + f_1(1 - D - u_1 - u_2) - \beta_1(u_1 + u_2)] \\ \frac{du_2}{dt} &= u_2[-\delta_2 + f_2(1 - D - u_1 - u_2) - \beta_2(u_1 + u_2)]\end{aligned}\quad (5)$$

The respective equilibria in monoculture are

$$\begin{aligned}u_1^m(D) &= \frac{f_1(1 - D) - \delta_1}{f_1 + \beta_1} \\ u_2^m(D) &= \frac{f_2(1 - D) - \delta_2}{f_2 + \beta_2}\end{aligned}\quad (6)$$

We assume

$$(i) \ u_1^m(0) > u_2^m(0) \text{ and } (ii) \ \frac{f_1}{\delta_1} < \frac{f_2}{\delta_2}$$

These conditions are illustrated in Fig. 5. There are four regions: species 1 wins; species 2 excludes 1; species 1 can no longer survive even in monoculture but species 2 can still survive; neither species can survive. We thus see a switch in dominance as  $D$  increases.

This switch is not caused by a competition–colonization trade-off as in the hierarchical model. Conditions (i) and (ii) are the key to understanding why the switch in dominance occurs. Condition (i) says that species 1 is the superior competitor in an undestroyed habitat in the sense that its monoculture equilibrium is higher. Condition (ii) says that species

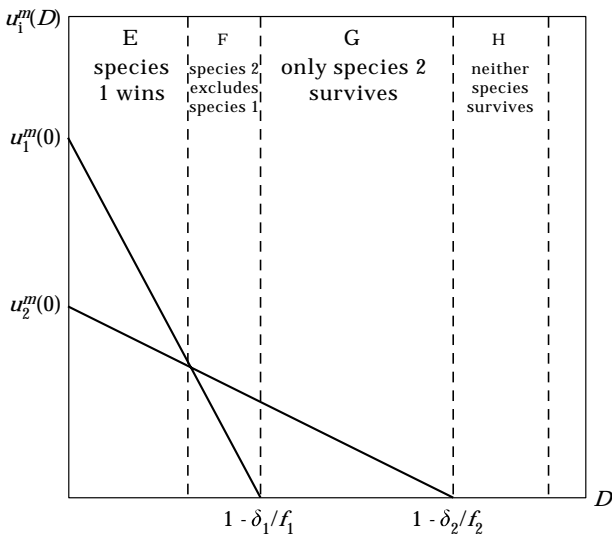


FIG. 5. Equilibrium proportional abundance of species  $i$  ( $u_i^m(D)$ ) as a function of the proportion of destroyed habitat ( $D$ ) in the mean-field case.

2 has a higher lifetime reproductive value in the absence of competition.

Since habitat destruction reduces the number of occupied sites simply by virtue of reducing the amount of available habitat, it also reduces the strength of competition. This mechanism causes the switch in dominance.

Based on the analysis of the hierarchical model in the three different environments, we can conjecture when the switch in dominance is likely to occur in a spatial version of the Lotka–Volterra model. Again the relative magnitude of the mean free path and the average dispersal distance are important. We will focus on environment II. In the spatial version of the model, each individual has a species specific neighborhood for dispersal and competitive interactions and the dynamics are extended to the spatial model in a similar fashion as before for the hierarchical model. For simplicity, we assume that the dispersal neighborhood and the neighborhood for the density dependent mortality are the same. That is, the neighborhood of an individual of species  $i$  at site  $x$  is  $x + \mathcal{N}_i$  where  $\mathcal{N}_i$  is defined in the same way as in the hierarchical model.

We assume now that  $M_1$  is much larger than  $L$ , whereas  $M_2$  is much smaller than  $L$  and species 1 excludes 2 when  $D = 0$ . A switch in dominance may occur since the proportional abundance of species 1 decreases as  $D$  increases, whereas the proportional abundance of species 2 in undestroyed patches which are contained in the respective infinite cluster, remains essentially unchanged as long as  $D < 1 - p_{c,1}$ . Once the monoculture proportional abundance of species 1 becomes too low relative to the monoculture proportional abundance of species 2, species 2 might be able to exclude species 1 in those  $L \times L$  squares which are accessible to species 2. Species 1 might still be able to survive in those  $L \times L$  squares which are undestroyed but inaccessible to species 2. This would allow for coexistence under spatial segregation. Note that the monoculture proportional abundance of species 2 is in general different from the mean-field value due to local density dependence. [It was actually shown in Neuhauser & Sudbury (1993) that when  $\delta_i = 0$ , the monoculture equilibrium of species  $i$  when  $D = 0$  is product measure, that is, all sites are independent, with density  $f_i/(f_i + \beta_i)$ , the mean-field value].

If we reverse the sizes of the respective neighborhoods, that is,  $M_1$  is now much smaller than  $L$  and  $M_2$  is much larger than  $L$ , a switch may not occur as long as there exists an infinite cluster for species 1. In this case, intraspecific competition is not reduced by habitat destruction since within an undestroyed

$L \times L$  square, which is accessible to species 1, species 1 will remain at its monoculture equilibrium density for  $D = 0$ . Coexistence might again become possible since species 2 may have access to many more patches than species 1, in particular, when  $D$  is close to the critical value for extinction of species 1. The two species would then essentially be spatially segregated.

If both  $M_1$  and  $M_2$  are much larger than  $L$ , the mean-field analysis can be applied again and a switch in dominance may occur. If both  $M_1$  and  $M_2$  are much smaller than  $L$ , a switch in dominance will likely not occur since in each  $L \times L$  square which is contained in the infinite cluster, the process essentially behaves as in the case  $D = 0$ .

#### 4. Discussion and Summary

Habitat destruction occurs in different patterns and it is important to understand how the spatial arrangement of unsuitable habitat affects species abundance and diversity. Randomly destroying relatively small patches to destroying the same amount in one large contiguous patch form the two extreme ends of the spectrum of the spatial pattern of destroyed habitat. We showed that the key to predicting the effect of the spatial pattern of habitat destruction on species abundance is the relative magnitude of the mean free path, a quantity that measures the average distance an individual has to disperse before encountering destroyed patches, and the size of its dispersal/competition neighborhood. The mean free path determines whether the small scale spatial structure of the model is important. That is, when the mean free path is much smaller than the size of the dispersal and competition neighborhood, habitat destruction can be treated analytically as in mean-field models.

In Tilman *et al.* (1994, 1997) it was pointed out that habitat destruction can actually aid the inferior competitor which in their case was the better disperser. It follows from our analysis that the effect of habitat destruction caused by this competition-colonization trade-off depends strongly on the spatial pattern of the destroyed patches. We saw in the case of the hierarchical model that habitat destruction may either aid the better disperser and harm the better competitor as was the case in environments I and II where patches were destroyed randomly and the average dispersal distance exceeded the mean free path, or may have the opposite effect as in environment III where sufficiently wide corridors were left for the superior competitor but the superior disperser lost most of its offspring due to dispersal into destroyed habitat.

A different trade-off is responsible for the effects seen in the Lotka-Volterra model in a habitat with destruction. The switch in dominance occurred due to the reduction of competition when the suitable habitat is reduced. Again, as in the hierarchical model, we found that the relative magnitude of the mean free path to the average dispersal distance is the key to predicting the dominance behavior as the proportion of destroyed habitat changes.

In summary, this article has shown that the spatial arrangement of destroyed habitat plays an important role in the effect on species abundance. The key quantities that allow one to predict this effect are the mean free path and the average dispersal distance.

Alfred P. Sloan Research Fellow during 1994–1996. Partially supported by the National Science Foundation under grants DMS-9403644 and DMS-9703694. This work was partially done while the author visited the Department of Ecology and Evolutionary Biology, Princeton University, during 1995/1996 and the author wishes to express her gratitude for their warm hospitality. The author also wishes to thank David Tilman and Clarence Lehman for discussions and Chris Klausmeier and Tony Ives for discussions and comments on an earlier version.

#### REFERENCES

- BEZUIDENHOUT, C. & GRIMMETT G. (1990). The critical contact process dies out. *Ann. Probab.* **18**, 1462–1482.
- BRAMSON, M., DURRETT, R. & SCHONMANN R. H. (1991). The contact process in a random environment. *Ann. Probab.* **19**, 960–983.
- BRAMSON, M., DURRETT, R. & SWINDLE, G. (1989). Statistical mechanics of crabgrass. *Ann. Probab.* **17**, 444–481.
- BROWER, R. C., FURMAN, M. A. & MOSHE M. (1978). Critical exponents for the Reggeon quantum spin model. *Phys. Lett.* **76B**, 2113–2119.
- CAMPANINO M., KLEIN, A. & PEREZ, J. F. (1991). Localization in the ground state of an Ising model with a random transverse field. *Commun. Math. Phys.* **135**, 499–515.
- DJORDJEVIC, Z. V., STANLEY, H. E. & MARGOLINA, A. (1982). Site percolation threshold for honeycomb and square lattices. *J. Phys. A*, **15**, L405–412.
- DURRETT, R. (1988). *Lecture Notes on Particle Systems and Percolation*. Pacific Grove, California: Wadsworth.
- DURRETT, R. (1991). A new method for proving the existence of phase transitions. In: *Spatial Stochastic Processes*, pp. 141–169. Boston: Birkhauser.
- DURRETT, R. (1995). Ten lectures on particle systems. In: *Lectures on Probability Theory*, pp. 97–201, Springer Lecture Notes in Math 1608. Berlin: Springer.
- DURRETT, R. & LEVIN, S. A. (1994). Stochastic spatial models: a user's guide to ecological applications. *Phil. Trans. R. Soc. London, Ser. B* **343**, 329–350.
- DURRETT, R. & MOLLER, A. M. (1991). Complete convergence theorem for a competition model. *Probab. Th. Rel. Fields* **88**, 121–136.
- DURRETT, R. & NEUHAUSER, C. (1991). Epidemics with recovery in  $d = 2$ . *Ann. Appl. Probab.* **1**, 189–206.
- DURRETT, R. & SCHINAZI, R. (1993). Asymptotic critical value for a competition model. *Ann. Appl. Probab.* **3**, 1047–1066.

- DURRETT, R. & SWINDLE, G. (1991). Are there bushes in the forest? *Stoch. Proc. Appl.* **37**, 19–31.
- GAUSE, G. F. (1935). *La théorie mathématique de la lutte pour la vie*. Paris: Hermann et Cie.
- GRASSBERGER, P. & DE LA TORRE, A. (1979). Reggeon field theory (Schlögl's second model) on a lattice: Monte Carlo calculations of critical behavior. *Ann. Phys.* **122**, 373–396.
- HARRIS, T. E. (1974). Contact interactions on a lattice. *Ann. Probab.* **2**, 969–988.
- HASTINGS, A. (1980). Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* **18**, 363–373.
- HURT, G. C. & PACALA, S. W. (1995). The consequences of recruitment limitation: reconciling chance history, and competitive difference between plants. *J. Theor. Biol.* **176**, 1–12.
- KANG, H., KRONE, S. & NEUHAUSER, C. (1995). Stepping stone models with extinction and recolonization. *Ann. Appl. Probab.* **5**, 1025–1060.
- KLEIN, A. (1994). Extinction of contact and percolation processes in a random environment. *Ann. Probab.* **22**, 1227–1251.
- LEHMAN, C. L. & TILMAN, D. (1997). Competition in spatial habitats. In: *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (Tilman, D. & Kareiva, P., eds). Princeton, NJ: Princeton University Press.
- LEVINS, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. America* **15**, 237–240.
- LIGGETT, T. M. (1985). *Interacting Particle Systems*. New York: Springer.
- LIGGETT, T. M. (1991). Spatially inhomogeneous contact processes. In: *Spatial Stochastic Processes. A Festschrift in Honor of the Seventieth Birthday of Ted Harris* (Alexander, K. C. & Watkins, J. C., eds) pp. 105–140. Boston: Birkhäuser.
- LIGGETT, T. M. (1992). The survival of one-dimensional contact processes in random environments. *Ann. Probab.* **20**, 696–723.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- MADRAS, N., SCHINAZI, R. & SCHONMANN, R. H. (1994). On the critical behavior of the contact process in deterministic environments. *Ann. Probab.* **22**, 1140–1159.
- MAY, R. M. (1981). Models for two interacting populations. In: *Theoretical Ecology: Principles and Applications* pp. 78–104. Sinauer Associates.
- NEE, S. & MAY, R. M. (1992). Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Anim. Ecol.* **61**, 37–40.
- NEUHAUSER, C. & SUDBURY, A. (1993). The biased annihilating branching process. *Adv. Appl. Prob.* **25**, 24–38.
- PACALA, S. W. & LEVIN, S. A. (1997). Biologically generated spatial pattern and the coexistence of competing species. In: *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (Tilman, D. & Kareiva, P., eds). Princeton, NJ: Princeton University Press.
- PACALA, S. W. & TILMAN, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *Am. Nat.* **143**, 222–257.
- SHAFFER, M. L. (1981). Minimum population sizes for species conservation. *BioScience* **31**, 131–134.
- SIMBERLOFF, D. (1984). Mass extinction and the destruction of moist tropical forests. *Zh. Obshch. Biol.* **45**, 767–778.
- SLOBODKIN, L. B. (1961). *Growth and Regulation of Animal Populations*. New York: Holt, Rinehart & Winston.
- SOULE, M. E. (1986). *Conservation Biology*. Sunderland, MA: Sinauer.
- TERBORGH, J. & WINTER, B. (1980). Some causes of extinction. *Conservation Biology: an Evolutionary Ecological Perspective*. (Soule, M. E. & Wilcox, B. A., eds) pp. 119–133. Sunderland, MA: Sinauer.
- TILMAN, D. (1982). *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.
- TILMAN, D. (1990). Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* **58**, 3–15.
- TILMAN, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2–16.
- TILMAN, D., MAY, R. M., LEHMAN, C. L. & NOWAK, M. A. (1994). Habitat destruction and the extinction debt. *Nature* **371**, 65–66.
- TILMAN, D., LEHMAN, C. L. & YIN, C. (1997). Habitat destruction, dispersal, and deterministic extinction in competitive communities. *Am. Nat.* **149**, 407–435.

## APPENDIX

### Rescaling

The proofs are based on a rescaling argument. The rescaling argument is by now a standard technique and has been applied frequently (the argument is reviewed in Durrett, 1991, 1995). The basic idea is to show that for given  $\delta > 0$ , members of the family of processes under consideration, when viewed on suitable length and time scales, dominate an oriented site percolation process in which sites are open with probability  $1 - \delta$ . (The sites may be  $j$ -dependent and the oriented site percolation process may be defined in a random environment).  $j$ -dependent oriented site percolation with density  $1 - \delta$  can be defined as follows. Let  $\mathcal{G} = \{(z_1, z_2) \in \mathbb{Z}^2: z_1 + z_2 \text{ even}\} = 2\mathbb{Z}^2 \cup ((1, 1) + 2\mathbb{Z}^2)$  and  $\mathcal{L} = \{(z, n): z \in \mathcal{G}, n \in \mathbb{Z}_0^+, \text{ with } z \in 2\mathbb{Z}^2 \text{ for } n \text{ even and } z \in (1, 1) + 2\mathbb{Z}^2 \text{ for } n \text{ odd}\}$ . The oriented site percolation process is a collection of random variables  $\{\omega(z, n): (z, n) \in \mathcal{L}\}$  with values in  $\{0, 1\}$ , that indicate whether the sites in  $\mathcal{L}$  are open (1) or closed (0). We say the process is  $j$ -dependent with density  $1 - \delta$  if for any sequence  $(z_k, n_k)$ ,  $1 \leq k \leq l$ , satisfying  $\|z_k - z_{k'}\| > 2j$  whenever both  $k \neq k'$  and  $n_k = n_{k'}$ , then

$$P(\omega(z_k, n_k) = 0 \text{ for } 1 \leq k \leq l) \leq \delta^l.$$

By an open path from  $(y, 0)$  to  $(z, n)$  we mean a sequence of points  $(z_0, 0) = (y, 0)$ ,  $(z_1, 1), \dots, (z_n, n) = (z, n)$  in  $\mathcal{L}$  such that for  $0 \leq k \leq n - 1$ ,  $\|z_k - z_{k+1}\| \leq m$ , for some appropriate  $m$ , and all the  $(z_k, k)$ 's with  $k \geq 1$  are open. If there is an infinite open path starting at  $(0, 0)$ , we say *percolation occurs*. It is a well known fact that for fixed  $m$ , oriented site percolation percolates for  $\delta$  close enough to 0. In addition, there exists a linearly, in all direction expanding region on which the processes have the desired properties. We refer the reader to Durrett & Neuhauser (1991) for some results on dependent percolation.

To apply the rescaling argument let  $R$  and  $T$  be positive integers to be chosen later and define

$$\psi(z) = (z_1 R, z_2 R) \text{ for } z = (z_1, z_2) \in \mathcal{G}$$

$$\psi(z, k) = (z_1 R, z_2 R, kT) \text{ for } (z, k) \in \mathcal{L}$$

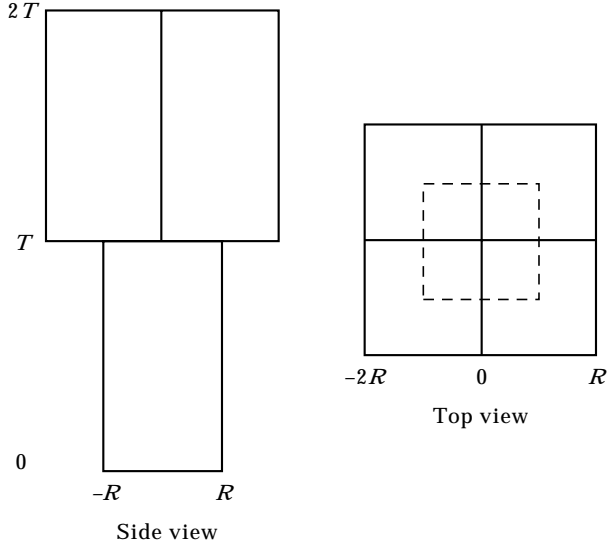


FIG. A1. Side and top views of rescaling boxes.

$$\begin{aligned}
 E &= (-R, R]^2 \\
 E(z) &= \psi(z) + E \\
 H &= (-R, R]^2 \times [0, T] \\
 H(z, k) &= \psi(z, k) + H
 \end{aligned} \tag{A.1}$$

Figure A1 shows side and top views of how these boxes are arranged. The heterogeneity of the environment will, in general, be reflected in the renormalized lattice and we will define certain good events  $G_1$  which describe “typical” environments and call a square  $E(z)$  a  $G_1$ -square if the event  $G_1$  occurs in  $E(z)$ . Depending on the case and type of result we wish to prove, we will then define certain good events  $G_2$  and show that if  $E(z)$ , for all  $\|z\| \leq 1$ ,  $z \in \mathcal{G}$ , are  $G_1$ -squares and if  $G_2$  occurs in  $E(0)$  at time 0, then with probability at least  $1 - \delta$ ,  $G_2$  occurs in all four boxes  $H(z, 1)$ ,  $\|z\| \leq 1$ ,  $z \in \mathcal{G}$ , at time  $T$ . Here,  $\|z\| \leq 1$  means  $\max(z_1, z_2) \leq 1$  for  $z = (z_1, z_2) \in \mathbb{Z}^2$ . [Note that the anchor points  $\psi(z, 1)$  of  $H(z, 1)$ ,  $\|z\| \leq 1$ , coincide with the corners of the top of  $H(0, 0)$  as illustrated in Fig. A1].

A comparison with an appropriate oriented site percolation process will then show that the  $G_1$ -squares in which the event  $G_2$  occur, dominate the wet sites in the corresponding oriented site percolation process in which sites are open with probability  $1 - \delta$ . Details can be found in Kang *et al.* (1995).

### Proofs for Environment I

The proofs of both survival/coexistence and extinction in the long range case utilize the rescaling

argument introduced in the previous section. We begin with the single species case. For the proofs, it will be convenient to define the model on a square lattice where the lattice spacing is  $1/2M_1$  instead of 1. We denote the rescaled lattice by  $\mathbb{Z}^2/2M_1$ . This will allow us to let  $M_1 \rightarrow \infty$  and still obtain a meaningful process since the  $[-M_1, M_1]^2 \cap \mathbb{Z}^2$  neighborhood on the original square lattice translates into a  $[-1/2, 1/2]^2 \cap (\mathbb{Z}^2/2M_1)$  neighborhood which is simply  $[-1/2, 1/2]^2$  in the limit  $M_1 \rightarrow \infty$ .

Since environment I is random, the rescaled squares  $E(z)$ ,  $z \in \mathcal{G}$ , defined in (A1) are not identical. We set  $\mathcal{N} = \{z \in \mathbb{Z}^2/2M_1 : 0 < \|z\| \leq 1/2\}$  and  $\mathcal{N}_x = x + \mathcal{N}$ . By choosing  $M_1$  sufficiently large, most squares will share similar statistical properties, namely the fraction of destroyed sites will be “sufficiently random”. To make this precise, we define the event  $G_1$  for the square  $E$ : for  $\eta > 0$  (which will be specified later), we let  $G_1$  be the event that for every  $x \in E \cap \mathbb{Z}^2/2M_1$

$$\left| \frac{\sum_{y \in \mathcal{N}_x \cap E} U_y}{|\mathcal{N}_x \cap E|} - (1 - D) \right| \leq \eta \tag{A.2}$$

where  $U_y = 1$  if  $y$  is undestroyed and  $U_y = 0$  if  $y$  is destroyed. Note that the  $U_y$ ’s are independent and identically distributed. If  $G_1$  occurs in  $E$ , we say  $E$  is a  $G_1$ -square. For translates of  $E$ , we define  $G_1$  analogously. The next lemma shows that for  $M_1$  sufficiently large, an arbitrarily high proportion of squares are  $G_1$ -squares.

### LEMMA A3

Fix  $R > 0$  and  $\epsilon_1 > 0$ . For any  $\eta > 0$  we can find  $M_0$  so that

$$P(G_1) \geq 1 - \epsilon_1 \tag{A.4}$$

for all  $M_1 \geq M_0$ .

### PROOF

This follows from a simple large deviations estimate since the  $U_y$ ’s are independent and identically distributed.

$$\begin{aligned}
 P(G_1^c) &\leq |E| \sup_{x \in E \cap \mathbb{Z}^2/2M_1} P \left( \left| \frac{\sum_{y \in \mathcal{N}_x \cap E} U_y}{|\mathcal{N}_x \cap E|} \right. \right. \\
 &\quad \left. \left. - (1 - D) \right| > \eta \right) \leq C_1 (RM_1)^2 e^{-\gamma_1 M_1^2}
 \end{aligned}$$

for appropriate  $C_1 < \infty$  and  $\gamma_1 > 0$  (depending on  $\eta$ ). Note that  $E$  is an  $(-R, R]^2$  box on the rescaled lattice  $\mathbb{Z}^2/2M_1$ , hence the factor  $(RM_1)^2$  in the estimate. For  $M_1$  sufficiently large, (A4) holds.

The survival result in the single-species case follows from Bramson *et al.* (1989); the coexistence result in the two-species case follows from Durrett & Swindle (1991) and Durrett & Moller (1991). We only state the modifications necessary to adapt their proofs, which were done for the case  $D = 0$ , to the case when  $D > 0$ . The basic idea is to define a mean-field (that is,  $M_1 = \infty$ ) version of the process under consideration and show that when viewed on suitable length and time scales, the process dominates super-critical oriented site percolation in a random environment determined by  $G_1$ -squares. A perturbation argument, i.e. continuity, then shows that the last conclusion holds for the process when  $M_1$  is finite but large.

To motivate the mean-field version  $X_t$  of the process of 1's, note that the contact process can be viewed as a branching random walk in which particles coalesce when they occupy the same site. Furthermore, if we start with a finite number of particles, the probability that a site is picked twice before some fixed time, goes to 0 as  $M_1 \rightarrow \infty$ . We therefore define  $X_t$  as a branching random walk on  $\mathbf{R}^2$  in which

- (i) particles die at rate 1;
- (ii) particles give birth at rate  $\lambda_1$ ;
- (iii) the offspring of a particle at  $x$  is sent to a site  $y$  chosen uniformly from  $\{y: \|x - y\| \leq 1/2\}$ . We flip a coin with probability  $1 - D - \eta$  of heads to see whether  $y$  is undestroyed. If  $y$  is undestroyed, the offspring can land at  $y$ ; if not, the birth is suppressed.

If  $X_0 = x$  and  $S_t^x$  denotes a random walk that starts at  $x$  and makes steps at rate  $\lambda_1(1 - D - \eta)$ , then for any Borel set  $A \subset \mathbf{R}^2$ ,

$$\mathbf{E}|X_t^x \cap A| = e^{\kappa t} P(S_t^x \in A)$$

where  $\kappa = \lambda_1(1 - D - \eta) - 1$ . The same argument as in Bramson *et al.* (1989) then shows that the process  $X_t$  exhibits the behavior described in the survival part of the single-species case if we choose  $\eta$  small. To get from  $X_t$  to the process under consideration, note that if  $E$  is a  $G_1$ -square, then each site  $x \in (-R + 1, R - 1]^2$  has at least a fraction  $1 - D - \eta$  of undestroyed sites in its neighborhood. Therefore, for  $M_1$  sufficiently large, the process under consideration dominates  $X_t$  with probability close to 1.

For the coexistence result in the two-species case, we first observe that 1's ignore 2's and are therefore in contact process equilibrium as described in single-species case. The mean-field version  $Y_t$  of the process of 2's in Durrett & Swindle (1991) needs to be modified in an analogous way. That is, we define  $Y_t$  as the process in which

- (i) particles die at rate  $1 + \lambda_1(1 - D - 1/\lambda_1) = \lambda_1(1 - D)$  (2's die if they meet a  $\delta$  or a 1 branches onto their site);
- (ii) particles give birth at rate  $\lambda_2$ ;
- (iii) the offspring of a particle at  $x$  is sent to a site  $y$  chosen at random uniformly from  $\{y: \|x - y\| \leq 1/2\}$ . We flip a coin with probability  $1/\lambda_1$  to see whether the chosen site is undestroyed and vacant. If it is, the birth is successful; if not, the birth is suppressed.

The process  $Y_t$  is therefore a branching random walk in which 2's die at rate  $\lambda_1(1 - D)$  and births occur at rate  $\lambda_2/\lambda_1$ . In order for 2's to survive, we therefore need  $\lambda_1(1 - D) < \lambda_2/\lambda_1$  which is the condition for coexistence in the two-species case provided 1's survive.

The density of 1's and 2's is then close to their mean-field values, that is, the density of 1's is the same as in the single-species case, namely close to  $1 - D - 1/\lambda_1$  and the density of 2's is close to  $(\lambda_2 - (1 - D)\lambda_1^2)/(\lambda_1\lambda_2)$ .

The proofs of these results follow very closely the proofs in Durrett & Swindle (1991) and Durrett & Moller (1991). We omit the details.

To show extinction of 1's in the single-species case and of 2's in the two-species case, we will again use a comparison with oriented site percolation in a random environment determined by the event  $G_1$  defined in (A2). Extinction is much harder to show than coexistence since the respective processes may survive quite well on squares in which  $G_1$  does not occur (we call these squares  $G_1^c$ -squares). Since we do not know anything about the properties of  $G_1^c$ -squares, we assume the worst possible case in which all sites in a  $G_1^c$ -square are *undestroyed*.

We call a site  $z_1 \in \mathcal{G}$   *$G_1$ -regular* if  $E(z_1)$  and all of its eight neighbors  $E(z_2)$ ,  $z_2 \in \mathcal{G}$ ,  $\|z_1 - z_2\| = 2$ , are  $G_1$ -squares; otherwise,  $z_1$  is called  *$G_1$ -singular*.

If  $z$  is  $G_1$ -regular, the 1's in the one-species model and the 2's in the two-species model are subcritical on  $E(z)$ , but may be supercritical if  $z$  is  $G_1$ -singular. There are infinitely many clusters of  $G_1$ -singular sites of all sizes which are cylinders infinitely extended in the time direction. We need to control these clusters. We will adapt the proof in Klein (1994) to show that these singular regions are rare enough, so that the process dies out even though the process is supercritical on the singular regions. Klein (1994) optimized the multi-scale analysis in Campanino *et al.* (1991) to show extinction for the contact process in a random environment.

We begin with describing the comparison process. We compare our process to the following oriented site



percolation process. For  $(z, n) \in \mathcal{L}$ , the probability that  $(z, n)$  is occupied is

$$p((z, n)) = \begin{cases} \epsilon & \text{if } z \text{ is } G_1\text{-regular} \\ 1 - e^{-\gamma_3 M_1^3} & \text{if } z \text{ is } G_1\text{-singular} \end{cases} \quad (\text{A.5})$$

We will first show that we can rescale our single-species process so that it is dominated by the process defined in (A.5). Because of translation invariance it is enough to show (A.5) for  $(z, n) = ((0, 0), 0)$ . Set  $R = M_1$  and define  $H_0 = (-3M_1, 3M_1]^2 \times [0, 2M_1]$  and  $H_1 = (-M_1, M_1]^2 \times [M_1, 2M_1]$ . We say that  $((0, 0), 0)$  is vacant if  $H_1$  does not contain any particles; otherwise we say that it is occupied. Similarly, vacant and occupied are defined for translates of  $H_1$ .

We need the notion of a dual process. To determine whether or not a site in the contact process is occupied at time  $t$ , one can work backwards in time and determine the possible set of ancestors. It turns out that the dual process is the same as the contact process, i.e. the process is self-dual. For details see Durrett (1988).

Suppose  $(0, 0)$  is  $G_1$ -regular. We will assume that initially all sites in  $(-3M_1, 3M_1]^2$  are occupied by 1's and that all sites in  $((-3M_1, 3M_1]^c)$  are occupied by 1's for all  $t \leq 2M_1$ . A site in  $H_1$  is occupied if the dual starting at that site survives and reaches either  $(-3M_1, 3M_1]^2$  or  $H_0^c \cap (\mathbf{Z}^2/2M_1) \times [0, 2M_1]$ . Since  $z$  is regular, the dual process starting at a fixed site in  $H_1$  can be dominated by a subcritical branching process and hence dies out. Since  $|H_1| \leq C_3 M_1^4$ , it follows that

$$P(H_1 \text{ is occupied}) \leq C_4 M_1^4 e^{-\gamma_4 M_1} \leq C_2 e^{-\gamma_2 m_1} \quad (\text{A.6})$$

for appropriate  $C_2 < \infty$  and  $\gamma_2 > 0$ .

Suppose now that  $(0, 0)$  is  $G_1$ -singular. We will take a rather crude approach.  $H_1$  will be vacant if all particles in  $(-M_1, M_1]^2 \times \{M_1 - 1\}$  die within one unit of time and no births occur in  $(-M_1, M_1]^2 \times [M_1 - 1, 2M_1]$ . The probability of this event is

$$\geq (1 - e^{-1})^{4M_1^2} (e^{-\lambda_1 M_1})^{4M_1^2} \geq e^{-\gamma_3 M_1^3} \quad (\text{A.7})$$

for appropriate  $\gamma_3 > 0$ . It is clear from our assumptions that sites are 2-dependent; that is, if  $(z, n), (z', m) \in \mathcal{L}$  with either  $\|z - z'\|/2 > 4$  or  $|m - n| > 2$ , then  $(z, n)$  and  $(z', m)$  are independent.

The multiscale analysis involves multiple rescaling. The first rescaling step produces  $G_1$ -regular and  $G_1$ -singular sites as described above together with the associated oriented site percolation process which serves as a comparison process. The subsequent rescaling steps will be used to demonstrate that the oriented site percolation process does not percolate

for  $M_1$  sufficiently large. Since in the original single-species model individuals are not born spontaneously, this will then imply that the single-species model dies out for  $\lambda_1 < 1/(1 - D)$  and  $M_1$  sufficiently large.

We follow the presentation in Klein (1994) closely and adopt his notation. This will make it easier to incorporate the necessary changes into his proof. Klein (1994) proved the extinction result for a continuous time, nearest neighbor contact process in a random environment whose birth and death rates were given by independent families of independent and identically distributed random variables.

Our first rescaling step results in a process with nearest neighbor structure. Adjacent sites will not be independent, but sites that are separated by at least a certain distance will be independent. This will suffice as we will see below. This step also fixes  $M_1$  in the following sense: for any  $\lambda_1$  and  $D$  satisfying  $\lambda_1 < 1/(1 - D)$ , we can find  $M_1$  large so that the first rescaling step can be carried out successfully in the sense that the resulting process is subcritical. For this choice of  $M_1$ , the subsequent steps are constructed. (In other words, the choices for the scales in subsequent steps depend on  $M_1$ ). After the first rescaling step, the new process evolves in discrete time. Proving results for discrete time systems is in some sense easier than for continuous time systems since it allows for better control of how quickly the process spreads.

To define the subsequent rescaling steps, we begin by recalling some notation and definitions from Klein (1994). For  $L > 0$ ,  $x \in \mathbf{Z}^2$ , let

$$\Lambda_L(x) = \{y \in \mathbf{Z}^2 : \|x - y\| < L\}$$

For  $X = (x, t) \in \mathbf{Z}^2 \times \mathbf{R}$ ,  $L > 0$  and  $T > 0$ , let

$$B_{L,T}(X) = \Lambda_L(x) \times [t - T, t + T]$$

and set

$$B_L(X) = B_{L,e^{Lv}}(X)$$

for some fixed  $v \in (0, 1)$ . The two-point connectivity function  $G_W^e(X, Y)$ ,  $X, Y \in \mathbf{Z}^2 \times \mathbf{R}$ , is the probability that there exists a path of certain good sites connecting  $X$  and  $Y$  which lies in  $W$ , a region in  $\mathbf{R}^3$ ;  $e$  denotes the fixed environment. A path of good sites at a certain rescaling level consists of sites along which the original process of 1's can spread.

We need the following definition. Let  $m > 0$ ,  $L > 1$ . A site  $x \in \mathbf{Z}^2$  is called  $(m, L)$ -regular if

$$G_{B_L((x, 0), \partial)}((x, 0), \partial) \leq e^{-mL} \quad (\text{A.8})$$

Otherwise the site is called  $(m, L)$ -singular. Here  $\partial$  is short for  $\partial B_L((x, 0))$ . A set  $\Lambda \subset \mathbf{Z}^2$  is  $(m, L)$ -regular if

every  $x \in \Lambda$  is  $(m, L)$ -regular otherwise it is  $(m, L)$ -singular.

The scaling rescaling step differs slightly from the subsequent rescaling steps in the sense that we require stronger conditions in the second step for a site to be regular. The underlying lattice structure is now the oriented site percolation lattice obtained in the first rescaling step. We need to show that we can find  $m_0 > 0$ ,  $p > 2$  and  $L_0 > 0$  so that

$$P(0 \text{ is } (m_0, L_0)\text{-regular}) \geq 1 - \frac{1}{L_0^p}$$

If we assume that all sites in  $B_L((0, 0))$  are  $G_1$ -regular, then the exponential estimate in (A.8) follows immediately from standard estimates from dependent percolation theory. We omit the details. Using Markov's inequality, the probability that there exists  $G_1$ -singular sites in  $B_L((0, 0))$  can be bounded by

$$\begin{aligned} &\leq (2L)^2 (2e^{L^v}) P(0 \text{ is } G_1\text{-singular}) \\ &\leq (2L)^2 (2e^{L^v}) C_1 (RM_1)^2 e^{-\gamma_1 M_1^2} \leq \frac{1}{L^p} \end{aligned}$$

provided  $L^v - \gamma_1 M_1^2 < -2p \log L$ . Since  $v \in (0, 1)$ ,  $L$  can be some large power of  $M_1$ . For any fixed  $M_1$  we can thus find  $L_0$  and  $m_0$  so that the second rescaling step can be completed.

We can now continue in the setup of Klein (1994) and the subsequent steps can be carried out essentially without changes. We give a brief description. We choose an increasing sequence of length scales  $L_k$ ,  $k \geq 1$  and a decay rate  $m_\infty \in (0, m_0)$  so that the probability that a site is regular at some scale is sufficiently large, then this probability will be sufficiently large on the next scale. [This is Theorem 3.2 in Klein (1994)].

In the third and all subsequent rescaling steps we allow singular regions in the rescaling squares, their density, however, will be quite small. Klein (1994) showed that the scales can be arranged so that with high probability singular sites are not adjacent. This allows one to show exponential decay for the connectivity function of a path from the center of the box to any of its vertical sides. Controlling the connectivity function for a path from the center of the box to the top (or bottom) of the box is harder since the paths can go through singular regions. Klein showed that by dividing up the box into vertical slices, with high probability at least one of the vertical slices is such that no path can go through a singular region. In our situation this is achieved by requiring that all sites of the oriented site percolation process after the first rescaling step are closed in the sense that the

original process dies out in the corresponding box. In this case, a path has to go around a singular region. The height of the slices is chosen so that this is unlikely, thus giving the desired result. This completes the sketch of the proof of extinction in the one-species model in environment I when  $\lambda_1 < 1/(1 - D)$  and the range is large.

In the two-species model we wish to show that 2's die out if  $\lambda_1 > 1/(1 - D)$  and  $\lambda_2 < (1 - D)\lambda_1^2$ ; that is, on  $G_1$ -squares, 1's are supercritical and 2's are subcritical when they live in a region in which 1's are in equilibrium. We will therefore say that  $(0, 0)$  is vacant at time 0, if  $D$  does not contain 2's but contains 1's. Otherwise, we say that  $(0, 0)$  is occupied at time 0.

The proof of extinction for the two-species model is similar to the corresponding proof in the single-species model. It follows from Durrett & Schinazi (1993) that for any  $\epsilon > 0$ ,  $p(z, u) \leq \epsilon$  for  $z$  regular provided  $\min(M_1, M_2)$  is sufficiently large. The estimate for singular sites is the same as in the single-species model, except that we replace 1's by 2's.

### Proofs for Environments II and III

As before, we will focus our attention to proving the results for the single-species case and will only indicate how to prove the analogous results for the two-species case.

We begin with the single-species model in environment II and assume  $M_1 \gg 1$ . If  $D < 1 - p_{c,2}$ , then the undestroyed squares percolate. A rescaling argument in a random environment analogous to the one used in Kang *et al.* (1995) will show survival of 1s. To apply the rescaling argument we set  $R = L$  in (A1). The event  $G_1$  is now simply the event that all sites in  $E$  are undestroyed. If  $E$  is a  $G_1$ -square, then we say  $G_2$  occurs in  $E$  if the density of 1's in  $E$  is close to  $1 - 1/\lambda_1$ . Using results in Bramson *et al.* (1989), it follows that for any  $\eta > 0$ , if  $E$  and  $E'$  are neighboring  $G_1$ -squares and  $E$  is  $G_2$  at time 0, then with probability at least  $1 - \eta$ ,  $E'$  will be  $G_2$  at time  $T = L^2$  and  $E$  will remain  $G_2$  for the entire time interval  $[0, T]$  for  $M_1$  sufficiently large. A slight modification in Kang *et al.* (1995) then shows that if  $D < 1 - p_{c,2}$  and  $1 - \eta$  is sufficiently close to one, then a shape theorem, for  $G_1$ -squares in which  $G_2$  occurs, holds. That is, the process spreads out linearly in time on  $G_1$ -squares. This produces the coexistence result in the single-species case in environment II. The extinction result in this case follows trivially since if  $D > 1 - p_{c,2}$ , the  $G_1$ -squares form only finite clusters and hence the process dies out.

To prove the corresponding results for the two-species case, we replace the argument in Bramson *et al.* (1989) by the argument in Durrett & Swindle (1991) to show coexistence in the two-species model. The rescaling argument is then the same as above. The extinction result follows for the same reason as above.

We now assume environment III. Suppose  $K$  and  $L$  are chosen so that  $(K/L)^2 = D$ . We will again use a rescaling argument to show survival. The  $L \times L$  squares and the  $K \times K$  squares are arranged as shown in Fig. 1(c). The squares we will use in the rescaling argument are  $(L - K) \times (L - K)$  squares at the intersections of corridors. These squares consist of undestroyed sites and are connected via  $K \times (L - K)$

rectangles of undestroyed sites. A similar argument as the one we used to show survival in the single-species model on environment II will show that for any  $\eta > 0$ , if the density of 1's in one of these squares at the intersection of two corridors is close to  $1 - 1/\lambda_1$  at time 0, then the density of 1's in a neighboring such square will be close to  $1 - 1/\lambda_1$  at time  $T = \kappa L^2$ ,  $\kappa$  appropriate, and the density of 1's in the former square will remain close to  $1 - 1/\lambda_1$  for all times in the interval  $[0, T]$ , with probability at least  $1 - \eta$  for  $M_1$  sufficiently large. To get across the corridor connecting the two squares, one can use standard estimates from percolation theory which can be found in Durrett (1988). We omit the details. Extinction is proved in a similar way.