

Extinction in Multispecies and Spatially Explicit Models of Habitat Destruction

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Submitted June 5, 1997; Accepted January 21, 1998

Keywords: habitat destruction, spatial model, extinction, competition.

Loss of habitat due to human activities is a major threat to biological diversity (Ehrlich and Ehrlich 1981; Wilson 1988). Recent models of competition among sessile organisms predict that as habitat is destroyed, the species that are first to become extinct will be those that are the superior competitors (Nee and May 1992; Tilman et al. 1994, 1997). In these models, competition occurs among individuals for suitable sites that can be occupied by at most one individual. Species are ordered in a strict competitive hierarchy. If a propagule lands in a site occupied by an individual of a species lower in the hierarchy, it immediately replaces the inferior competitor. In order to allow coexistence of many species, these models assume a trade-off between competitive and colonization abilities, with those species higher on the competitive hierarchy assumed to be less able to make propagules to colonize sites that are empty or occupied by an inferior competitor. This trade-off allows coexistence, because the inferior competitors can survive as fugitive species.

The result that habitat destruction can lead to the extinction of the best competitor is a consequence of the assumed trade-off between competitive and colonization ability. Habitat destruction occurs through the loss of habitable sites, thereby decreasing the effective colonization rate of all species. This loss is felt most heavily by the poorest colonizers (the best competitors). With habitat destruction, the reduction in the effective colonization

rate of superior competitors makes them incapable of persisting. Stated more directly, the conclusion of these models is that habitat destruction leads to the extinction first of the poor colonizers.

Here, I investigate two assumptions of these models. First, by relaxing Tilman et al.'s (1994, 1997) assumptions about the colonization rates of successive species in the competitive hierarchy, I show that in fact the best competitors may not be the first to become extinct during habitat destruction. Moreover, as habitat destruction proceeds, some species may be driven to extinction only to reestablish in the community following more extensive habitat destruction that drives more competitive species to extinction. Thus, the models of Tilman et al. (1994, 1997) and others allow a much richer collection of results than initially suspected.

Second, Tilman et al.'s (1994, 1997) analytical model does not account for the spatial location of sites on the landscape; dispersing propagules are equally likely to land in any site in the universe of habitat. Here, I investigate the consequences of spatial structure by analyzing the simple case in which dispersing propagules are more likely to land in sites closer to their source. In this case, dispersal of propagules depends on both the number of propagules produced and the distance that they travel from their source. In contrast, spatially implicit models characterize the colonization ability of species only by the number of propagules produced, because dispersal distance is effectively infinite. For the spatially explicit case, I assume that habitat destruction reduces the total size of contiguous habitat but does not fragment the area of suitable habitat. I show that when there is a trade-off between the number of propagules produced and competitive abilities, the consequence of habitat destruction is similar to that exhibited by the spatially implicit model: although the best competitor may become extinct first with the reduction in the size of the area of suitable habitat, this is not necessarily the case. Furthermore, even though greater production of propagules increases the persistence of a species, greater dispersal distance decreases the persistence of a species. Therefore, these two components of colonization have opposite effects on persistence.

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The Spatially Implicit Model

Consider a large collection of sites, each of which can be permanently destroyed, empty, or inhabited by an individual of species i , where i is between 1 and N . Individuals of species i produce propagules at rate c_i (called the colonization rate) and individuals of all species die at rate m (see table 1 for a summary of variables). In the spatially implicit model, dispersal is assumed to be uniform over the habitat. If the site where a propagule lands is empty but not destroyed, the site is successfully colonized by an individual of species i . Furthermore, following others (Hastings 1980; Nee and May 1992; Tilman et al. 1994, 1997), the species are ordered by their competitive ability: if a propagule of species i lands on a site occupied by an individual of species j , it instantly displaces the current resident if $i < j$ and fails to colonize the site if $i \geq j$. In this article, competitive ability refers to the ability of a species to win a given site and does not refer to the overall proportion of sites occupied by that species. With these assumptions, the proportion of sites occupied by species i , p_i , is determined by the mean-field equations

$$\begin{aligned} \frac{dp_i}{dt} &= c_i p_i \left(1 - D - \sum_{j=1}^i p_j \right) - m p_i - \sum_{j=1}^{i-1} c_j p_i p_j \\ &= \left[\begin{array}{c} \text{successful colonization} \\ \text{of available sites} \end{array} \right] \\ &\quad - \left[\begin{array}{c} \text{density-independent} \\ \text{mortality} \end{array} \right] \\ &\quad - \left[\begin{array}{c} \text{displacement by} \\ \text{superior competitors} \end{array} \right], \end{aligned} \quad (1)$$

where D is the proportion of destroyed sites (Nee and May 1992; Tilman et al. 1994, 1997). Note that equations (1) are appropriate as a model of competition in metapopulations and are not limited to the individual-based interpretation taken here.

To coexist in the community with no habitat destruction, inferior competitors must produce more propagules than superior competitors. The criteria for species 1 through i to coexist when $D = 0$ are

$$c_{i \text{ odd}} > \left(\frac{c_2 c_4 \dots c_{i-1}}{c_1 c_3 \dots c_{i-2}} \right)^2 m$$

and

$$c_{i \text{ even}} > \left(\frac{c_1 c_3 \dots c_{i-1}}{c_2 c_4 \dots c_{i-2}} \right)^2 \frac{1}{m}. \quad (2)$$

Nee and May (1992) analyzed equations (1) for two species and found that species 1, the superior competitor, is always driven to extinction by less destruction than species 2. Tilman et al. (1994, 1997) extended this work to N species with equal mortality rates and found that species become extinct in order from best to worst competitor when their abundances in the pristine ($D = 0$) habitat are geometrically decreasing from species 1 to N , equal, or increasing from species 1 to N .

Will the best competitor always be the first to become extinct in communities where species have equal mortality? No. It is possible to construct a community of three or more species in which a species other than the best competitor becomes extinct first. In general, to determine when this will occur, I solve for the N -species equilibrium as a function of D :

$$\hat{p}_{i \text{ odd}} = \frac{c_1 c_3 \dots c_{i-2}}{c_2 c_4 \dots c_{i-1}} (1 - D) - \frac{c_2 c_4 \dots c_{i-1}}{c_1 c_3 \dots c_i} m$$

and

$$\hat{p}_{i \text{ even}} = \frac{c_1 c_3 \dots c_{i-1}}{c_2 c_4 \dots c_i} (D - 1) + \frac{c_2 c_4 \dots c_{i-2}}{c_1 c_3 \dots c_{i-1}} m. \quad (3)$$

When no species has been driven to extinction, increasing habitat destruction decreases the equilibrium density of odd-ranked species and increases the equilibrium den-

Table 1: Summary of symbols used

Symbol	Description
p_i	Proportion of sites occupied by species i
c_i	Colonization rates of species i (rate of propagule production)
m	Mortality rate
D	Proportion of sites destroyed
\bar{D}_i	Smallest value of D at which species i becomes extinct locally
D_i	Largest value of D at which species i can persist locally
L	Length of habitat in one dimension
$k_i(x)$	Dispersal kernel of species i
$1/\alpha_i$	Standard deviation of $k_i(x)$; mean dispersal distance of species i
L_c	Critical habitat size below which the population cannot persist

sity of even-ranked species. This alternation occurs because habitat destruction decreases the proportion of sites occupied by species 1 to the benefit of species 2 (species 2 can colonize neither destroyed sites nor those occupied by species 1, but species 1 can actively displace individuals of species 2). The increase of species 2 depresses the density of species 3, and so on. Defining \bar{D}_i as the smallest amount of destruction at which species i becomes extinct (i.e., the amount of destruction at which $\hat{p}_i = 0$),

$$\bar{D}_{i\text{odd}} = 1 - \frac{c_2^2 c_4^2 \dots c_{i-1}^2}{c_1^2 c_3^2 \dots c_{i-2}^2 c_i} m. \tag{4}$$

For species 1 to become extinct before all other species, \bar{D}_1 must be less than $\bar{D}_{i\text{odd}}$ for all species i ; that is,

$$c_i > \frac{c_2^2 c_4^2 \dots c_{i-1}^2}{c_1^2 c_3^2 \dots c_{i-2}^2} \tag{5}$$

must hold for all odd i . These inequalities are met for communities in which $c_i/c_{i-1} > c_{i-1}/c_{i-2}$ for all i (“noninteractive communities,” sensu Hastings 1980); in words, the relative rate of propagule production of species i to its next better competitor must be more than the relative rate of propagule production of this next better competitor to its next better competitor. This condition need not hold for all communities, and when it does not hold, an inferior competitor will become extinct before a better competitor.

Tilman et al. (1997) define D_i as the smallest amount of destruction such that species i cannot persist for any value of D greater than D_i and show that if $c_1 < c_2 < \dots < c_m$, then $D_1 < D_2 < \dots < D_i$. The variable \bar{D}_i as I describe above defines the least amount of destruction that will drive species i extinct, regardless of whether species i can persist for greater D . The variable D_i does not necessarily equal \bar{D}_i : if species i becomes extinct before a superior competitor, there is a finite range of D in which its equilibrium density is 0 but above and below which it persists (fig. 1). The upper limit of this range can be found by setting the appropriate densities equal to 0 in equations (3) and solving for D , renumbering species to account for those that are extinct. Thus, a species may be driven to extinction in a community and yet can reenter the community as habitat destruction increases to a value where the species has a positive equilibrium. If the community reaches equilibrium faster than habitat destruction increases, such a species will become extinct locally and must rely on recolonization from another remnant patch in the region to attain its positive equilibrium. If the amount of habitat destruction increases rapidly, the species may never reach its zero equilibrium and there-

fore may rebound in density as D increases without the need for recolonization from outside.

The main result from the spatially implicit model is that extinction need not proceed in order from best to worst competitor in communities of three or more species with equal mortality rates. The order of extinction depends on the ratios of colonization rates of species adjacent in the competitive hierarchy.

The Spatially Explicit Model

Equations (1) imply that all destroyed habitat is equally accessible to all propagules and therefore treats all patterns of habitat destruction in the same way. This limitation has been partially addressed through simulation models (Tilman et al. 1994, 1997; Dytham 1995; Lavorel et al. 1995; Moilanen and Hanski 1995; Bascompte and Solé 1996) and verbal arguments (Budiansky 1996; Loehle and Li 1996; McCarthy et al. 1997) but has not been examined analytically. Here I derive a model that incorporates space explicitly, treating all remnant habitat as a contiguous block surrounded by destroyed habitat.

Suppose that sites are arranged in a one-dimensional habitat of length L . The only significant difference between the one- and two-dimensional cases is that the one-dimensional case is easier to analyze; I briefly discuss a two-dimensional analog later. As in the spatially implicit model, c_i is the rate at which propagules are produced and m is the rate at which adults die. Instead of landing on each site with equal probability as in the spatially implicit model, propagules of species i are sent to a site a distance x from the parent with probability $k_i(|x|)$. The distribution k_i is a nonincreasing function of distance called a “dispersal kernel,” with $\int k_i(x) dx = 1$. If dispersal occurs over a spatial scale sufficiently larger than the size of an individual, the density of sites occupied by species i is given by

$$\begin{aligned} \frac{\partial p_i(x, t)}{\partial t} &= \int_{-L/2}^{L/2} c_i k_i(x-y) p_i(y, t) dy \left[1 - \sum_{j=1}^i p_j(x, t) \right] \\ &\quad - m p_i(x, t) - p_i(x, t) \sum_{j=1}^{i-1} \int_{-L/2}^{L/2} c_j k_j(x-y) p_j(y, t) dy \\ &= \left[\begin{array}{l} \text{propagules arriving at } x \\ \text{from all sites in habitat} \end{array} \right] \left[\begin{array}{l} \text{vacant sites} \\ \text{at } x \end{array} \right] \\ &\quad - \left[\begin{array}{l} \text{density-independent} \\ \text{mortality} \end{array} \right] - \left[\begin{array}{l} \text{displacement} \\ \text{by superior} \\ \text{competitors} \end{array} \right], \end{aligned} \tag{6}$$

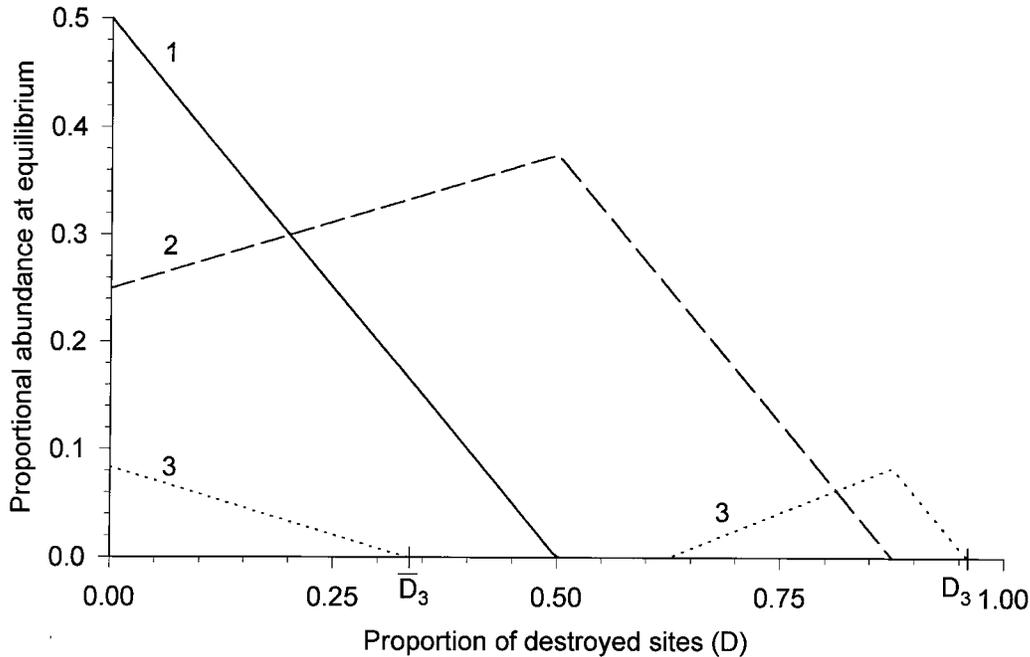


Figure 1: Equilibrium abundance of three competing species obeying spatially implicit equations (1) as a function of habitat destruction. Parameters are: $c_1 = 2.0 \text{ yr}^{-1}$, $c_2 = 8.0 \text{ yr}^{-1}$, $c_3 = 24.0 \text{ yr}^{-1}$; $m = 1.0 \text{ yr}^{-1}$. Species 1 is represented by a solid line, species 2 is represented by a dashed line, and species 3 is represented by a dotted line. $\bar{D}_1 = D_1 = 0.5$, $\bar{D}_2 = D_2 = 0.875$, and $\bar{D}_3 = 0.3333 < D_3 = 0.9583$. Notice that species 3 becomes extinct locally first but can reestablish as destruction is increased.

where population density p_i now varies in space, which is indexed by $-L/2 < x < L/2$. The first term of the right-hand side of equations (6) accounts for successful colonization (a weighted sum of propagules from all individuals in the habitat multiplied by the density of empty sites at x), the second term accounts for density-independent mortality, and the final term accounts for displacement by superior competitors; compare equations (6) with the spatially implicit equations (1). Colonization of sites outside the habitat is impossible ($p_i(x, t) = 0$ for $x < -L/2$ or $x > L/2$). Analytically, I will consider the one species equation,

$$\frac{\partial p(x, t)}{\partial t} = \int_{-L/2}^{L/2} ck(x-y)p(y, t)dy[1 - p(x, t)] - mp(x, t). \quad (7)$$

Equation (7) is a cousin of the more widely studied reaction-diffusion equations (see Okubo 1980 and Holmes et al. 1994 for reviews), and, like some reaction-diffusion models (Skellam 1951; Kierstead and Slobodkin 1953; Ludwig et al. 1979; Cantrell and Cosner 1994), it has a critical habitat size L_c below which too many propagules disperse out of the habitat to allow the population to persist. The variable L_c tells us how much habitat must be left undestroyed for a population to persist and

can be thought of as inversely related to D_i from the spatially implicit model. If the dispersal kernel is an exponential distribution ($k(x) = \alpha e^{-\alpha|x|}/2$, where $1/\alpha$ is the mean dispersal distance), using a result of Kot and Schaffer (1986),

$$L_c = \frac{2}{\alpha} \sqrt{\frac{m}{c-m}} \tan^{-1} \left(\sqrt{\frac{m}{c-m}} \right) \quad (8)$$

(see appendix for details). The exponential distribution often fits seed dispersal kernels well (Willson 1993), and numerical solutions of equation (7) using other non-increasing kernels with exponentially bounded tails give similar results. This result also holds for square two-dimensional habitats of area L^2 . Numerically solving a two-dimensional analog of equation (7) using the dispersal kernel analogous to the exponential, $k(x, y) = \alpha e^{-\alpha\sqrt{x^2+y^2}}/(2\pi\sqrt{x^2+y^2})$, I found that the square root of the critical habitat area follows equation (8).

The variable L_c is a strictly decreasing function of c (fig. 2). If species 1 and 2 have the same dispersal kernel and can coexist in the pristine habitat, when habitat is reduced to the L_c of species 1, species 2 can persist because $c_1 < c_2$. Analytical treatment of communities of three or more species is complicated by the fact that species 1 through species $i-1$ are not guaranteed to be extinct

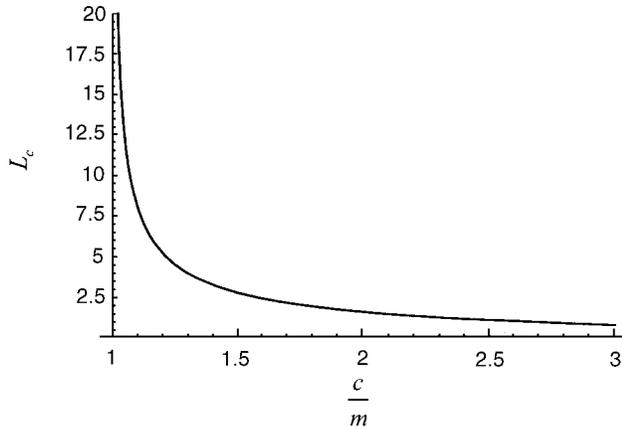


Figure 2: Critical habitat length, L_c , predicted by equation (8) as a function of the ratio of colonization to mortality rate, c/m , with mean dispersal distance $1/\alpha = 1$. Because the critical habitat size is directly proportional to the mean dispersal distance, the critical length is plotted in terms of multiples of the mean dispersal distance.

when species i first becomes extinct. In this case, the critical habitat length given by equation (8) does not necessarily hold and cannot be determined by linearizing around the zero solution as in the appendix. Van Kirk and Lewis (1997) describe a technique that can be used to approximate the critical lengths in the spatially explicit model, but I will focus on numerical results here. Numerical solutions of equations (6) show extinction order similar to the spatially implicit case discussed above (fig. 3).

Until now, I have assumed that all species have identical dispersal kernels. The effect of different dispersal distances can be seen from equation (8): L_c increases linearly with the mean dispersal distance $1/\alpha$. If farther dispersal is correlated with a higher colonization rate, poorer competitors would be relatively more susceptible to extinction. In this case, extinction can proceed in any order as habitat is destroyed, including species 2 becoming extinct first (fig. 4). Two characters commonly associated with weedy species, production of many propagules (large c) and long-range dispersal (large $1/\alpha$), have opposite effects on susceptibility to habitat destruction in this model.

By accounting for the actual location of destroyed sites in a spatially explicit model, I found the amount of habitat needed to support a population (eq. [8]). This critical habitat size decreases with colonization rate and increases with mean dispersal distance. Numerical solution of the model showed that if dispersal distances of all species are the same, extinction order will be similar to that of the spatially implicit model (fig. 3). If poorer competitors disperse farther than better competitors, they lose more

propagules to destroyed sites and require more habitat to persist; extinction can proceed in any order (fig. 4).

Discussion

I have expanded on previous models of competition and habitat destruction (Nee and May 1992; Tilman et al. 1994, 1997) in two ways: by investigating a wider range of parameters of the multispecies spatially implicit model than had been done, and by deriving an analytical spatially explicit model that retains the spatial nature of habitat loss. In both models, the extinction order depends on the relative colonization rates of competitors. Using the spatially explicit model, I derived the critical habitat size required for a single species to persist and numerically investigated extinction in communities of more than two competitors.

The amount of habitat that can sustain a population in the spatially explicit model is often extremely small. For example, consider the dogbane *Apocynum sibirica*, a prairie plant that disperses 63% of its propagules within 20 m (Willson 1993). If its colonization rate in empty habitat is twice its mortality rate, then its critical habitat size $L_c^2 = (31.4 \text{ m})^2 = 990 \text{ m}^2$. Under the simplifying assumptions of this model, habitat destruction has to be massive to cause the deterministic extinction of sessile species that coexist because of a colonization-competition trade-off. Spatially explicit simulations show this same result (Dytham 1995; Tilman et al. 1997). In an experiment, Holt et al. (1995) created patches of different sizes (32, 288, and 5,000 m^2) in a recently abandoned agricultural field and tracked the vegetation through the first 6 yr of secondary succession. They found similar plant communities in patches of all sizes and no effect of patch size on species richness per unit area sampled.

Because the critical habitat size in this model is so small, it is likely that species would feel other effects of habitat destruction before the loss of propagules to destroyed sites becomes important. This may deemphasize the extinction risk of superior competitors. McCarthy et al. (1997) reviewed the empirical literature and found no evidence of increased extinction risk of superior competitors. While it is important to know that common, superior competitors may be at risk of extinction, it may be premature to focus conservation effort on these species instead of rare ones.

In these models, I do not consider the effect of fragmentation as addressed by percolation theory (O'Neill et al. 1988; Turner 1989) and as studied using simulations (Lavorel et al. 1995; Bascompte and Solé 1996). Fragmentation can induce a metapopulation structure when the populations in patches of remnant habitat are susceptible to extinction due to local disasters or demo-

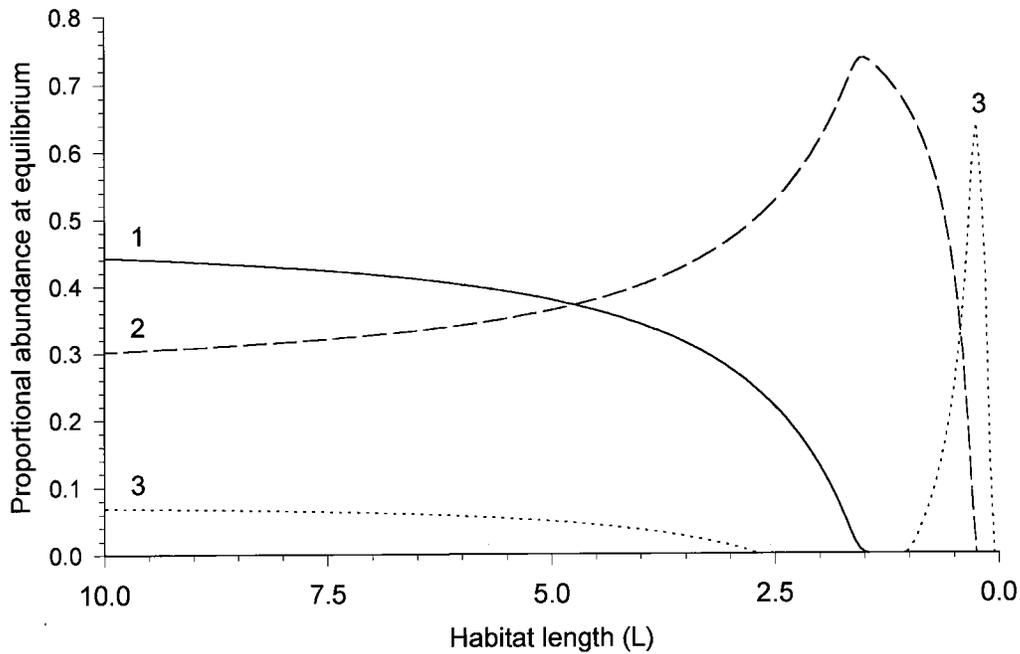


Figure 3: Equilibrium abundances averaged across the intact habitat of three competing species obeying the spatially explicit equations (6). Dispersal parameters $\alpha_i = 1.0$ for all species; all other parameters are as in figure 1. Compare this figure with the corresponding figure from the spatially implicit case (fig. 1). Notice that destruction has negligible effects on species proportions in relatively large habitats (species proportional abundances are nearly constant for large L).

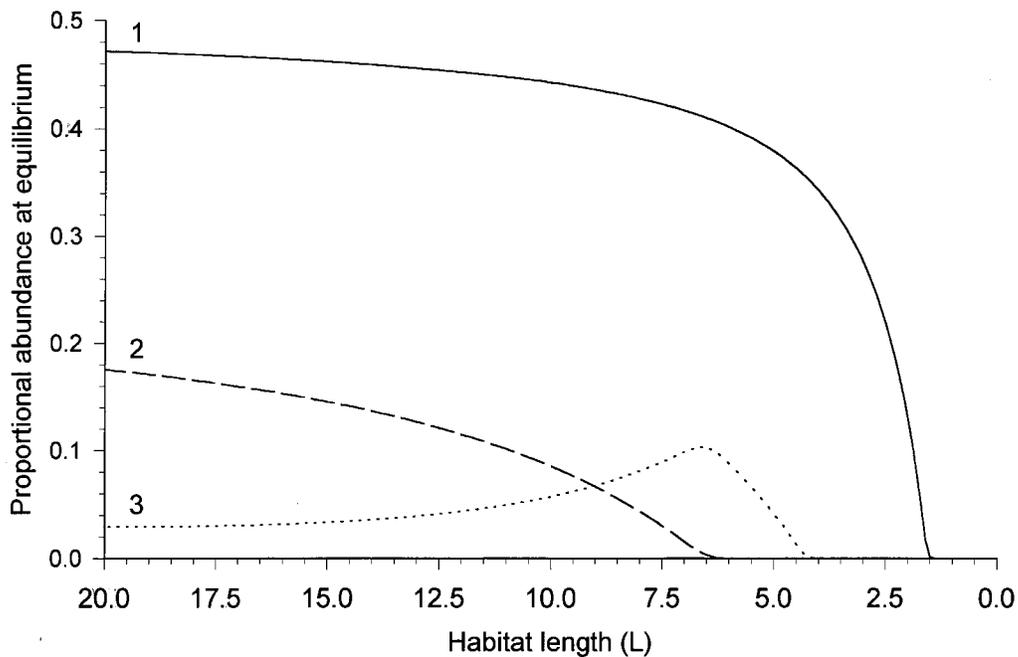


Figure 4: Equilibrium abundances averaged across intact habitat of three competing species obeying the spatially explicit equations (6). Here poorer competitors disperse farther: $\alpha_1 = 1.0$, $\alpha_2 = 0.15$, and $\alpha_3 = 0.05$; other parameters are as in figures 1 and 3. Because species 2 and 3 disperse farther than in figure 3, they become extinct when less habitat is destroyed.

graphic stochasticity. Recolonization of an isolated patch after a local extinction would rely on long-range dispersal from another remnant patch. When the population has been fragmented into isolated, extinction-prone patches, increased dispersal distance could aid persistence, in contrast to the results of my spatially explicit model, which focuses on one unfragmented remnant patch. Lavorel et al. (1995) investigated the optimal dispersal distance in a fragmented landscape and found it was often quite small.

Although the critical patch sizes I found are small, these results should not be taken as license to continue the destruction of native habitat. In this note I consider only one mechanism of coexistence, and the models analyzed ignore demographic and environmental stochasticity (Leigh 1981; Lande 1993). More realistic models must be considered when further evaluating the relationship between habitat size and extinction.

Acknowledgments

C. Lehman, E. Litchman, S. Naeem, C. Neuhauser, E. Siemann, and D. Tilman helped this note through discussions and valuable comments on drafts. I also thank A. Ives, E. G. Leigh, Jr., and an anonymous reviewer for constructive remarks. I was partially supported by a University of Minnesota Graduate School Fellowship during this work.

APPENDIX

Finding the Critical Habitat Size

To determine the critical patch length, I analyze the linear stability of the trivial solution $p(x) = 0$. Let the solution have the form $p(x, t) = e^{\lambda t} \mu(x)$, substitute into equation (7), and linearize around $p(x)$ to get

$$\lambda e^{\lambda t} \mu(x) = c \int_{-L/2}^{L/2} k(x-y) e^{\lambda t} \mu(y) dy - m e^{\lambda t} \mu(x). \quad (\text{A1})$$

After simplifying,

$$(m + \lambda) \mu(x) = c \int_{-L/2}^{L/2} k(x-y) \mu(y) dy. \quad (\text{A2})$$

Following Kot and Schaffer (1986), the exponential form of the dispersal kernel $k(x)$ allows this to be recast as the boundary value problem

$$\begin{cases} \mu''(x) + \alpha^2 \frac{c - (m + \lambda)}{m + \lambda} \mu(x) = 0 \\ \mu'(-L/2) = \alpha \mu(-L/2) \\ \mu'(L/2) = -\alpha \mu(L/2) \end{cases}. \quad (\text{A3})$$

When largest eigenvalue $\lambda = 0$, the trivial solution loses stability. This determines the critical length L_c , which satisfies the following equality

$$\tan \frac{\alpha \beta L_c}{2} = \frac{1}{\beta}, \quad \beta = \sqrt{\frac{c-m}{m}}. \quad (\text{A4})$$

Solving for L_c , I find

$$L_c = \frac{2}{\alpha} \sqrt{\frac{m}{c-m}} \tan^{-1} \left(\sqrt{\frac{m}{c-m}} \right). \quad (\text{A5})$$

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Associate Editor: Anthony R. Ives