HABITAT DESTRUCTION, DISPERSAL, AND DETERMINISTIC EXTINCTION IN COMPETITIVE COMMUNITIES

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Abstract.—An analytical model of competitive coexistence in spatial habitats, modified to address habitat destruction, predicts that the most abundant species can be among the first species driven extinct by habitat destruction, given that abundant species are the poorest dispersers and best competitors. This contrasts with the classical view of biased extinction of rare species. Here we explore the robustness of this prediction both analytically and in spatially explicit simulations of more realistic cases. The prediction proved surprisingly robust. The poorest dispersers, which in this model generally are the best competitors and may be the most abundant species, were among the first driven extinct by habitat destruction whether they were abundant or rare, had short or long range dispersal, or reproduced continuously or periodically; whether competitive displacement was immediate or gradual; whether habitat destruction was clumped, uniform, or random and whether destruction occurred at once or progressively; and whether the habitat was large or small. The amount of destruction sufficient to produce extinctions changed considerably as model assumptions changed, but the biased extinction remained. The underlying reason for the robustness of our conclusions is the broad assumption that inferior competitors persist by virtue of greater dispersal ability and/or lower mortality rates. Further work on the forces allowing multispecies coexistence is thus essential for understanding the effects of habitat destruction on extinction.

Habitat destruction has long been thought to lead to the biased extinctions of rare species. It directly causes the immediate extinction of rare endemic species that reside only in the areas destroyed. It also reduces population densities (Herkert 1994) and causes stochastic extinction of rare species by increasing the probability that demographic fluctuations force population size to 0 (e.g., Terborgh and Winter 1980; Shaffer 1981; Simberloff 1984; Soule 1986). However, it recently has been hypothesized (e.g., Spies et al. 1994) that habitat destruction and the accompanying fragmentation also can cause the biased, deterministic, but time-delayed extinction of abundant species in remnant undisturbed habitat fragments by modifying the local dynamics of colonization and extinction (e.g., Nee and May 1992; Tilman et al. 1994; Moilanen and Hanski 1995). It is this third novel but potentially important effect of habitat destruction that we explore here. Because abundant species can be major controllers of ecosystem processes, their biased extinction can have significant ramifications for ecosystem functioning (e.g., McNaughton 1993; Vitousek and Hooper 1993; Tilman et al. 1996).

To predict the effects of habitat destruction on the abundances and extinction...
of individual species in a multispecies community, it is first necessary to know
the mechanisms of interspecific interaction that allow species to coexist in an
intact community. This is so because species can be highly interactive, with
changes in abundances of one or more species after habitat destruction propagat-
ing through the entire community in a manner that depends on the mechanisms
of interspecific interaction. Here we explore one such model of multispecies
coexistence and how it predicts that diversity and species composition should
respond to habitat destruction. Such analyses are needed for other models of
coeexistence.

Our model has the potential to explain the stable coexistence of a potentially
unlimited number of species competing as if for a single limiting resource within
local neighborhoods of a spatially subdivided habitat (Tilman 1994). It is a model
of a single community in which each individual organism occupies a site, in which
all interspecific competition occurs at such sites, and in which sites, each the size
of a single individual, are joined together by the movement of propagules among
them (Tilman 1994). It is thus an implicitly individual-based model of local com-
petition and dispersal in a multispecies community. It seems to explain much of the
plant diversity in the prairie grasslands of Cedar Creek Natural History Area
(Tilman 1990, 1994) and incorporates the essential processes that are thought to
explain diversity in numerous other habitats (e.g., Levin and Paine 1974; Arm-
Hanski 1983, 1990; Paine 1984; Shmida and Ellner 1984; Connell 1985; Cohen

The model that we use is not a metapopulation model in the strict sense of that
word, but rather an individual-based model. However, it commonly has been
referred to as a metapopulation model because of its history (e.g., Levins 1969;
A metapopulation model should mimic the dynamics of a patchy, segregated
habitat in which there are numerous local populations (rather than individuals)
joined together by dispersal (colonization) among them (e.g., Harrison 1994;
Harrison et al. 1995). Levins's (1969) original formulation, on which our model
is based, does not do this well but can be modified to be a reasonable model
of individual-based competition in a spatially subdivided habitat (Tilman 1994).
Levins's model also has been modified to make it a better mimic of true metapop-
ulation dynamics (e.g., Gotelli 1991; Hanski 1991). To distinguish our model
from metapopulation models, we refer to ours as a model of multispecies spatial
competition.

The traits of species threatened by habitat destruction, and the number of
resulting extinctions, depend on the mechanisms that allow species to persist in
an intact habitat. Skellam (1951), Levins and Culver (1971), Horn and MacArthur
(1972), Werner and Platt (1976), Hastings (1980), Shmida and Ellner (1984), and
others have shown that a trade-off between local competitive ability and dispersal
ability can explain the coexistence of two species. Other studies have found this
trade-off in intertidal communities (Levin and Paine 1974; Paine 1984), grassland
communities (Werner and Platt 1976; Platt and Weis 1977; Gleeson and Tilman
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1991), and coral reefs (Stone 1996). Here we use a simple model (Tilman 1994, modified from Hastings 1980) that predicts that a potentially unlimited number of species can stably coexist in a homogeneous but spatial habitat in which all species compete for a single limiting resource (Tilman 1994). This requires interspecific trade-offs among dispersal, competition, and/or longevity and a limit to similarity.

Nee and May (1992) used a similar but two-species model and found that habitat destruction led to reduced abundance of the superior competitor (but poorer disperser) and increased abundance of the inferior competitor (but better disperser) in undisturbed remnant habitat fragments. The shift to greater abundance of the poorer competitor (better disperser) occurred even though sites did not undergo any internal intrinsic changes. This model was extended (Tilman et al. 1994) to any number of competing species, but only for a case in which species had a geometric abundance sequence; it revealed biased extinction of the most abundant species following habitat destruction. In this article, we first present the model and analytically explore the effects of habitat destruction for five cases. Next we develop a spatial simulator that we use to examine the robustness of the analytical model when its simplifying assumptions are made more realistic.

THE ANALYTICAL MODEL

Let a habitat be subdivided into sites, each the size of a single adult for sessile species or of an individual’s territory for motile species. The proportion of sites occupied by individuals of this species is \( p \), the dispersal (propagule production or colonization) rate is \( c \), the mortality rate is \( m \), and the proportion of permanently destroyed sites is \( D \). The initial proportion of occupied sites must not exceed \( 1 - D \). Propagules that enter a destroyed site do not survive, and destroyed sites do not produce propagules. This leads to a model slightly modified from that of Levins (1969):

\[
\frac{dp}{dt} = cp(1 - D - p) - mp. \tag{1}
\]

To extend this to numerous species, we assume throughout this article that species compete as if for a single limiting resource, with species always ranked from the best competitor (species 1) to the worst (species \( n \)). This approach is comparable to ranking the species from that with the lowest \( R^* \) value for the resource (Tilman 1982) to that with the highest. Species 1, the best competitor (lowest \( R^* \)), would displace all other species from any site that it invaded. Species 1 could invade any intact site. Species 2, the next best competitor, could displace all species except species 1, and so on, to the last species, species \( n \), which would be displaced by all other species, could displace none, and could invade only unoccupied sites. Such invasion and displacement abilities have been observed in experimental studies of nutrient competition among both algae and grasses (Tilman and Sterner 1984; Tilman and Wedin 1991; Wedin and Tilman 1993).

Using subscripts to identify species \( i \) and \( j \), the model can be extended to any
number of species, with one equation per species and with the equation for the \( i \)th species being

\[
\frac{dp_i}{dt} = c_i p_i \left( 1 - D - \sum_{j=1}^{i-1} p_j \right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j.
\]  

(2)

Here dispersal and mortality have specific parameters, but the competitive hierarchy is implicit in the form of the equations. The sums in equation (2) establish a hierarchy by having the abundance of a species only be affected by species of greater competitive rank (i.e., lower values for \( j \)). The summed initial abundances of all species must not exceed \( 1 - D \), \( D \) is a constant, and \( p_j \geq 0 \) for all \( i \). This model applies to permanent habitat destruction. It can be modified to determine the effects of periodic disturbances or changes in mortality rates (Loehle and Yi 1996). The rate of change in the abundance of each species depends on its rate of dispersal to intact sites not occupied by superior competitors or by itself, on the rate at which it dies, and on the rate at which it is displaced by superior competitors. The competitive hierarchy means that a species is only affected by its superior competitors.

In intact (virgin) habitats (defined as \( D = 0 \), the appropriate interspecific trade-offs among competitive ability, dispersal \( (c) \), and mortality \( (m) \) can allow stable coexistence of an unlimited number of species (Tilman 1994). Here we explore the effects of permanent habitat destruction on multispecies communities that stably persist in intact habitats. For such a community of \( n \) competing species (Tilman 1994), at equilibrium the proportion of sites occupied by the \( i \)th species is

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

(3)

This is derived from equation (2) by setting \( dp_i/dt = 0 \). The equations are solved in order starting with species 1 and are subject to the constraint that \( \hat{p}_i \geq 0 \) for all \( i \).

**Effects of Habitat Destruction on a Single Species**

Let us start by considering a single species, living by itself. From equation (1), its equilibrial proportion of sites occupied is

\[
\hat{p} = 1 - D - \frac{m}{c}.
\]

This species would go extinct (\( \hat{p} = 0 \)) in a habitat in which a portion of the habitat, \( D \), was destroyed, where

\[
D = 1 - \frac{m}{c}.
\]  

(4)

This means that the amount of habitat destruction required to drive this species
extinct increases with its dispersal rate, $c$, assuming that $c > m$ and $m$ is a constant (fig. 1A). The greater the dispersal rate of the species is, or the lower its mortality rate is (fig. 1A), the more habitat destruction it can endure. It is interesting to note that the critical amount of habitat destruction, $D$, is equal to the equilibrrial proportion of sites occupied by this species in an intact habitat:

$$\hat{p}_i = 1 - \frac{m}{c}.$$ 

Thus, if this species occupied 5% of the sites in an intact habitat, it would be driven to eventual extinction in undisturbed remnant patches by the permanent random destruction of just 5% of the sites in that habitat (Tilman et al. 1994). However, as shown later, this value depends critically on many of the assumptions of the analytical model, especially on the spatial patterning of dispersal and habitat destruction.

Habitat Destruction and Multispecies Extinction

Next consider the effects of habitat destruction on a community of many species that can coexist in an intact habitat. The best competitor, species 1, would behave as described by equation (4), becoming extinct once $D \geq 1-m_i/c_1$. As $D$ increases, abundances of other species may rise and fall and even reach 0 several times, but for each species there would be a value of $D_i$ called $D_i$, at all values above which species $i$ would be unable to invade into or persist in the community. These $D_i$ values are derived later for each of four markedly different cases. These four cases are necessary because there is no a priori reason to assume a particular relationship between the equilibrrial abundances of species in an intact habitat and their dispersal or competitive abilities. These relationships, though, determine the quantitative dependence of the number of extinctions on the amount of habitat destroyed (e.g., Tilman et al. 1994). The four cases include having the best competitor be either the most abundant or least abundant species and having species experience equal or differing mortality rates. The methods of analysis for the four cases are identical, differing only in the functional relations among dispersal ability, competitive ability, and mortality. To avoid redundancy, we derive one case and summarize the full results in figure 2.

Four Analytical Cases

Case 1. Best competitors most abundant and equal mortality.—For this case, the equilibrrial species abundances in an intact habitat are taken to be a geometrically decreasing function of competitive rank, and all species are assumed to experience a mortality rate of $m$. The abundance of the best competitor is $\hat{p}_1 = z$, and that of the $i$th species is $p_i = z(1 - z)^{i-1}$; that is, the best competitor is the most abundant species.

Case 2. Equally abundant species and equal mortality.—For this case, all species have identical abundances, $\hat{p}_i = z$, in an intact habitat and have identical mortality rates, $m$. The maximum number of species, $n$, would be $n < 1/z$.

Case 3. Poorer competitors more abundant and equal mortality.—For this case, the poorest competitor is the most abundant species. Equilibrrial abundances
Fig. 1.—Dispersal ability and the amount of habitat destruction required for extinction. 
A. The amount of habitat destruction that leads to the extinction of the best competitor of a single species living by itself depends on its dispersal and mortality rates, as illustrated for three different mortality rates. 
B. In a multispecies competitive community in which all species experience the same mortality rate, the amount of habitat destruction that leads to extinction of each species (numbered 1–8) depends on dispersal, with each species falling at a point on the curve determined by its dispersal rate. This illustrates case 1, using the same parameters described in the legend to figure 3 for case 1. Graphs for cases 2 and 3 would be similar.
## Equation Table

**Case 1**

\[ c_i = \frac{m}{(1 - z)^{2i-1}} \]
\[ D_i = 1 - (1 - z)^{2i-1} \]
\[ E = \frac{\ln (1 - D) + \ln (1 - z)}{2\ln (1 - z)} \]
\[ \frac{\delta E}{\delta D} = \frac{1}{2(D - 1) \ln (1 - z)} \]

**Case 2**

\[ c_i = \frac{m}{(zi - 1)(zi - 1 - 1)} \]
\[ D_i = z(2i - 1 - z(i - 1)) \]
\[ E = \frac{2 + z - \sqrt{4 - 4D + z^2}}{2z} \]
\[ \frac{\delta E}{\delta D} = \frac{1}{z\sqrt{4 - 4D + z^2}} \]

**Case 3**

\[ c_i = \frac{2m - 2 - z(i - 1)(1 - m)}{(2 - z(i - 1))(2 - z(i + 1))} \]
\[ D_i = \frac{\sqrt{4z(4 + z(1 - 0)(1 + 0))}}{4} \]
\[ E = \sqrt{\frac{4 + z - \sqrt{16 - 16D + 8z + z^2}}{2z}} \]
\[ \frac{\delta E}{\delta D} = \frac{4}{\sqrt{2z(16 - 16D + 8z + z^2)} \left(4 + z - \sqrt{16 - 16D + 8z + z^2}\right)} \]

**Case 4**

\[ c_i = \frac{iz(1 - z(i - 1))}{(1 - zi)(1 - z(i - 1))} \]
\[ D_i = \frac{2(1 - 3i + 2iz(i - 1))}{z(i - 1) - 2} \]
\[ E = \frac{3 + 2D - 2z - \sqrt{9 - 10D + D^2 + 4z - 4Dz + 4z^2}}{4z} \]
\[ \frac{\delta E}{\delta D} = \frac{1}{4z} \left(1 + \frac{5 - D + 2z}{\sqrt{9 - 10D + D^2 + 4z - 4Dz + 4z^2}}\right) \]

**Fig. 2.** Equilibrium mathematical relations for the four analytical cases described in the text. Here \( c \) is dispersal rate, \( m \) is mortality rate, \( z \) is the equilibrium abundance of species \( i \) in an intact habitat, \( i \) refers to the \( i \)th species in the competitive hierarchy, \( D_i \) is the amount of habitat destruction required for extinction of species \( i \), and \( E \) is the number of species driven extinct, at equilibrium, by permanent destruction of a portion \( D \) of the habitat.

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in an intact habitat are an increasing function of competitive rank, with $\bar{p_i} = iz$.

The value of $z$ is subject to the constraint $z < 2/(n^2 + n)$, where $n$ is the number of species.

Case 4. Equally abundant but poorer competitors with higher mortality.—In this case, poorer competitors have progressively higher mortality rates and species are equally abundant, with $p_i = z$ and $m_i = iv$ (where $v$ is the mortality rate of the best competitor). Here the total number of species must be less than $1/z$.

A fifth class of cases, considered separately, involves inferior competitors that are outliers (i.e., are unusually rare and/or have markedly different mortality rates than superior competitors). These five cases thus explore the effects of habitat destruction on a variety of multispecies communities that differ in the relationships among abundance, dispersal ability, competitive ability, and mortality. In all cases, diversity is maintained in intact habitats by a trade-off among competition, dispersal, and mortality.

**Analytical Solution of the Four Cases**

To analyze each of these cases, it is first necessary to determine the dispersal rates, $c_i$, that allow species 1 through $n$ to coexist stably in an intact habitat. To do this, we substitute the mortality rate and equilibrial abundance of species $i$ into equation (3) and solve for $c_i$, the dispersal rate of species $i$. For case 1, this gives

$$c_i = \frac{m}{(1 - z)^{2v - 1}}.$$  \hspace{1cm} (5)

Comparable calculations give $c_i$ for cases 2, 3, and 4 (fig. 2). For all four cases, $c_i < c_i + 1$ (i.e., poorer competitors have progressively greater dispersal rates) (fig. 3A).

The critical relationship determining the order of extinction of species is, as proven in the appendix, the ranking of species by the proportion of sites that each would occupy in an equilibrial monoculture in an intact habitat. This is $\bar{p}_i = 1 - m/c_i$. If and only if $1 - m_1/c_1 < 1 - m_2/c_2 < \ldots < 1 - m/c_i$ will species go extinct in ranked competitive order (i.e., species 1 followed by 2, by 3, \ldots) as habitat destruction increases. This is comparable to extinction being ordered from the poorest to the best disperser if all species experience the same mortality rate. As already discussed, species 1 goes extinct if $D \equiv 1 - m_1/c_1$ because its colonization rate is insufficient to compensate for losses to mortality and habitat destruction. If species 1 is extinct, species 2, because it is the best remaining competitor, would necessarily go extinct once $D \equiv 1 - m_2/c_2$. Similarly, species $i$ must necessarily go extinct once $D > 1 - m_i/c_i$. Interactions with superior competitors might make a species go extinct at a lower $D$, but its extinction is unavoidable for $D > 1 - m/c_i$. Thus, species go extinct in ranked competitive order if $D_1 < D_2 < \ldots < D_i < D_{i+1}$, which is comparable to having $1 - m_1/c_1 < 1 - m_2/c_2 < 1 - m_i/c_i < 1 - m_{i+1}/c_{i+1}$. The complete proof is in the appendix.

For cases 1–3, species have identical mortality rates, $m$. Because $c_i$ increases with competitive rank, $i$ (fig. 3A), this necessarily means, for cases 1–3, that $1 - m/c_i < 1 - m/c_{i+1}$ and that species go extinct, as habitat destruction is
increased, in order of their dispersal abilities, with the poorest dispersers going extinct first. For case 4, \( m_i = iv \). Using the relationship for \( c_i \) from table 1 gives \( 1 - m/c_i = 1 - ((1 - iz)(1 - z(1 - i))/((1 - z(i - 1)/2)). \) The partial derivative of this, with respect to \( i \), is positive for \( i < 1/z \). Even for the limiting case of \( i = 1/z \), which is a completely full habitat (impossible at equilibrium; Tilman 1994), the partial is \( 2z^2/(1 + z) \), which is positive. Positive partial derivatives mean that species of higher rank (higher \( i \)) have higher \( 1 - m_i/c_i \) and thus again go extinct in order of their dispersal abilities, the poorest dispersers first, as habitat destruction increases (appendix).

For all four cases, the amount of habitat destruction sufficient to cause the extinction of species \( i \) is \( D_i = 1 - m_i/c_i \). This is easily illustrated for cases 1–3, for which all species have mortality of \( m \) (fig. 1B). The dispersal rate of each species \( (c_i) \) determines the amount of habitat destruction at which it goes extinct. The abundance of each species and its competitive rank determine its \( c_i \). As figure 1B shows for case 1, these species all fall on the same extinction curve, with the position determined by their dispersal rate. Thus, with identical mortality rates, the species most susceptible to extinction are those with the lowest dispersal rates, which, given a dispersal-competition trade-off, are necessarily the better competitors. If species do not have equal mortality rates, the amount of habitat destruction that a species can endure before extinction depends on its dispersal relative to mortality (i.e., on \( 1 - m/c \)), and a better disperser with a high mortality rate could go extinct at a lower level of destruction than a poorer disperser with a relatively lower mortality rate.

Substitution of the \( c_i \) for each case gives the \( D_i \) for each case (fig. 2). For case 1,

\[
D_i = 1 - (1 - z)^{2i-1}.
\]  

Let the total number of species driven extinct, at equilibrium, by a given amount of habitat destruction be \( E \). Because species are driven extinct in order starting with species 1, habitat destruction of \( D_i \) leads to the eventual loss of \( i \) total species. Thus, for a given \( D \), \( E \) is equal to the \( i \) of equation (6). Substituting \( E \) for \( i \) in equation (6) and solving for \( E \) give the dependence of the number of species driven extinct on the proportion of habitat destroyed for case 1:

\[
E = \frac{\ln[(1 - D)(1 - z)]}{2\ln(1 - z)}.
\]  

Similar analyses lead to the values of \( E \) for cases 2, 3, and 4 (fig. 2). Although \( E \), thus defined, need not be an integer, the number of extinct species is \( E \) rounded down to the nearest integer. In all four cases, the number of extinctions that would occur at equilibrium is an increasing function of the amount of habitat destroyed (fig. 3B), but the shape of this important function differs markedly from case to case and depends on the quantitative relationships among abundance, competitive rank, dispersal, and mortality.

Stone (1996) suggested that coral reefs are unusually sensitive to destruction-related extinction because superior competitors are rare. Consider, for instance, a situation in which better competitors are rarer, as in case 3, but in which
equilibrial abundances in an intact habitat are an exponentially (rather than linearly) increasing function of competitive rank, with \( \hat{p}_i = p_0e^{ik} \). This causes the number of species driven to eventual extinction to increase rapidly with destruction (curve labeled \textit{Rare}, for best competitors rare, in fig. 3C), in marked contrast to the case in which better competitors are more abundant. This illustrates the effect of the relationship between competitive ability and abundance on extinction.

The number of additional extinctions caused by a small increase in the proportion of habitat destroyed is given by the partial derivative of \( E \) with respect to \( D \) (fig. 2). For case 1, this is

\[
\frac{\partial E}{\partial D} = \frac{1}{2(D-1) \ln(1-z)}
\]

The dependence of \( \partial E/\partial D \) on \( D \) shows that a given increment in habitat destruction leads to many more eventual extinctions when a larger proportion of a habitat has already been destroyed for cases 1, 2, and 4 (fig. 3D). However, if inferior competitors are increasingly more abundant than their superior competitors, a situation that Stone (1996) suggests occurs in coral reefs, the greatest number of extinctions per unit of habitat destroyed can occur when an intact habitat experiences its first destruction (e.g., case 3; fig. 3D).

\textit{Outlier Species}

As \( D \) is increased for the preceding four cases, species go extinct in order of dispersal ability, with the poorest dispersers (best competitors) going extinct first. However, if species have different mortality rates, it is possible to assemble multispecies communities for which this does not occur (appendix; fig. 4). Given that species can coexist in an intact habitat, the necessary condition for extinctions to occur in an order other than by dispersal ability is for one or more species to have \( 1 - m_i/c_i \) values that are smaller than those of one or more superior competitors. Although it is mathematically impossible for species 2 to go extinct before species 1 (appendix), it is possible for species 3 to go extinct before species

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**Fig. 3.**—Relationships among variables in the four analytical cases, with \( J \) referring to case 1, that is, geometric abundance series (here \( z = \frac{n}{i} \)) and equal mortality; 2, the case with equally abundant species (here \( z = \frac{n}{5} \)) with equal mortality; 3, the case with poorer competitors more abundant (here \( z = \frac{n}{5n} \)) and equal mortality; and 4, the case with equal abundance (here \( z = \frac{n}{25} \)) and higher mortality of poorer competitors. In all cases, \( m = 0.05 \). Curves are based on the equations in table 1. A, Dispersal rates \( c_i \) of species for each case (species ranked from best competitor, species 1, to poorest). B, Extinction debt, \( E \), for each case (i.e., number of species driven to time-delayed extinction after destruction of a portion, \( D \), of the habitat). C, The number of time-delayed extinctions caused by a given amount of habitat destruction for two cases. For the case labeled \textit{Rare}, the better competitors are progressively rarer \( (p_i = p_0e^{ik}, p_0 = 0.01, k = 0.039, 1 \leq i \leq 40) \). The curve \textit{Abundant} is for case 1 with \( z = 0.075 \) (eq. [7]). Modified from Stone (1996). D, Partial derivative of \( E \) with respect to \( D \) (i.e., additional extinction caused by additional habitat destruction, for each case).
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Note.—All species had identical mortality rates of 0.05 yr$^{-1}$. Dispersal rates ($c$) for each species were chosen such that, for each of 24 cases, abundances in an intact habitat were at the level desired for one of three abundance series (a geometric series, a series in which all competitors were equally abundant, or a series in which poorer competitors were more abundant in the intact habitat). See the legend to fig. 7 for more details.
Fig. 4.—A case in which the third best competitor (species 3) is driven extinct at a lower amount of habitat destruction than the other species. Here \( m_1 = m_2 = 0.001, m_3 = 0.3, c_1 = 0.002, c_2 = 0.008, \) and \( c_3 = 1.6. \)

1 and 2 (fig. 4). To estimate the likelihood of such events, we repeatedly drew \( c_i \) and \( m_i \) from uniform random distributions \((0 < c_i < 4; 0 < m_i < 1)\). From many such draws, we selected all cases in which either three or four species had parameters that led to stable coexistence in an intact habitat. In 97% of such three-species communities, the top three species were driven extinct in order of dispersal ability. Similarly, species went extinct in order of dispersal ability in 75% of the four-species communities. Moreover, even when a superior disperser went extinct out of order, the species that had \( 1 - m_i/c_i \) values in order of their competitive ranks went extinct in order and at the predicted \( D_i \) value.

The Dynamics of Extinction and the Extinction Debt

All of the relationships discussed so far apply at equilibrium. However, the model predicts a time delay between habitat destruction and the resulting extinctions. Consider, first, an intact habitat containing 25 coexisting species (with parameters chosen to mimic grassland species, i.e., \( m_i = 0.05 \), or a 20-yr average life span) that experienced a single act that destroyed 35% of the habitat (fig. 5A). This led to the predicted extinction of the four poorest dispersers (best competitors), but it took from 175 to 400 yr for the abundances of these species in remnant patches to fall to 1/10 of their initial abundances. Destruction of 70% of the habitat led to the time-delayed extinction of the 12 poorest dispersers (12 best competitors; fig. 5B). The number of species driven extinct and their identities are correctly predicted by the previously derived equilibrial relationships.
Such delayed extinctions have been considered analogous to a destruction-caused "debt" that is paid with the future extinction of species; thus, they are termed the extinction debt (Tilman et al. 1994).

Assuming that \( D \) is constant, a species undergoes an approximately exponential decline to extinction. Species \( i \) goes extinct when \( D > 1 - m_i/c_i \), which can be rewritten as \( D = k_i(1 - m_i/c_i) \), where \( k_i \) is an arbitrary constant greater than 1. From equation (2) it is seen that \( dN_i/dt \sim (k_i - 1)(m_i - c_i) \) when the abundance of species \( i \) is sufficiently low and all its superior competitors nearly are extinct. Because this species can only persist in an intact habitat if \( c_i > m_i \), and because \( k_i > 1 \), the term on the right-hand side of this approximation must be negative. This means that there is an approximately negative exponential decline in the abundance of species \( i \) once \( D > 1 - m_i/c_i \). The approximate time required for the abundance of a species to fall to 1/100 of its original abundance in remnant patches would thus be \( t_{1/100} = \ln(100)/(k_i - 1)(c_i - m_i) \). Thus, the smaller the difference between \( m \) and \( c \) is (but still constrained only to cases in which species can coexist in an intact habitat) and the smaller \( k \) is (i.e., the closer \( D \) is to \( D_i \)), the greater the time lag is between habitat destruction and extinction.

Consider, also, what would happen if the same 25-species community experienced continual, incremental (linear) increases in habitat destruction such that 5,000 or 500 yr were required for complete destruction of an intact habitat. With equal mortality rates and slow but incremental habitat destruction (fig. 5C), extinctions also are in order of dispersal ability. There is a "competitive cascade" in which even and odd levels in the competitive hierarchy respond as groups, and each group undergoes successive, out-of-phase increases and decreases in abundance as the poorest remaining disperser in a group is being driven extinct. When habitat destruction is more rapid (fig. 5D), all species decrease in abundance, but the poorest dispersers decrease the most rapidly and are the first to go extinct.

SPATIAL SIMULATIONS

How robust are these predictions—that is, how strongly do they depend on the numerous simplifying assumptions of the analytical model? Our analytical model assumes, for simplicity, that habitats are infinitely large, that dispersal is random across the entire habitat, that individual sites are permanently destroyed at random, that competitive displacement is instantaneous, and that reproduction and dispersal are continuous. To determine how these simplifying assumptions

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Fig. 5.—A, Dynamics of extinction following permanent destruction of 35% of an intact habitat originally containing 25 stably coexisting species. B, Dynamics of extinction for this same habitat, but after permanent destruction of 70% of the habitat. C, Dynamics of extinction for this same 25-species community during linearly increasing permanent habitat destruction that required 5,000 yr for the intact habitat to experience complete destruction. D, Similar dynamics, but for a case in which complete destruction required 500 yr. All cases are based on numerical solution of equation (2) with \( m = 0.05 \) yr\(^{-1}\), a geometric abundance series with \( z = 0.04 \), and the dispersal (colonization) rates of equation (5).
influenced the predictions given earlier, we developed a spatial simulator of multispecies competition that allowed us to relax these assumptions singly and in combination.

Our simulations use a hexagonal array of sites, each site being the size of the area occupied by a single individual. Each site could be in one of three states: permanently destroyed, habitable but presently unoccupied, or habitable and presently occupied by one or more species. In any instant of time, each occupied site produces propagules that either are immediately transmitted to the set of neighboring sites (for cases with continuous reproduction) or are transmitted once each year (for cases with seasonal dispersal). Depending on conditions being tested, the set of neighboring sites may be as small as the six immediately adjacent hexagonal sites or as large as the entire habitat. The higher the dispersal rate of a species is, the greater the probability is that a neighboring site will be colonized. If a propagule lands on a site that is destroyed or occupied by a superior competitor, it is lost. If it lands either on an unoccupied site or one occupied by an inferior competitor, it colonizes the site. Upon colonizing a site, an individual either may immediately displace an inferior competitor or may do so with some time delay. These processes are repeated each time step in the spatial simulator.

The simulations can be considered to be a stochastic cellular automaton (Lee et al. 1990) with a few states per site and with rules ascribing probabilities to transitions between states. When the rules are consistent with all assumptions made by the analytical model, simulations behave just as does equation (1), even though only the transition probabilities, not the mathematical equations themselves, are in the spatial simulator. Results become more stochastic, however, as eigenvalues are closer to 0 (Lehman and Tilman 1997). The relevant eigenvalues, for the model with $D = 0$, are given elsewhere (Tilman 1994).

**Relaxing Assumptions for Dispersal, Reproduction, and Displacement**

To determine how the assumptions of the analytical model influence the effects of habitat destruction on multispecies interactions, we used simulations to explore all eight combinations of global versus neighborhood (six neighboring sites) dispersal, continuous versus seasonal (once per year) dispersal, and immediate versus delayed (5-yr lag between invasion and displacement) competitive displacement. For each of these eight combinations, we established three different four-species communities, giving 24 combinations in total. Species parameters were chosen to mimic grassland herbaceous species in which competitive displacement occurs in 2–5 yr (e.g., Tilman and Wedin 1991; Wedin and Tilman 1994). All species had identical mortality rates of 0.05 yr$^{-1}$, which gives an average generation time of 20 yr. The three communities differed in the relative abundances of the four competitors in an intact habitat, with the following distributions: a geometric abundance sequence in which the best competitor was most abundant, all species were of approximately equal abundance, or the best competitor was the rarest and poorer competitors were increasingly more abundant. All species had identical mortality rates. Most simulations used a grid of 49 × 50 sites. Propagules that fell outside this region were lost (absorbing boundaries). Most simulations ran for 5,000 simulated years. Equilibrium was usually reached in about 1,000 yr.
HABITAT DESTRUCTION AND EXTINCTION

Each of the assumptions of the analytical model, when relaxed, had a detectable effect on the equilibrial abundance of one or more of the four competitors in an intact habitat. Specifically, local dispersal and seasonal dispersal led to markedly lower abundances of the best competitor or of any of the species when living in the absence of competitors. For multispecies communities, decreased abundance of the best competitor, and also changes in dispersal of all species, had ramifications down the competitive hierarchy. Delayed competitive displacement led to increased abundance of the second best competitor, and its increased abundance, plus the changes in competitive displacement, had ramifications down the competitive hierarchy.

The main purpose of the 24 cases was to determine the impacts of the relaxed assumptions on extinction. To do this, we first adjusted dispersal rates for each case such that each species had the desired equilibrial abundance in an intact habitat (i.e., the correct abundance for its geometric, equal, or decreasing series). We then determined the amount of habitat destruction required for extinction of each species in each of the 24 cases. In every case, species went extinct in order of their dispersal (and competitive) ability, with the poorest disperser (best competitor) first. The most ecologically realistic case, that in which there was local, seasonal dispersal and delayed displacement, shows this for all three abundance distributions (fig. 6A-C).

For all 24 cases, ANOVA was used to determine whether $D$, was significantly dependent on dispersal, reproduction, competitive displacement, or abundance distribution. The amount of habitat destruction needed for extinction of species 1, $D_1$, was significantly dependent on dispersal and on abundance distribution, but independent of reproduction and competitive displacement (table 1; fig. 7). Thus, making the later two assumptions more ecologically realistic had such minor effects on the extinction of species 1 as to be undetectable within the noise of the spatial simulator, given that dispersal rates already had been adjusted, as discussed earlier. As in the analytical model, greater abundance of the superior competitor in an intact habitat was associated with greater destruction needed for its extinction. Species 2, 3, and/or 4 were significantly affected by dispersal, competition, and abundance (table 1; fig. 7). Reproductive mode (continuous vs. discrete) did not have a detectable effect on $D$, for any species. Local dispersal, even though dispersal rates had been adjusted, still led to extinction of all four species at markedly lower destruction than that which occurred with global dispersal.

In total, these simulations demonstrate that our analytical model of multispecies spatial competition predicts the qualitative effects of habitat destruction but that the quantitative effects are dependent on the simplifying assumptions of the analytical model. In general, the analytical model predicts fewer extinctions at a given level of habitat destruction than do spatial simulations that include local dispersal and delayed reproduction.

Habitat Size

To determine the effects of the size of a remnant habitat fragment on extinction, we performed simulations of a case in which four competing species had a geometric abundance sequence in a large habitat. Holding mortality and dispersal
rates constant, we varied the size of a remnant habitat fragment (i.e., the total number of sites in the fragment) from six sites ($2 \times 3$) to 2,450 sites ($49 \times 50$). In all cases, the fragment was totally isolated. It was embedded in a region that provided no propagules and in which all propagules that left the fragment were lost (i.e., absorbing boundaries). We performed numerous simulations at each size, with more simulations for smaller sizes (e.g., 1,600 replicates for the $2 \times 3$ habitat) and fewer for large habitats (e.g., four replicates for the $49 \times 50$ case).

As fragment size decreased, species went extinct in order of their dispersal ability, with the poorest disperser (best competitor) going extinct first (fig. 8). The sharp decrease in the abundance of species 1, the poorest disperser and best competitor, as fragment size decreased from 20 (400 sites) to 10 (100 sites), is caused by the sharply increasing proportion of edge, which increased the loss of propagules, and differentially impacted it because of its low rate of propagule production. Its demise allowed species 2 to increase. However, in even smaller habitats, it similarly was impacted by edge effects and went extinct. This process continued as habitats were made smaller, with the best disperser, species 4, dominating the smallest fragments that could sustain life. Other simulations showed that species were driven extinct in order of dispersal ability as the shape of a habitat of fixed size was changed from a square block to an increasingly long and thin corridor. In all cases, increasing the proportion of habitat edge reduced the effective dispersal rate of a species until dispersal was less than mortality and the species went extinct. Species can go extinct sooner than this because of stochastic simultaneous mortality. Indeed, there is some probability of extinction in any finite habitat, and this probability can sometimes be large (Hanski et al. 1996).

**Spatial Patterning of Habitat Destruction**

With local dispersal, the spatial pattern of habitat destruction and the size and location of remnant fragments should influence extinction. To quantify this, we simulated equally sized habitats, each containing 9,900 sites ($99 \times 100$), that were divided into a checkerboard pattern of squares. Habitat destruction was imposed by permanently destroying a contiguous portion, $D$, of each square in the checkerboard. We did this for checkerboards containing from 1 to 625 squares. For any given $D$, this gave spatial patterns of habitat destruction ranging from one large

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**Fig. 6.**—Abundances of four competitors at 1,000 yr after various amounts of habitat destruction ($D$) were imposed, as predicted by the spatial simulator. For all cases, the spatial simulator was formulated to have local dispersal (to the six sites neighboring a given hexagonal site), delayed dispersal (once per year), and delayed competitive displacement. All species had $m = 0.05$ yr$^{-1}$. Numbers 1–4 refer to species 1–4, with species 1 being the best competitor. A. Dispersal rates ($c_3 = 0.095$, $c_4 = 0.183$, $c_5 = 0.4$, and $c_6 = 0.85$) given a geometric series in the intact habitat, with the best competitor most abundant. B. Dispersal rates ($c_3 = 0.088$, $c_4 = 0.132$, $c_5 = 0.270$, and $c_6 = 1.08$) chosen to have species approximately equally abundant in the intact habitat. C. Dispersal rates ($c_3 = 0.082$, $c_4 = 0.111$, $c_5 = 0.263$, and $c_6 = 5.99$) chosen to give greater abundance for poorer competitors in an intact habitat.
block of destruction to 625 uniformly spaced small blocks. For each checkerboard, the amount of habitat destruction required for extinction of species 1-4 was determined via spatial simulations. Compared to the analytical case, which corresponds to spatially random destruction of individual sites (dotted lines in fig. 9), checkerboard destruction led to much less extinction when there were a few large blocks of remnant habitat and to much more extinction when there were many small uniformly spaced remnants (fig. 9). For all but the smallest and largest checkerboard patterns of fragmentation, species went extinct in order from the poorest to the best disperser as habitat destruction increased (fig. 9).

Spatially random patterns of habitat destruction lie between uniform and clumped patterns. Our analytical model, which assumes spatially random habitat destruction, thus explores an intermediate case. For any given size of destroyed sites, the analytical case predicts extinctions that are intermediate between the greater extinctions expected from uniformly dispersed habitat destruction and the lower extinctions expected from clumped habitat destruction.

DISCUSSION AND SUMMARY

The random thinning of populations caused by habitat destruction is well known to lead to biased but stochastic extinction of rare species. We have shown that abundant species, if they are inferior dispersers, may also be subject to biased but deterministic extinction following habitat destruction, even when they are the best competitors in the community. This occurs, in essence, because of their low dispersal abilities relative to their mortality (i.e., to their lower $1 - m_i/c_i$ values).

This prediction of the potential for biased, time-delayed extinction of the originally most abundant species of intact habitats proved to be remarkably robust. Species went extinct in inverse order of their dispersal abilities and in order of their competitive ability, as single intact habitats were made progressively smaller, as habitats were fragmented by spatially random destruction of individual sites, as habitats were fragmented into a checkerboard pattern, and as habitats of a fixed size were made into increasingly longer and thinner corridors. This biased extinction following permanent habitat destruction occurred whether these

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Fig. 7.—Amount of habitat destruction required for extinction of species 1 ($D_1$), species 2 ($D_2$), and so forth, for each of the “treatments” used in the 24 cases run with the spatial simulator. Abun refers to the abundance distribution that was geometrically decreasing (I), all species equally abundant (2), or poorer competitors more abundant (3). Comp refers to the competition treatment, which was either immediate competitive displacement (I) or delayed competitive displacement (2). Disp refers to dispersal, which was either global (I) or local (2). Repr refers to the timing of reproduction and dispersal, which was either continuous (I) or annual (2). For each combination of parameters for a given abundance series, the dispersal rates of each species were adjusted to give each species the desired abundance in an intact habitat. These same dispersal parameters were then used for all of the intensities of habitat destruction for that case. See table 1 for results of ANOVA. Thin lines show standard errors.
species were the most or the least abundant species and whether there was local or global dispersal, continuous or seasonal dispersal, and immediate or delayed competitive exclusion.

The strength of our analytical prediction of biased extinction is the result of two intuitive processes: first, that poorer dispersers are more likely to go extinct following habitat destruction, and second, that inferior competitors must be better dispersers to coexist in a simple spatial habitat. As such, our model of multispecies spatial competition makes the robust prediction that species, including abundant species, that are good competitors but poor dispersers are highly susceptible to biased, deterministic, time-delayed extinction following habitat destruction. The loss of such species would leave behind a community composed of more rapidly dispersing, weedy species. Because the best competitor is relatively poor at replacing itself in this model, it is disproportionately inhibited by the decreased dispersal caused by habitat destruction. Similarly, it would be disproportionately harmed by increased mortality. For communities in which diversity depends on a colonization-competition trade-off, perhaps the best rule of thumb suggested
by this work is that the species most susceptible to deterministic extinction, whether abundant or rare in a pristine habitat, would be those with the poorest dispersal relative to mortality.

The number of extinctions resulting from a given amount of habitat destruction was highly dependent on the various simplifying assumptions of the analytical model. The analytical model predicted that species $i$ would go extinct once at least $D_i = 1 - m_i/c_i$ of a habitat was destroyed. However, results of our spatial simulations show that this should not even be used as a rule of thumb. Local dispersal, finite habitat size, and small, uniformly spaced remnant sites can lead to extinctions at much lower levels of habitat destruction than predicted by the analytical formula. In contrast, large, clumped remnant sites can allow species to survive at much higher levels of habitat destruction than analytically predicted. However, even the results from our spatial simulator must be viewed with caution because we assumed that mortality is a random and independent factor with a time-invariant mean and constant variance. In nature, climatic variation, epidemics, and outbreaks of predators tend to affect all individuals in a given region simultaneously. Such variability and regional synchrony in mortality may
threaten an entire region, greatly decreasing long-term viability even in large, clumped remnant habitats compared with simulation predictions (Hanski 1991).

This model predicts that the massive habitat destruction that has already occurred in many regions may be leading to extinction of some of the most abundant species on Earth, if they are among the best competitors and poorest dispersers. If superior competitors but inferior dispersers are rare, then the theory presented in this article and in Stone (1996) predicts that even low levels of habitat destruction can lead to the time-delayed extinctions of large numbers of such species (fig. 3C). It is thus critically important to determine the actual relationships among competitive ability, abundance, dispersal ability, and mortality in various communities because these determine the quantitative dependence of extinction on destruction. Diamond (1972) reported time lags of several hundred to several thousand years for extinctions of animals on land bridge islands formed by isolation by rising seas levels about 10,000 yr ago. However, it is not known how these species coexisted in intact habitats and whether the species that went extinct were poorer dispersers and superior competitors. This merits substantial additional research.

In total, this article has shown that the qualitative predictions (Nee and May 1992; Tilman et al. 1994) concerning biased extinctions are surprisingly robust to changes in biological assumptions. This robustness comes from our broad assumption that inferior competitors persist by virtue of greater dispersal ability or lower mortality rates, and it is to such communities that this theory applies. These theoretical predictions thus challenge us to better understand the mechanisms of interspecific interactions that allow species to coexist in various habitats, because we must know these to predict the qualitative and quantitative effects of habitat destruction on extinction.

ACKNOWLEDGMENTS

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APPENDIX

ORDERED EXTINCTION OF SPECIES

PROPOSITION

In the analytical model with $n$ species coexisting in a pristine habitat, random habitat destruction drives species extinct in competitive order if and only if their abundances in monoculture are also in competitive order. That is,

$$D_1 < D_2 < D_3 < \ldots < D_n \Leftrightarrow 1 - \frac{m_1}{c_1} < 1 - \frac{m_2}{c_2} < 1 - \frac{m_3}{c_3} < \ldots < 1 - \frac{m_n}{c_n}.$$
1. Proof of the Forward Direction

We assume \( D_1 < D_2 < D_3 < \ldots < D_n \) and prove that \( 1 - m_i/c_1 < 1 - m_2/c_2 < \ldots < 1 - m_i/c_i \). The proof is by induction, first establishing the condition for \( i = 2 \), then showing that it holds for all \( i \).

a) Recall that the equilibrial abundance of species \( i \) is

\[
\hat{p}_i = 1 - D - \frac{m_{i-1}}{c_i} \sum_{j=1}^{i-1} \hat{p}_j \left( 1 + \frac{c_j}{c_i} \right).
\]  

(A1)

Thus, when \( D = 0 \), the equilibrial abundance of species 2 is

\[
\hat{p}_i = 1 - \frac{m_2}{c_2} - \hat{p}_1 \left( 1 + \frac{c_1}{c_2} \right)
\]

\[= 1 - \frac{m_2}{c_2} - \left( 1 - \frac{m_1}{c_1} \right) \left( 1 + \frac{c_1}{c_2} \right)\]

\[= \frac{m_1}{c_1} - \frac{m_2}{c_2} - \hat{p}_1 \frac{c_1}{c_2}.
\]

Because the species coexist in virgin habitat, \( \hat{p}_1 \) and \( \hat{p}_2 \) above are both positive when \( D = 0 \), and because all the \( c_i \) are also positive, the right term immediately above is always negative. For \( \hat{p}_2 \) to be positive, therefore, it is necessary that the left term be positive, which means

\[
\frac{m_1}{c_1} > \frac{m_2}{c_2} \Rightarrow 1 - \frac{m_1}{c_1} < 1 - \frac{m_2}{c_2}.
\]

In other words, given coexistence in virgin habitat, the monocultural abundance of the second species is necessarily greater than that of the first (regardless of the relationship between \( D_1 \) and \( D_2 \)).

b) Next assume that the monocultural abundances are in competitive order for the first \( k \) species. That is, assume

\[
1 - \frac{m_1}{c_1} < 1 - \frac{m_2}{c_2} < 1 - \frac{m_3}{c_3} < \ldots < 1 - \frac{m_k}{c_k}, \text{ for } k < n.
\]

(We have just established this for \( k = 2 \).) Given that all species are driven extinct in competitive order (i.e., given that \( D_1 < D_2 < D_3 < \ldots < D_n \)), does the monocultural abundance for species \( k + 1 \) also fall in order? That is, we would like to prove that

\[
1 - \frac{m_k}{c_k} < 1 - \frac{m_{k+1}}{c_{k+1}}.
\]

Because we are given that \( D_k < D_{k+1} \), species 1 through \( k \) are all extinct when \( D = D_k \), but species \( k + 1 \) survives. At precisely this level of destruction, from equation (A1),

\[
\hat{p}_1 = \hat{p}_2 = \ldots = \hat{p}_{k-1} = 0,
\]

\[
\hat{p}_k = 1 - D_k - \frac{m_k}{c_k} = 0,
\]

and

\[
\hat{p}_{k+1} = 1 - D_k - \frac{m_{k+1}}{c_{k+1}} > 0.
\]
The last two relations jointly imply that
\[ \frac{m_k}{c_k} = 1 - D_k > \frac{m_{k+1}}{c_{k+1}}, \]
or
\[ 1 - \frac{m_k}{c_k} < 1 - \frac{m_{k+1}}{c_{k+1}}, \]
which was the inductive condition to be proved. Thus, we know that \( D_1 < D_2 < \ldots < D_n \) implies that \( 1 - m_1/c_1 < 1 - m_2/c_2 < \ldots < 1 - m_n/c_n \).

2. Proof of the Backward Direction

a) We assume \( 1 - m_1/c_1 < 1 - m_2/c_2 < \ldots < 1 - m_n/c_n \) and prove that \( D_1 < D_2 < \ldots < D_n \), again by induction. First, we have
\[ 1 - \frac{m_1}{c_1} < 1 - \frac{m_2}{c_2}, \]
which means
\[ 1 - D_1 - \frac{m_1}{c_1} < 1 - D_2 - \frac{m_2}{c_2}. \]  \hspace{1cm} (A2)

The left-hand side of inequality (A2) is the equilibrial abundance of species 1 when \( D = D_1 \), and by the definition of \( D_1, \hat{p}_1 = 0 \) there. This makes the right-hand side positive. But when \( \hat{p}_1 = 0 \), the right-hand side is simply the equilibrial value \( \hat{p}_2 \) at \( D = D_1 \), Thus, species 2 always survives at levels of destruction sufficient to drive species 1 extinct; hence, \( D_1 < D_2 \).

b) Next assume that the first \( k \) species are driven extinct in competitive order. That is, assume that
\[ D_1 < D_2 < D_3 < \ldots < D_k, \quad \text{for} \quad k < n. \]
(We have just established this for \( k = 2 \).) Given that all monocultural abundances are in order, does species \( k + 1 \) survive when species \( k \) is extinct? That is, we would like to prove that
\[ D_k < D_{k+1}. \]
When \( D = D_k \), we are given that species 1 through \( k \) are all extinct. As before, from equation (A1), when \( D = D_k \),
\[ \hat{p}_1 = \hat{p}_2 = \ldots = \hat{p}_{k-1} = 0, \]
\[ \hat{p}_k = 1 - D_k - \frac{m_k}{c_k} = 0, \]
and
\[ \hat{p}_{k+1} = 1 - D_k - \frac{m_{k+1}}{c_{k+1}}. \]
But since we have assumed that \( 1 - m_k/c_k < 1 - m_{k+1}/c_{k+1} \), we can write
\[ 1 - D_k - \frac{m_{k+1}}{c_{k+1}} > 1 - D_k - \frac{m_k}{c_k} = 0, \]
which is the same as
\[ \hat{p}_{k+1} > 0. \]
Thus, when \( D = D_k \), species 1 through \( k \) are extinct, but species \( k + 1 \) survives. Therefore, 
\[ 1 - m_1/c_1 < 1 - m_2/c_2 < \ldots < 1 - m_n/c_n \]
implies that \( D_1 < D_2 < \ldots < D_n \), and both directions (i.e., if and only if) of the proposition have been established.

**PROPOSITION**

In the analytical model with two or more species coexisting in a pristine habitat, random habitat destruction always drives the best competitor (species 1) extinct before the next best (species 2).

**Proof**

Part 1a shows that coexistence in a virgin habitat is sufficient to assure that 
\[ 1 - m_1/c_1 < 1 - m_2/c_2 \]
Part 2a shows that this inequality in turn is sufficient to assure that 
\( D_1 < D_2 \). Hence, species 1 always precedes species 2 to extinction.

**LITERATURE CITED**


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