Habitat destruction is the major cause of species extinctions. Significant species often are considered to be free of this threat because they are abundant in the undisturbed fragments that remain after destruction. Here we describe a model that explains multispecies coexistence in patchy habitats and which predicts that their abundance may be fleeting. Even moderate habitat destruction is predicted to cause time-delayed but deterministic extinction of the dominant competitor in constant patches. Further species are predicted to become extinct, in order from the best to the poorest competitor, as habitat destruction increases. Moreover, the more fragmented a habitat already is, the greater is the number of extinctions caused by added destruction. Because such extinction occurs generations after fragmentation, they represent a threat—a future, ecological cost of current habitat destruction.

The predictions are made by an extension of metapopulation models to multispecies competitions. Such models assume that organisms interact within a site, and that sites are linked via dispersal. If species that are competitively superior within sites are poorer dispersers, multispecies coexistence occurs, such predictions appear to explain biodiversity in many natural and plant communities. The models can be extended to incorporate habitat destruction. Our model includes the proportion of sites occupied by species (i.e., species-specific colonization rates (C), mortality or local extinction rates (m)), and habitat destruction (D): proportions of sites permanently destroyed. Sites may be as large as local populations14-18, as small as single individuals. Colonization and local extinction rates are relative to site size. Species are ranked from the best competitor (species 1) to the poorest. In lieu of competition coefficients, we assume that any occupied site dominated by a superior competitor (instantaneous) loses the inferior competitor. Thus species can colonize undestroyed sites not occupied by superior competitors (the first term of equation (1)), but is extinguished from any site (mediated by superior competitors) the last term. The equations for species i is:

$$\frac{dN_i}{dt} = \alpha_i(c_i - p_i e^{-(t/D_i)m_i} - \sum_{j \neq i} c_j p_j e^{-(t/D_j)m_j})$$

In equilibrium ($\alpha = 0/\mu = 0$) abundance is:

$$N_i = \frac{\alpha_i}{1 + \sum_{j \neq i} (1 + C_j)}$$

This must be solved from species 1 to $n$ with $\alpha = 0$ and $\beta > 0$ for all $i$. The best competitor has $N_i = 1 - (1/\beta + \mu)$, it undergoes deterministic extinction into a portion of habitat equal to its abundance in a virgin habitat is destroyed, because $\beta = 0$ when $D > 1 - m_i / \mu$, and $N_i = 1 - m_i / \beta$, which $D < 0.1$. If the dominant competitor occupies 10% of a virgin habitat, and this proportion of sites is randomly chosen and destroyed, its occupancy of 10% of sites in the undestroyed 90% might be enough to assure its survival. Surprisingly, the destruction of random sites has the same eventual effect as selectively destroying precisely those sites occupied by the dominant competitor. Although each species is always subject to stochastic extinction, this shows that the less abundant the dominant competitor is, the less habitat can be destroyed before its populations in undestroyed fragments are subject to deterministic extinction.

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FIG. 1 a. Results of an explicitly model simulation model of competition in which individuals are located and occupied only in one site. The habitat was divided into a hexagonal grid of 50 by 40 hexagons. Populations were initiated at sites distant from the hexagons, and population size was recorded at each site. In millions of years, population size was recorded at each site. b. Mortality for all species as a function of time, with a time delay $\tau$ of 0.1. c. Mortality for all species as a function of time, with a time delay $\tau$ of 0.1. d. Mortality for all species as a function of time, with a time delay $\tau$ of 0.1. 

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The $D$ that leads to extinction of other species depends on their traits. Let numerous coexisting species obey equation (1), and let species abundances in a virgin habitat form a geometric series $q^k$, where $q$ is the abundance of the best competitor. If all species experience the same loss ($m$), the required colonization rates are $c_i = m/(1 - q)^{1/m}$. Substituting into equation (3) and solving for $D$ predicts extinction of the $i$th species if $D > (1 - q)^{1/m}$. Because $D_i < D_i < D_j$, species go extinct from the best to the poorest competitors as habitat destruction increases. Similar results were obtained for three other abundance series and for equilibrium dispersal (Fig. 1a). Although our model is simple, more realistic elaborations that include explicit structural space, slower displacement of inferior competitors, and stochastic effects will not change its key results.

These results are surprising because the species initially most abundant in undisturbed habitat fragments can be the most susceptible to eventual extinction. Habitat destruction lowers effective colonization rates of all species, but those most adversely impacted species with lower colonization rates, that is better competitors. Because this requires an interspecific trade-off between colonization and competitive ability, one test of its applicability is to determine where this trade-off occurs.

Species dynamics after a bout of habitat destruction are shown for cases approximating tropical or temperate forests (Fig. 2). Properties of species that differ in habitat destruction and extinction of dominant competitors. Because extinctions occur after fragmentation, they are a "death" that comes due in the future. This model thus provides a mechanism for the slow extinctions that have occurred after habitat isolation, such as on islands created by rising sea levels6-8, or after experimental habitat fragmentation11, or deforestation8.

The number of species competitors driven extinct by habitat destruction (the extinction extent, $E$) increases sharply with habitat destruction (Fig. 1b).

$$ E = \left(1 - D \right)^{-1} - q $$

This comes from solving for $i$ in the inequality for $D_i$, because species go extinct in order from 1 to $n$. A slight increase in habitat destruction threatens many species if a large portion of a habitat already is destroyed (Fig. 1d). For instance, destroying an additional 1% of habitats causes extinction of $8$ times more species if $90\%$ versus $50\%$ of a region already is destroyed. Because $E$ is higher when the best competitor has low abundance (for example, $5\%$ as in a tropical forest, versus $99\%$ as in a temperate forest; Fig. 1b), increased habitat destruction threatens more superior competitors for tropical than temperate forests, and for forest interior than forest trail. Finally, the area-specific equation for landscapes and metapopulation models that predict that the fraction of total species threatened with extinction is a steeply rising function of habitat destruction (Fig. 1d), again showing that additional habitat destruction threatens more species in already fragmented habitats.

Although it is well known that habitat destruction causes extinctions, our results warn that an unanticipated effect of habitat destruction may be the selective extinction of the best competitors. These species are often the most efficient users of resources12 and major controllers of ecosystem functions13. Their extinction may have an insidious effect on ecosystems14-16 and field work is now required to determine the generality of the requisite competition-colonization trade-off, the applicability of this theory to particular species and ecosystems, and the spatial scale to which it may apply.