

Habitat destruction and the extinction debt

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HABITAT destruction is the major cause of species extinctions¹⁻³. Dominant 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 habitats⁴ 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 remnant patches. Further species are predicted to become extinct, in order from the best to the poorest competitors, 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 extinctions occur generations after fragmentation, they represent a debt—a future ecological cost of current habitat destruction.

The predictions are made by an extension of metapopulation models⁵⁻⁹ to multispecies competition⁴. 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 occurs⁴. Such processes seem to explain biodiversity in many animal¹⁰⁻¹⁶ and plant^{4,17-19} communities. The models can be extended to incorporate habitat destruction²⁰. Our model⁴ includes the proportion of sites occupied by species i (p_i), species-specific colonization rates (c_i), mortality (or local extinction) rates (m_i), and habitat destruction (D); proportion of sites permanently

destroyed). Sites may be as large as local populations^{5-8,12-14} or as small as single individuals⁴. Colonization and loss rates are determined relative to site size. Species are ranked from the best competitor for a limiting resource (species 1) to the poorest. In lieu of competition coefficients, we assume that any occupied site colonized by a superior competitor instantaneously loses the inferior competitor. Thus species i can colonize undestroyed sites not occupied by superior competitors (the first term of equation (1)), but is extinguished from any site invaded by superior competitors (the last term). The equation for species i is:

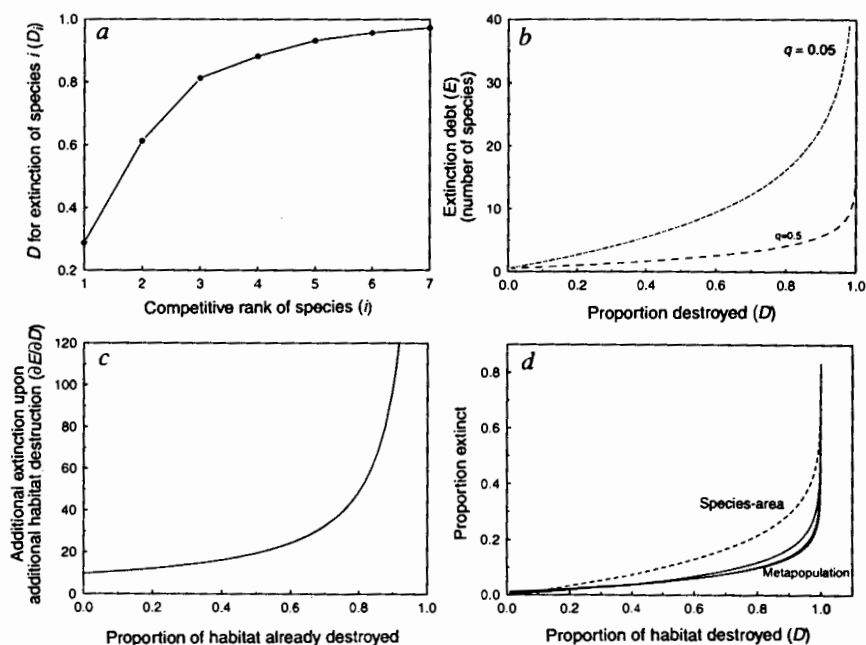
$$\frac{dp_i}{dt} = c_i p_i \left(1 - D - \sum_{j=1}^i p_j \right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j \quad (1)$$

Its equilibrium ($dp_i/dt=0$) abundance is:

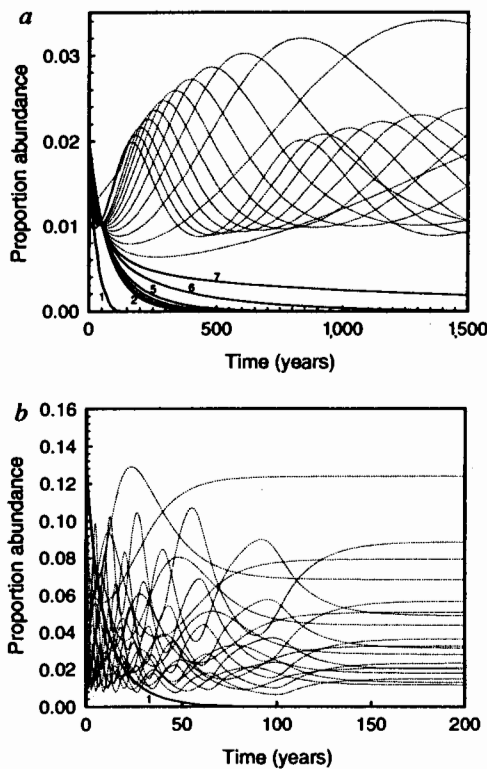
$$\hat{p}_i = 1 - D - \frac{m_i}{c_i} - \sum_{j=1}^{i-1} \hat{p}_j \left(1 + \frac{c_j}{c_i} \right) \quad (2)$$

This must be solved from species 1 to i , with $c_i > 0$ and $\hat{p}_i \geq 0$ for all i . The best competitor has $\hat{p}_1 = 1 - D - m_1/c_1$. It undergoes deterministic extinction once a portion of habitat equal to its abundance in a virgin habitat is destroyed²⁰ because $\hat{p}_1 = 0$ when $D \geq 1 - m_1/c_1$, and $\hat{p}_1 = 1 - m_1/c_1$ when $D = 0$. 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 undisturbed 90% might seem 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 rare species are always subject to stochastic extinction, this shows that the less abundant a dominant competitor is, the less habitat can be destroyed before its populations in undisturbed fragments are subject to deterministic extinction.

FIG. 1 a, Results of an explicitly spatial simulation model of competition in which individuals dispersed locally and interacted only in their site. The habitat was divided into a hexagonal grid of 50×49 sites. Propagules produced at a site dispersed randomly across the four neighbouring rings of sites. In hundreds of such simulations, permanent destruction of a proportion, D , of sites always led first to extinction of the best competitor, followed by the next best competitor, etc., at progressively greater D . Less habitat destruction was required for extinction in simulations than in equations (1-3), apparently because of a percolation effect. b, The dependence of E on D , as predicted by equations (1-3). Here, q is the abundance of the best competitor (species 1), and species abundances form a geometric distribution. More species are driven extinct when the dominant competitors are rare ($q=0.05$) than abundant ($q=0.5$), even though total species richness is identical. c, The more habitat that is already destroyed, the greater is the effect of additional destruction on extinction. This is based on $\partial E/\partial D = 1/(2(D-1) \ln(1-q))$. Here $q=0.05$, but the curve has similar shape for all $0 < q < 1$. d, The species-area curve for mainland habitats^{2,3} is $S = cA^z$ (where S is species richness, c is a constant, A is area, and z is a constant). We reformulated this to predict the proportion, P_s , of species lost because of habitat destruction, $P_s = 1 - (1-D)^z$ (dashed curve, labelled 'species-area', with $z=0.15$). For the metapopulation model, consider two regions—one species-rich and one species-poor—with roughly the same total numbers of individuals, N , and geometric abundance series. If the population size of the rarest



species is v , then $v = Nq(1-q)^{s-1}$. This gives $S = \ln[(1-q)/Nq]/\ln[1-q]$. The proportion, P_m , of species lost to destruction is thus $P_m = E/S$. Surprisingly, P_m is fairly independent of q but highly dependent on D (three solid curves; for q of 0.05, 0.2, 0.5).



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 series²¹, that is, $p_i = q(1-q)^{i-1}$, where q is the abundance of the best competitor. If all species experience the same loss (m), the required colonization rates⁴ are $c_i = m/(1-q)^{2i-1}$. Substituting into equation (2) and solving for D predicts extinction of the i th species if $D_i \geq 1 - (1-q)^{2i-1}$. Because $D_1 < D_2 < D_3 \dots$, 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 neighbourhood dispersal (Fig. 1a). Although our model is simple, more realistic elaborations that include explicit spatial structure, 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 most greatly impacts species with lower colonization rates, that is better competitors. Because this requires an interspecific trade-off between colonization and competitive abilities, 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.

FIG. 2 Species dynamics after habitat destruction. a, In numerical solution of equation 1, destruction of 1/3 of a habitat led to extinction of the 7 best competitors (solid curves). The 13 inferior competitors (dotted curves) persisted. Parameters were chosen to give a geometric abundance series in a virgin habitat, with the best competitor occupying 3% of sites (that is, $q = 0.03$) and with $m = 0.02 \text{ yr}^{-1}$, mimicking a tropical forest. Lower mortality rates would lead to slower extinctions. b, Same as a, except that the best competitor occupied 20% of the virgin habitat ($q = 0.2$), mimicking a temperate forest. Here only the best competitor (solid curve) was driven extinct by habitat destruction, and the remaining 19 species (dotted curves) persisted.

2a, b). Both cases show the 50 to 400 or more year lag between habitat destruction and extinction of dominant competitors. Because extinctions occur generations after fragmentation, they are a 'debt' 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 levels²²⁻²⁴, or after experimental habitat fragmentation²⁵, or deforestation²⁶.

The number of superior competitors driven extinct by habitat destruction (the extinction debt, E) increases sharply with habitat destruction (Fig. 1b):

$$E = \frac{\ln [(1-D)(1-q)]}{2 \ln [1-q]} \quad (3)$$

This comes from solving for i in the inequality for D_i , because species go extinct in order from 1 to i . A slight increase in habitat destruction threatens many more species if a large portion of a habitat already is destroyed (Fig. 1c). For instance, destroying an additional 1% of habitat causes extinction of 8 times more species if 90% versus 20% 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 50%, as in a temperate forest; Fig. 1b), increased habitat destruction threatens more superior competitors for tropical than temperate forests, and for larger and rarer vertebrates than for smaller, more abundant species. Finally, the species-area equation for mainlands and our metapopulation model both 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 resources²⁷ and major controllers of ecosystem functions²⁸. Thus, the extinction debt associated with habitat destruction may have an insidious effect on ecosystems²⁹⁻³⁰. Field work is now required to determine the generality of the requisite competition-colonisation trade-off, the applicability of this theory to particular species and ecosystems, and the spatial scales to which it may apply. □

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- Ehrlich, P. & Ehrlich, A. *Extinction* (Ballantine Books, New York, 1981).
- Wilson, E. O. *Biodiversity* (National Academy, Washington DC, 1988).
- Simberloff, D. *Zh. Obshch. Biol.* **45**, 767-778 (1984).
- Tilman, D. *Ecology* **70**, 2-16 (1994).
- Levins, R. & Culver, D. *Proc. natn. Acad. Sci. U.S.A.* **68**, 1246-1248 (1971).
- Horn, H. S. & MacArthur, R. H. *Ecology* **53**, 749-752 (1972).
- Cohen, D. & Levin, S. A. *Theo. Pop. Bio.* **39**, 63-99 (1991).
- Hastings, A. *Theo. Pop. Bio.* **18**, 363-373 (1980).
- Hanski, I. *Ecology* **64**, 493-500 (1983).
- Levin, S. A. & Paine, R. T. *Proc. natn. Acad. Sci. U.S.A.* **71**, 2744-2747 (1974).
- Gaines, S. & Roughgarden, J. *Proc. natn. Acad. Sci. U.S.A.* **82**, 3707-3711 (1985).
- Harrison, S., Murphy, D. D. & Ehrlich, P. R. *Am. Nat.* **132**, 360-382 (1988).
- Hanski, I. in *Living in a Patchy Environment* (eds Shorrocks, B. & Swingland, I. R.) 127-145 (Oxford Univ. Press, UK, 1990).
- Shorrocks, B. *Biol. J. Linn. Soc.* **43**, 211-220 (1991).
- Sale, P. F. *The Ecology of Fishes on Coral Reefs* (Academic, New York, 1991).
- Doherty, P. & Fowler, T. *Science* **263**, 935-939 (1994).
- Werner, P. A. & Platt, W. J. *Am. Nat.* **110**, 959-971 (1976).

- Shmida, A. & Ellner, S. *Vegetatio* **66**, 29-55 (1984).
- Grubb, P. J. in *Community Ecology* (eds Diamond, J. & Case, T.) 207-226 (Harper & Row, New York, 1986).
- Nee, S. & May, R. M. *J. Anim. Ecol.* **61**, 37-40 (1992).
- May, R. M. in *Ecology and Evolution of Communities* (eds Cody, M. L. & Diamond, J. M.) 81-120 (Harvard Univ. Press, Cambridge, MA, 1975).
- Diamond, J. M. *Proc. natn. Acad. Sci. U.S.A.* **69**, 3199-3203 (1972).
- Terborgh, J. *BioScience* **24**, 715-722 (1974).
- Case, T. J., Bolger, D. T. & Richman, A. D. in *Conservat. Biology* (eds Fielder, P. L. & Jain, S. K.) 91-125 (Chapman & Hall, New York, 1992).
- Lovejoy, T. E. et al. in *Extinctions* (ed. Nitecki, M. H.) 295-325 (Univ. of Chicago Press, Chicago, 1984).
- Bucher, E. H. *Curr. Ornithol.* **9**, 1-36 (1992).
- Chapin, F. S. A. *Rev. Ecol. System.* **11**, 233-260 (1980).
- Pastor, J., Aber, J. D., McCaugherty, C. A. & Melillo, J. M. *Am. Mid. Nat.* **108**, 266-277 (1982).
- Tilman, D. & Downing, J. A. *Nature* **367**, 363-365 (1994).
- Naem, S., Thompson, L., Lawler, S., Lawton, J. H. & Woodfin, R. *Nature* **368**, 734-737 (1994).