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HABITAT DESTRUCTION AND THE EXTINCTION DEBT REVISITED

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A very important analysis of the problem of habitat destruction¹ concluded that such destruction may lead to an extinction debt, which is the irreversible loss of species following a prolonged transient or delay. An error in interpretation of this model led the authors to apply the results to all types of habitat destruction, but in fact the model applies only to an across-the-board decrease in fecundity, not to disturbances. For repeated, spatially random disturbance, a different model applies. For habitat destruction on regional scales (reduction in ecosystem area without disturbance in remnant areas), one must, in contrast, apply species-area relations based on the distribution of different habitat types (e.g., elevational and rainfall gradients, physiographic and edaphic variability). The error in interpretation of the basic model is presented, followed by clarification of model usage and development of a new model that applies to disturbance events.

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The basic model assumes a uniform area gridded into cells of a size that one individual adult can occupy. Sites are linked via dispersal. If species that are competitively superior within sites are poorer dispersers, multispecies coexistence occurs². The model is defined in terms of 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). Species are ranked from the best competitor for a limiting resource (species 1) to the poorest. Superior competitors instantly outcompete inferior ones on undestroyed sites. The abundance equation for species i is

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

The terms on the right are, respectively, the reproduction, random mortality, and mortality due to competitive displacement. From (1), the equilibrium ($dp_i/dt = 0$) abundance is:

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

which must be solved from species 1 to i , with $c_i > 0$ and $\hat{p}_i \geq 0$ for all i .

Analysis of the reproduction term in (1) shows where the error has occurred. By rearrangement, reproduction is

$$c_i p_i - c_i p_i D - c_i p_i \sum_{j=1}^i p_j, \quad (3)$$

which is the maximum reproduction minus the effect of " D " (whatever D is), minus reproduction that fails because of superior competitors. Specifically, of the total average reproduction for species i ($c_i p_i$), a proportion $\sum_{j=1}^i p_j$ falls on sites that have superior competitors, and a proportion D falls on "destroyed" sites and also fails. The net effect is that D reduces fecundity across the board by $D\%$ for all species.

The spatially explicit simulation of this process in Tilman *et al.*¹ illustrates this interpretation. The authors created a hexagonal grid of 50 x 49 sites, with $D\%$ of the randomly located sites being destroyed and with reproduction dispersing randomly to neighbors. (Imagine $D\%$ of a grassland being covered by large stones.) In this case, reproduction falling on destroyed sites is not successful. This situation again corresponds to a $D\%$ reduction in fecundity across all species. Note, however, that this result depends on the random placement of destroyed sites at the scale of the dispersal of individuals (as in the Tilman *et al.*¹ simulation). Consider, by contrast, a case where destroyed sites are concentrated rather than scattered. For a 100 x 100 grid, with a central square block 30 cells wide destroyed ($D = 0.09$ or 9%), only the cells next to the edge of the destroyed area (4 x 30 cells) have their fecundity reduced by 50%, giving an overall reduction of $120 \times 0.5/9,100 = 0.0066$ or 0.66% effective D , not the nominal 9%. (Only the percentages in the remnant area are evaluated by p_i ; thus the 9,100 cells.)

This analysis shows that the result of Tilman *et al.*¹ is strongly dependent on the spatial configuration of destroyed sites and overestimates the extinction risk when disturbances are clustered. The random configuration of D sites at the scale of effective dispersal is essentially an extreme level of fragmentation equivalent to the suburbification of a forest, where the sizes of roads and home sites compared to tree dispersal and tree size form the proper analogy. Thus, the model of Tilman *et al.* does not apply generally to reduction in habitat area, but only to the limiting case of uniformly distributed, patchy habitat destruction on scales comparable to the patch occupancy size and dispersal distance of individuals. This case would not apply to prairie or forest remnants, for example, but it might apply to animals whose scale of landscape use (e.g., minimum territory size) is comparable to the scale of habitat fragmentation due to roads, fields, etc.

With respect to general reductions in habitat area, one cannot compare the loss of species predicted from (1) and (2) with the predictions of the species area curve model, which predicts species number as a function of area for islands and continents. Much of the increase in observed species number with area predicted by this model results from the progressive inclusion

of more habitat types (due to gradations in elevation, soil, rainfall, etc.) in larger areas³. In very uniform habitats, the change in species number with area can be very gradual. In remnant forest patches, patch area and species number may be unrelated if remnants represent uniform topographic sites⁴. The extinction debt model, in contrast, is specifically based on a model that seeks to explain multispecies coexistence within a uniform habitat. To relate this model to regional-scale habitat destruction and compare it to the species area curve, one would have to create a model of multiple habitats with relations within each habitat being governed by (1). To do this, one would have to remember that most species occur in more than one habitat. In fact, many species are weeds (high c_i and high m_i , low competitive ability) in some habitats but are good competitors in others. Thus, direct comparison of (1) and the species area curve model (as in Fig. 1d of Tilman *et al.* is not possible without a version of (1) with much more explicit spatial structure.

When fecundity is in fact reduced directly, (1) would also apply. For example, chemical pollutants could reduce fecundity of plants or animals across the board. If pesticides reduced pollinator abundance, then fecundity could again be reduced (more or less) across the board, as in (1). In this case, D does not represent "destroyed sites" but just a reduction in fecundity. For these cases, all of the results of Tilman *et al.*¹ about the extinction debt and the nonlinear effect of D hold. This argument suggests that heavily polluted areas could, in fact, be accruing substantial extinction debts that current assessment methods do not detect.

A final application of (1) concerns a type of habitat destruction that we often observe, which is temporary but patchy and repeated. Examples include diver damage to reefs, slash-and-burn agriculture, fuel wood cuttings, and hunting. Random, patchy mortality as in slash-and-burn agriculture is equivalent to fixing $D = 0$ and increasing m_i , the random mortality rate, by a fixed amount k . This gives a population dynamics equation differing from the original:

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^i p_j\right) - (m_i + k) p_i - \sum_{j=1}^{i-1} c_j p_i p_j. \quad (4)$$

Here, equilibrium for species i is given by

$$\hat{p}_i = 1 - \frac{(m_i + k)}{c_i} - \sum_{j=1}^{i-1} \hat{p}_j \left(1 + \frac{c_j}{c_i}\right). \quad (5)$$

The effect is similar to that of varying D , except that increasing m across the board has less effect on species with higher per capita fecundity, c_i , because of the term $(m_i + k)/c_i$. The best competitor, for example, has $\hat{p}_1 = 1 - (m_1 + k)/c_1$ and undergoes extinction when $m_1 + k = c_1$. In this case, as one moves toward species that are less competitive but more fecund (c_i is larger), the effect of random mortality becomes less and less severe. This is particularly so, because the longer life span of competitively superior species typically makes the normal m_i lower. The net result favors poor competitors (good dispersers or weeds). In this case, the extent of extinctions as k increases is even more severe among the good competitors, and more species are at risk, than in the case studied by Tilman *et al.*¹. That is, for random disturbances that produce mortality, the extinction debt is even more severe than the original analysis projected.

In conclusion, the extinction debt model is very powerful, but it must be related with care to real-world situations. For highly fragmented landscapes (where fragmentation is at the scale of species' use of space) and for general reductions in fecundity, the original extinction debt analysis applies directly. For habitat destruction that leaves large patches undisturbed, the model overestimates likely extinctions. For random, patchy mortality, such as slash-and-burn agriculture, the proper analysis modifies m , not D , and the result is even more severe extinctions of superior competitors than in the original analysis.

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