species (*a* in the figure). The analytical model of Tilman *et al.* implicitly assumes this spatial homogeneity.

Should the destruction of habitat be concentrated in a contiguous block along the perimeter, however, then the undestroyed sites occupied by the dominant species will each remain surrounded in their immediate vicinity by the same proportion of available colonization sites as before the habitat loss occurred (*b* in the figure), and the effective colonization rate will remain unchanged. Indeed, the very fact that the equilibrium condition and extinction predictions of the analytical model are independent of the absolute size of the original habitat force this conclusion. Without fragmentation, the equilibrium condition of a 1-million-acre-forest will be unchanged from that of a geometrically similar, "intact" 10-million-acre forest.

Thus if destruction is concentrated at the perimeter, the analytical model would predict no deterministic extinctions through competitive effects. In such a case, extinctions would only occur when the absolute area of the habitat is reduced to the point that the populations become small enough to fall victim to stochastic extinction processes[2].

Extinction predictions based on species–area relations have been criticized[3,4] for assuming a functional relation between area loss and species loss where in fact none may exist. Metapopulation models offer a convincing mechanism to predict species loss in highly fragmented habitats, but offer no support for the notion that area loss *per se* results in extinction. Predictions of global extinction rates based on estimates of area loss alone seem to be unreliable, unless it can be shown that permanent habitat destruction (and not just temporary forest clearing) is occurring in a highly random fashion that fragments the habitat consistently on a very local scale.

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TILMAN *ET AL.* REPLY — Budiansky raises an important issue — that the quantitative relationship between the amount of habitat destroyed and the number of resulting species extinctions may depend on the spatial pattern of habitat destruction. Our analytical model[1] has no provision for habitat shape or size and cannot directly address this issue. However, a modified analytical model and extensive simulations of explicitly spatial versions of our model[5] reveal two important effects.

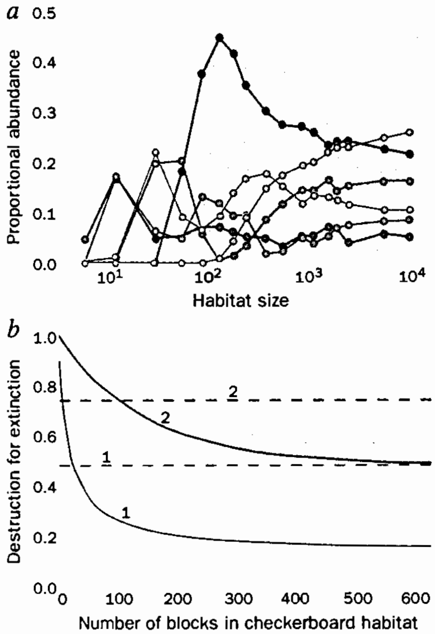

FIG. 2 *a*, Mean equilibrial species abundance versus habitat size from replicate spatially explicit simulations of competition[1] among 6 species. Species 1 (green) is the best competitor but poorest disperser, species 2 (grey) the next best competitor and next poorer disperser, (species 3, 4, 5 and 6 are brown, blue, red and purple, respectively) . Mortality was 0.05 yr^{-1} and colonization was 0.076, 0.146, 0.2975, 0.601, 1.24 and 2.53 yr^{-1} for species 1 to 6, with absorbing boundaries, annual reproduction, and propagules dispersed randomly across the neighbouring four rings of sites in a hexagonal array of $n \times (n-1)$ sites. *b*, Solid curves, amount of habitat destruction required to drive the best competitor (species 1) or the next best competitor (species 2) extinct when an explicitly spatial habitat was destroyed in a checkerboard pattern. Dashed lines, amount of habitat destruction required for extinction of species 1 and 2 as predicted by our analytical model[1]. Here, a 100 x 99 hexagonal habitat was divided into from 1 to 625 equal-sized blocks in a checkerboard pattern. Solid curves show the contiguous proportion of each block that had to be destroyed to cause extinction of species 1 or 2 for various numbers of blocks.

First, the novel prediction of our analytical model[1] holds: for all spatial patterns of habitat destruction we tried, destruction leads to the biased extinction of superior competitors[5]. Even when they originally were the most abundant species, superior competitors become extinct at lower levels of destruction than inferior competitors when an otherwise pristine habitat is reduced in size, such as by the loss of edge (Fig. 2). This biased extinction is a deterministic effect, caused by poor dispersal abilities, not the stochastic effect alluded to by Budiansky.

For habitats as large as those containing 104 sites, loss of edge differentially harms the best competitor. As edge is lost, the best competitor goes extinct first (species 1; Fig. 2*a*) in habitats of the size that Budiansky (his Fig. 1) suggested would have no edge effects. Further reductions in habitat size causes progressive extinction of species in order of competitive abilities (Fig. 2*a*), as occurred with destruction in our analytical model[1]. Simulations show that better competitors, because of poorer dispersal, require larger areas for survival. 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.

It follows that better competitors, because of poorer dispersal, have larger minimal demands for habitat size. Furthermore, similar predictions of biased deterministic extinction of superior competitors arose when we modified our analytical model[1] by adding a term for the proportion of propagules lost to edges[5] (via decreases in colonization rate proportional to $S^{-1/2}$ for square habitats, with S being habitat size). Other simulations showed that patch shape also influenced extinctions: for patches of a given area, those with greater perimeters caused more extinctions, with extinctions again biased toward the best competitors.

Second, additional simulations showed that extinctions can occur at amounts of habitat destruction markedly greater than, markedly less than, or similar to those predicted analytically[1], depending on the spatial pattern of destruction (Fig. 2*b*). Extinctions occur at less destruction than analytically predicted if uniformly spaced blocks and/or small blocks of habitat are destroyed, and at more if large and/or clumped blocks are destroyed. Destruction of random small patches led to results like those predicted by our analytical model. In all cases, there is biased extinction of abundant, superior competitors.

These spatially explicit versions of our analytical model demonstrate that control of the spatial pattern of habitat destruction can be a significant management tool for minimizing extinctions. Equally as important, they show that habitat destruction can differentially harm abundant, superior competitors that are poor dispersers. This novel and alarming prediction of biased extinction was the central point of our paper. Its robustness, in response to many alternative spatial patterns of destruction, reaffirms our warning that the time-delayed extinction of originally abundant species may be an unexpected consequence of habitat destruction.

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1. Tilman, L. *et al. Nature* **371**, 65–66 (1994).
2. Soule, M. E. (ed.) *Viable Populations for Conservation* (Cambridge Univ. Press, 1987).
3. Budiansky, S. *Nature* **370**, 105 (1994).
4. Heywood, V. H. & Stuart, S. N. in *Tropical Deforestation and Species Extinction* (eds Whitmore, T. C. & Sayer, J. A.) 91–117 (Chapman & Hall, London, 1992).
5. Tilman, D. & Lehman, C. in *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions* (eds Tilman, D. & Kareiva, P.) (Princeton University Press, in the press).