

CHAPTER TEN

Habitat Destruction and Species Extinctions

David Tilman and Clarence L. Lehman

INTRODUCTION

The expansion of humans across the earth has caused a long string of species extinctions (see Ehrlich and Ehrlich 1981; Wilson 1992; May, Lawton, and Stork 1995; Pimm et al. 1995). Unfortunately, all of these past extinctions pale in comparison to the projected effects of recent and anticipated human habitat destruction (e.g., May et al. 1995; Pimm et al. 1995). Human conversion of natural ecosystems into managed ecosystems or into roads, rights-of-way, housing, and industry continues at an astounding rate. Already, about 43% of earth's terrestrial ecosystem area is directly harnessed for human benefit (Daily 1995) with some ecosystem types, especially those with fertile soils or favorable climates, much more heavily exploited. For instance, less than 1% of the original tallgrass prairie and less than 0.2% of the original oak savanna of Minnesota still remains. In this chapter we explore the potential effects of such habitat destruction by comparing and contrasting the predictions of spatially explicit models, spatially implicit models, and extensions of island biogeographic theory.

SPECIES-AREA AND SPECIES-ABUNDANCE RELATIONSHIPS

Early island biogeographers reported an empirical relationship between habitat size and species richness (Darlington 1957). The number of species in a given taxonomic group on islands of a given geographic region is a power function of

island area:

$$S = cA^z, \quad (10.1)$$

where S is the number of species (species richness), A is the surface area of an island, z is an exponent observed to range from about 0.18 to 0.3, and c is a constant unique to each taxonomic group and set of islands. In this, as in all cases that follow, c is unique to each equation and situation. Similar relationships occur when areas of different sizes are sampled in mainland ecosystems, for which z values have been found to range from about 0.12 to 0.2. The lower z values of mainlands have been attributed to mainlands having a larger proportion of "transient" species (MacArthur and Wilson 1967).

The species-area relationship has been used to estimate how many species might be threatened with extinction following habitat destruction (Simberloff 1984; Wilson 1988, 1992). Consider a virgin habitat of area A_v that contains S_v species. If a proportion, D , were destroyed, the number of species, S_D , remaining would be

$$S_D = c[(1 - D)A_v]^z. \quad (10.2)$$

This means that the proportion of the original species that survived after destruction of a proportion D of the original virgin habitat would be

$$\frac{S_D}{S_v} = (1 - D)^z. \quad (10.3)$$

The proportion of the original species driven extinct would thus be

$$P_D = 1 - (1 - D)^z. \quad (10.4)$$

To evaluate the potential validity of this expression for P_D , consider what is encompassed in the empirical species-area relationship. In essence, it is a sampling function that shows how the number of observed species depends on the size of the

area sampled. Why, though, might diversity increase with area sampled? Area encompasses at least three distinct factors that influence diversity. First, on average, larger areas contain more individuals. It is clearly impossible to observe more species than individuals, but the issue is deeper than this. The species in a given community have some characteristic distribution of abundances, such as a log-normal distribution (Preston 1948), a broken-stick distribution (MacArthur 1960), or a geometric distribution (May 1975). Species also have a minimal population size below which demographic stochastic fluctuations lead to extinction (May 1973b, 1975). May showed that these two relationships led to

$$S = c \left(\frac{I}{m_I} \right)^z, \quad (10.5)$$

where m_I is the minimum population size required for species survival, I is the total number of individuals of all species in the community of interest, and the value of z for this relationship depends on the underlying distribution (May 1975; Preston 1948).

A second reason for diversity to increase with area comes from the statistical distribution of areas required for the survival of a minimum population of each species. A species of small herbivorous mammal, for instance, can survive in a much smaller area than a large carnivore. Such species-specific minimum areas for survival are likely to be distributed, within a community, with log-normal, geometric, or broken-stick relationships, leading to a power function analogous to that above,

$$S = c \left(\frac{A}{m_A} \right)^z, \quad (10.6)$$

where m_A and z are derivable from the underlying distribution of minimal areas. This equation states that diversity increases with area because species differ in how much area they require to survive, and larger areas allow the survival of species that cannot survive in small areas.

A third reason why diversity should increase with area is heterogeneity. Habitats differ in their physical and biotic characteristics. Each species has some combinations of habitat characteristics at which it does best and some combinations in which it cannot maintain a viable population. Larger areas are likely to contain a larger range of habitat conditions and thus to encompass conditions conducive to the survival of more species. Habitat heterogeneity can be incorporated into Equation 10.6 by partitioning the effects of area into that caused by the minimum area requirement of species and the heterogeneity effect:

$$S = c \left(\frac{A}{m_A} \right)^{z_1} (Ah_A)^{z_2}. \quad (10.7)$$

Equations 10.5–10.7 predict the types of species expected to go extinct following habitat destruction, based on island biogeographic theory and its derivatives. First, the abundance distribution relationship behind Equation 10.5 predicts that as I is decreased by habitat destruction, rarer species have a much higher chance of extinction. In its most literal interpretation, Equation 10.5 states that species should go extinct in order from the least to the most abundant as D increases. Equation 10.6 predicts that species should go extinct in order from those with the largest to those with the smallest home ranges as habitat destruction increases. Equation 10.7 adds the expectation that some species will be driven extinct, independent of the first two factors, as their unique habitat requirements are lost following habitat destruction. This corresponds to the extinction of local endemics following destruction of their habitat. All three of these are predictions of biased extinction of rare species, with the latter two predictions including a more explicit reason for their rarity (i.e., large home range or unique but rare habitat requirements). Thus, the island biogeographic model leads to the general expectation that habitat destruction should lead to the biased extinction of rare species. The individual-based metapopulation-like models and explicitly

spatial models that are analyzed next make a markedly different prediction (e.g., Nee and May 1992; Tilman et al. 1994; Tilman, Lehman, and Yin 1997).

INDIVIDUAL-BASED MODELS OF COEXISTENCE AND DIVERSITY

The metapopulation models of Levins (1969), Horn and MacArthur (1972), Levin and Paine (1974), Hastings (1980), Hanski (1983), Shmida and Ellner (1984), Cohen and Levin (1991), and others have been used to predict the effects of alternative management practices on survival of rare or endangered species (e.g., Harrison, Murphy, and Ehrlich 1988; Wootton and Bell 1992) and to predict the effects of habitat destruction on communities of numerous coexisting species (Nee and May 1992; Tilman et al. 1994; Moilanen and Hanski 1995; Loehle 1996; Tilman et al. 1997). We use such theory to explore the traits of species and numbers of species predicted to be threatened with extinction following habitat destruction.

The Analytical Model

As in Chapter 1, let an infinitely large habitat be divided into sites, each the size occupied by a single adult. Let the proportion of sites occupied by individuals of a species be p , the mortality rate m , the colonization rate c , and the proportion of permanently destroyed sites D . Assume that colonists entering a destroyed site do not survive, and that destroyed sites cannot produce colonists. As proposed by Nee and May (1992), this gives

$$\frac{dp}{dt} = cp(1 - D - p) - mp. \quad (10.8)$$

Note that the rate of propagule production, cp , is multiplied by the proportion of open and viable sites, $(1 - D - p)$, to give the rate of increase in site occupancy. The rate of mortality within sites, mp , is subtracted from this to give the rate of change in site occupancy. This is called a metapopulation

model, but it is more correctly considered an implicitly spatial model of site occupancy by individuals and of competitive interactions among individuals. Here we use a multispecies extension of this model in which all species compete, as if for a single limiting resource (Tilman et al. 1994). This model was derived in Tilman et al. (1994) from the models of Hastings (1980), Nee and May (1992), and Tilman (1994). In our model, there is a simple competitive hierarchy, with species ranked from the best competitor (species 1) to the worst (species n). Species 1, the best competitor, displaces all other species from any site that it invades, and species 1 can invade any undestroyed site. The next best competitor, species 2, displaces all species except species 1, and so on to species n , which is displaced by all other species, can displace none, and only can invade empty undestroyed sites. The dynamics of site occupancy by the i^{th} species, where subscripts i and j identify species, are (Eq. 10.9)

$$\frac{dp_i}{dt} = c_i p_i \left(1 - D - \sum_{j=1}^i p_j \right) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j. \quad (10.9)$$

Here D is a constant, which means that habitat destruction is permanent. The abundances of all species must be greater than or equal to zero. The competitive hierarchy means that a species is not affected by its inferior competitors. Interspecific trade-offs among competitive ability, colonization ability, and mortality are required to allow an unlimited number of species to stably coexist in a virgin, undestroyed habitat, even though they compete as if for a single resource (Tilman 1994). What are the effects of permanent habitat destruction on the diversity of such multispecies communities?

Consider the impact on the best competitor of destruction of a proportion, D , of the habitat. From Equation 10.9, at equilibrium (i.e., $dp_i/dt = 0$), the proportion of sites occupied by the i^{th} species will be (Eq. 10.10)

$$\hat{p}_i = 1 - D - \frac{m_i}{c_i} - \sum_{j=1}^{i-1} \hat{p}_j \left(1 - \frac{c_j}{c_i} \right), \quad (10.10)$$

where equations are solved in order starting with species 1 and must have $p_i \geq 0$ for all i . When applied to the best competitor, species 1, this predicts that its abundance will be zero when $D_1 = 1 - m_1/c_1$. The equilibrium abundance of species 1 in a virgin, undestroyed habitat is also $p_1 = 1 - m_1/c_1$. This means that, independent of the abundances of inferior competitors, the best competitor is predicted to be driven extinct once a proportion, D_1 , of habitat equal to its site occupancy in a virgin habitat is destroyed. Note that this is deterministic, not stochastic, extinction. Thus, if at equilibrium in a virgin habitat the best competitor occurred in 25% of the sites, this model predicts that permanent destruction of a randomly selected set of 25% of habitat sites would lead to its eventual extinction. The more abundant the best competitor, the greater is the random permanent destruction of sites required to drive it extinct. But, within the framework of this analytical model, habitat destruction of a randomly chosen proportion of D_1 sites has the same eventual effect—extinction—as if there had been the selective destruction of exactly those D_1 sites in which the species occurred.

What are the effects of habitat destruction on the extinction of inferior species? Tilman et al. (1994) derived results for a case in which species abundances form a geometric series, with the most abundant species being the best competitor, and increasingly less abundant species being increasing poorer competitors. This can be expressed as $p_i = q(1 - q)^{i-1}$, where q is the abundance of the best competitor and i refers to the species of competitive rank, i . It is possible to analytically calculate the D at which each species will go extinct, with D_i being the proportion of destroyed habitat beyond which species i can no longer survive (Tilman et al. 1994). In this case, $D_i = 1 - (1 - q)^{2i-1}$, which means that $D_1 < D_2 < D_3 \dots < D_n$. Thus species are predicted to go extinct in order from the most abundant (best competitor and poorest disperser) to the least abundant (poorest competitor and best disperser) as habitat destruction increases. This prediction stands in direct contrast to the prediction of biased extinction of rare species made by derivatives of the species-area curve.

This surprising prediction seems counterintuitive at first. How could the most abundant species, which are also the best competitors, be the species most threatened with extinction following habitat destruction? How could deterministic extinction of species 1 occur when only a proportion, D_1 , of an infinitely large habitat has been destroyed? An intuitive answer to these questions is provided by a consideration of the traits required of other species if they are to stably coexist in a virgin habitat with superior competitors. Within this model, a major way for an inferior competitor to coexist with a superior competitor in a virgin habitat is for the inferior competitor to be a better disperser. In contrast, the best competitors are the poorest dispersers of all, and their abundance is the most dispersal limited of all species. This makes them be the most susceptible to extinction from habitat destruction.

Tilman et al. (1997) explored three other analytical and several numerical cases to determine how general and robust the prediction of competitively ordered extinction was. In addition to the case in which poorer competitors were less abundant and all species had equal mortality, they considered cases in which (1) all species were equally abundant with equal mortality, (2) poorer competitors were more abundant with equal mortality, and (3) all species were equally abundant but poorer competitors had progressively greater mortality. Analytical solutions showed that, in all cases, species were predicted to go extinct in order of their competitive abilities, with the best competitors first, as habitat destruction increased. However, there are special cases in which some species go extinct out of this order (Tilman et al. 1997).

This biased extinction of the best competitors does not depend on the precise formulation of the model. For example, consider an analytical model that allows for the loss of seed at the edge of a habitat island. The length of habitat edge is proportional to \sqrt{A} , where A is the area of the habitat. This means that the fraction, L , of all seeds lost over the edge is proportional to \sqrt{A}/A , which is to say $L = K/\sqrt{A}$, where K is a constant. Thus each c_i in Equation 10.9 is replaced by $(1 - L) c_i = (1 - [K/\sqrt{A}]) c_i$. When $A = \infty$, seed loss L is

zero, just as assumed in Equation 10.9. When $S = K$, seed loss L is one, and all seeds are lost over the edge. Thus L in this model corresponds roughly to D in the original model, though it enters the equations differently:

$$\frac{dp_i}{dt} = (1 - L)c_i p_i \left(1 - \sum_{j=1}^i p_j\right) - m_i p_i - p_i \sum_{j=1}^{i-1} (1 - L)c_j p_j. \quad (10.11)$$

The equilibrium values for Equation 10.11 are

$$\hat{p}_i = 1 - \frac{m_i}{(1 - L)c_i} - \sum_{j=1}^{i-1} \hat{p}_j \left(1 + \frac{c_j}{c_i}\right). \quad (10.12)$$

The important questions are: How does the abundance \hat{p}_i of species i change with L , and for what value of L does species i become permanently extinct? For the best competitor, setting Equation 10.12 to zero and solving for L yields $L_1 = 1 - m_1/c_1$. Notice that this L_1 for extinction is identical to D_1 for extinction in the original model. Indeed, for cases in which species have a geometric abundance series of a large habitat ($A = \infty$), simulations have shown that decreasing habitat size (A) leads to the same biased extinction as previously discussed. The first species to go extinct is the best competitor (poorest disperser), and it is followed, in order, by progressively better dispersers (poorer competitors) as the habitat has more and more edge, that is, as it is effectively smaller. Other models have also led to similar effects (Moilanen and Hanski 1995; Loehle and Li 1996).

In total our metapopulation-like models make a markedly different prediction than the models derived from the species-area relationship. The latter predict that extinction should be biased toward rare species, whereas the former predict that extinction should be biased toward superior competitors and poor dispersers, which could be among the most abundant species. These divergent predictions are caused by the different mechanisms of coexistence assumed in each

model. The species-area models do not include any interspecific interaction and apply to species for which persistence depends only on the amount of available area. This causes species that require large areas (because they have large home ranges or small population sizes) to go extinct first. In contrast, the mechanism of coexistence in the metapopulation-like models comes from an interspecific trade-off among competitive ability, dispersal ability, and mortality. This model only applies to those species for which superior competitors are inferior dispersers (or have higher mortality) and thus predicts the biased extinction of superior competitors. It may be that aspects of both models operate in many natural habitats, causing the total number of species driven extinct by habitat destruction to be a weighted sum of metapopulation and species-area model predictions.

The number of species driven extinct by a given amount of habitat destruction depends on the traits of the species (Tilman et al. 1994; Stone 1995). If, in the virgin habitat, the best competitors are the most abundant species, and progressively poorer competitors are progressively less abundant, then the qualitative relationship of Figure 10.1 (curve B) would apply (Tilman et al. 1994), which is qualitatively similar to that predicted by the species-area relationship (Eq. 10.4). However, if, in the virgin habitat, the best competitors are rare, and poorer competitors are progressively more abundant, then the pattern will be more like that of curve A of Figure 10.1 (Stone 1995). Clearly the number of extinctions resulting from habitat destruction depends on the processes controlling species abundances in a community and may be markedly greater than that predicted by the classical species-area relationship (Stone 1995). This represents a second major difference between the species-area models and metapopulation-like models.

Extinction Dynamics

Although the ultimate outcome of habitat destruction is predicted to be the extinction of all species for which $D \geq D_i$, this gives no insight into the dynamics of these extinctions. All species that are driven extinct by destruction of D have an

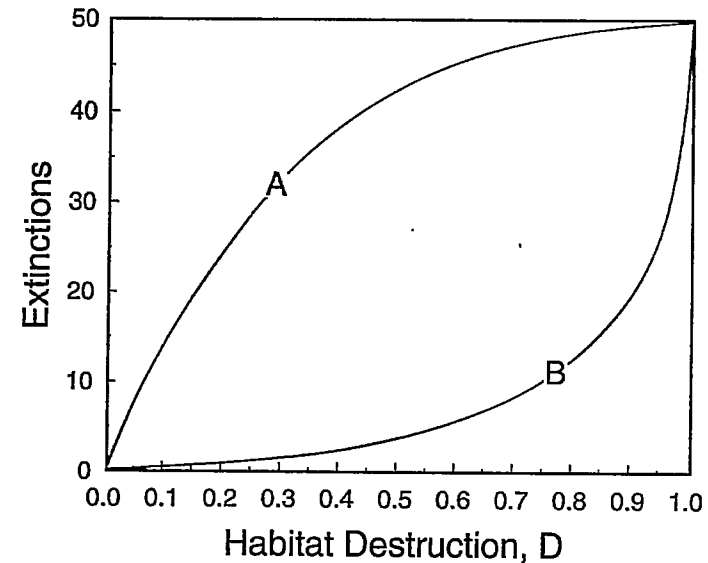


FIGURE 10.1. The number of extinctions predicted by the analytical multispecies version of Levins's model (Eq. 10.9). (A) Case in which the best competitor is the rarest species and progressively poorer competitors are more abundant (from Stone 1995). (B) Case in which the best competitor is the most abundant and progressively poorer competitors are less abundant (geometric abundance series of Tilman et al. 1994).

approximately negative exponential approach to an abundance of zero (Figure 10.2). The rate of this decay toward extinction depends on the c and m values of species relative to the amount of habitat destroyed. Values of c and m that seem realistic for grassland and tropical forest species yield a time delay between habitat destruction and species abundances falling to 1% of their original values that ranges from fifty to more than two thousand years.

Diamond (1972) reports time delays of this magnitude, and greater, between the formation of new islands by rising sea levels and the extinction of isolated bird populations. Terborgh (1974) and Case, Bolger, and Richman (1992) report similar cases of slow extinction following habitat isolation and fragmentation. Such time delays suggest that current habitat

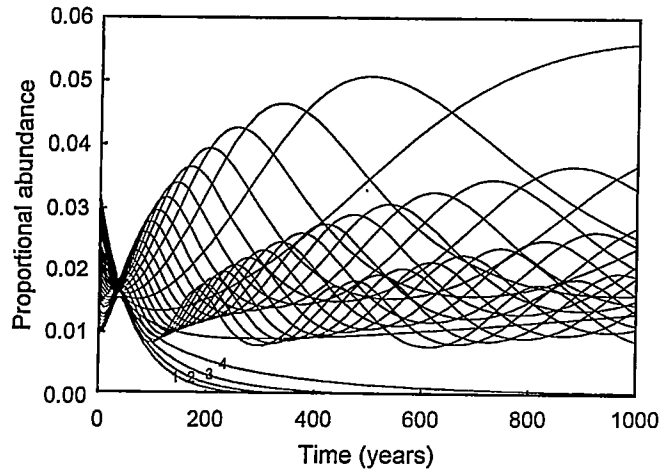


FIGURE 10.2. The dynamics of extinction following habitat destruction. Note that all twenty species coexisted in the virgin habitat. After permanent destruction of 25% of the habitat at time 0, the four best competitors (species 1-4) went extinct, and the other species persisted, eventually attaining new equilibrium abundances (from Tilman et al. 1994).

destruction is creating an extinction “debt.” Many species that survive the initial act of destruction, and that may have been among the most abundant species in the remnant patches, are predicted eventually to go extinct. Thus, current acts of habitat destruction create a debt that is repaid by the delayed, selective extinction of species that are poor dispersers but superior competitors. Data regarding this idea are scarce. Bucher (1992) suggested that extinction of the passenger pigeons, which may have been the most abundant bird species in North America, was caused more by fragmentation of the oak forests upon which they depended, than by overhunting. However, their great dispersal abilities seem to argue against the metapopulation hypothesis proposed here. The African primates most harmed by habitat fragmentation may be those that are superior competitors (e.g., Skorupa 1986). Other studies of the effects of fragmentation on the loss of bird and mammal species also suggest biased extinctions (e.g., Lovejoy et al. 1984;

Laurance 1990, 1991; Stouffer and Bierregaard 1995). Diamond (1972) suggested that the species most threatened with extinction following island formulation from a mainland were poor dispersers. This possibility of biased extinction of formerly abundant species merits further study.

EXTINCTIONS IN EXPLICITLY SPATIAL HABITATS

Might any of the predictions we have discussed change if we were to make the metapopulation-like model explicitly spatial? To find out, we let each individual organism occupy a site within a hexagonal array of adjacent cells, with each cell being the size of the region occupied by an individual adult, as in Chapter 1. If any site is invaded by a propagule of a species that is a superior competitor to the current resident, the current resident is displaced by the invader. Residents produce propagules with a probability proportional to $c \cdot dt$ and experience mortality with a probability of $m \cdot dt$. Propagules disperse in the immediate neighborhood of a source cell, producing a “seed shadow” that can extend out one, two, three, or more hexagonal “rings” from the source cell. Our explicitly spatial simulations allowed us to determine the effects of relaxing the simplifying assumptions of the analytical model.

The analytical model assumed that dispersal was continuous, whereas many organisms reproduce seasonally. It assumed global dispersal of propagules across the entire habitat, whereas actual dispersal is local. It assumed immediate competitive displacement following invasion by a superior competitor, whereas actual competitive displacement occurs with some time delay. We relaxed all eight possible combinations of these three simplifying assumptions for a case in which four species coexisted as competitors in a virgin habitat. In all eight cases, as D increased the four competitors went extinct in order of their competitive abilities, just as in the analytical models (Tilman et al. 1997). However, the amount of habitat destruction required to drive a species extinct differed, sometimes markedly, from the analytical model and depended on which simplifying assumptions were relaxed. Thus, a more realistic treatment of space changed the quantitative nature of the

effects of habitat destruction on extinction, but not the major qualitative feature, which is the selective loss of the superior competitors. This suggests that analytically predicted D_i values are of little, if any, quantitative value.

Spatial Patterning of Destruction

So far we only have considered destruction of randomly chosen individual sites in a spatial habitat, which is akin to destroying a habitat plant by plant. This was done for mathematical tractability but does not mimic the actual ways that humans destroy habitats. Most anthropogenic habitat destruction occurs in blocks. What might be the effects of having a habitat be destroyed in spatial blocks of various sizes? To explore this question, we again created a case in which four species coexisted in a virgin spatial habitat. We then destroyed this habitat in numerous alternative checkerboard patterns. For any given proportion, D , of habitat destroyed, we created alternative checkerboards ranging from 625 uniformly spaced small blocks of destruction to one large block of destruction. We then determined, for each type of checkerboard, the amount of destruction required to drive species 1, 2, 3, and 4 extinct. As might be expected, more destruction was required to drive a species extinct when large blocks were left intact than when the same undestroyed area was dispersed among many small blocks. However, except at the extremes, species went extinct in order of their competitive ability, with the best competitor being driven extinct first (Figure 10.3; Tilman et al. 1997).

The amount of habitat destruction required to drive a given species extinct was highly dependent on the size of the blocks into which a habitat was divided. The requisite amount of habitat destruction differed greatly from that predicted by the analytical model (i.e., for random destruction of single sites). For instance, the analytical model predicted that the best competitors would be driven extinct upon random destruction of 50% of all sites. However, in the spatially explicit cases the

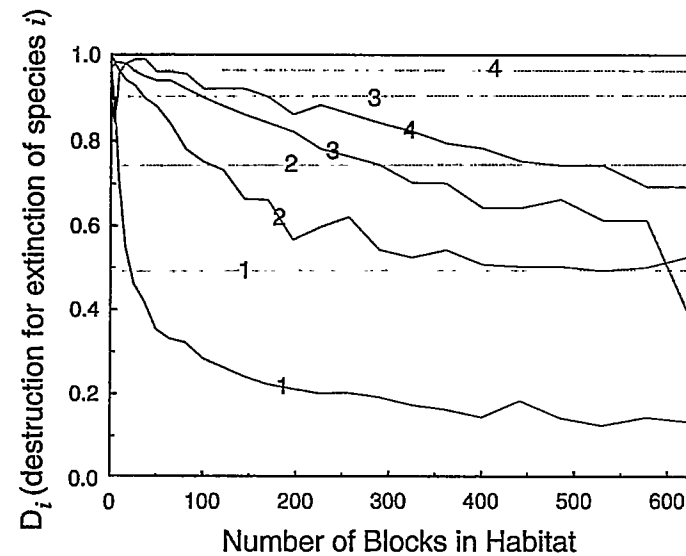


FIGURE 10.3. The effect of the spatial pattern of habitat destruction on the number of species driven extinct. In these simulations, a habitat was destroyed in a checkerboard pattern, with the total number of blocks into which a habitat was divided ranging from 1 to 625 (i.e., 25×25). The numbers refer to species, with 1 being the best competitor, 2 the next best, etc. The solid lines show the effect of the various patterns of habitat destruction on extinction by giving the proportion of each block that had to be destroyed to cause extinction of each species for any given total number of blocks. The dotted lines show the amount of habitat destruction required to cause extinction of these same species for the analytical model (Eq. 10.9). Figure from Tilman et al. (1997).

best competitors went extinct following anywhere from 95% to 15% habitat destruction, depending on the sizes of the blocks destroyed, and thus on the sizes of the areas left intact. For all four species, much more habitat destruction than analytically predicted was required to cause the extinction of a species if destruction left large intact blocks of habitat, and much less than analytically predicted was required if the intact habitat was left as many small but isolated patches. Thus, the analytical

D_i values predict the ordering of species extinctions, but not the level of habitat destruction at which this occurs. The latter only can be predicted by a more explicitly spatial consideration of fragment size, fragment locations, the patterning of corridors that link fragments, and movement patterns among fragments. The incidence function approach of Hanski (Chapter 2) provides one tool for such analyses. Detailed simulations that include spatial structure and incorporate knowledge of organismal movement patterns and behaviors are another approach that could be used to achieve this goal. However, as Wennergren, Ruckelshaus, and Kareiva (1995) have pointed out, the predictions of such models, especially when used to make management decisions about particular endangered species that live in highly fragmented habitats, may be highly sensitive to the model parameters, especially the estimated dispersal rate.

CONCLUSIONS

All organisms live in spatial habitats and interact mainly with neighboring organisms. Habitat destruction is also a spatial process, with some regions destroyed, others left in their pristine condition, and others modified intermediate amounts. Some of the effects of such habitat destruction can be understood in a qualitative manner by using nonspatial models, such as the species-area relationship and its derivatives. However, each incremental increase in the spatial realism in our models provided unique insights and predictions about the effects of habitat destruction on biodiversity. One such effect seems to be the tendency for biased extinction, following habitat destruction, of superior competitors that are poor dispersers. This effect, predicted by metapopulation-like models, was found to be remarkably robust when explored using explicitly spatial simulations. However, the level of habitat destruction required to drive a given species extinct was highly dependent on model assumptions, especially on the spatial patterning of destruction, and often differed dramatically from analytical D_i values de-

rived from the metapopulation-like model. Such effects illustrate the limitation of the implicitly spatial metapopulation-like models and the need for greater spatial realism in considering the effects of habitat destruction on species extinctions.

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