
Habitat Loss, Fragmentation, and Restoration

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Abstract

The loss and fragmentation of habitat is a major threat to the continued survival of many species. We argue that, by including spatial processes in restoration management plans, the effects of habitat loss and fragmentation can be offset. Yet few management plans take into account spatial effects of habitat conservation/restoration despite the importance of spatial dynamics in species conservation and recovery plans. Tilman et al. (1997) found a "restoration lag" in simulations of species restoration when randomly selecting habitat for restoration. Other studies have suggested that the placement of restored habitat can overcome effects of habitat loss and fragmentation. Here we report the findings of simulations that examine different regional management strategies, focusing on habitat selection. We find that nonrandom restoration practices such as restoring only habitat that is adjacent to those occupied by the target species can dramatically reduce or negate any restoration lag. In fact, we find that the increase in patch occupancy of the landscape can be greater than two-fold in the adjacent versus the random scenarios after only two restoration events, and this increase can be as great as six-fold during the early restoration phase. Many restoration efforts have limitations on both funds and available sites for restoration, necessitating high potential success on any restoration efforts. The incorporation of spatial analyses in restoration management may drastically improve a species' chance of recovery. Therefore, general principles that incorporate spatial processes and sensible management are needed to guide specific restoration efforts.

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Introduction

Many species face extinction given the current rate of habitat loss, fragmentation, and degradation (Hastings 1980; Ehrlich & Ehrlich 1981; Wilcox & Murphy 1985; Wilcove et al. 1986; Hassell et al. 1993; Fahrig 1997; Tilman et al. 1994). Although the implications of spatial pattern and arrangement have been studied in terms of species persistence (Dytham 1995a), they have not been adequately addressed for species recovery plans. Here, using simple spatial models, we argue that by including spatial processes in restoration management plans, the effects of habitat loss and fragmentation can be offset (Lewis et al. 1996). The decision as to which habitat should be restored may be as important as to how much is to be restored. Yet few management plans take into account spatial effects of habitat conservation/restoration, despite the importance of spatial dynamics in species conservation and recovery plans. Tilman et al. (1997) investigated species restoration in cellular automata, in which habitat in a landscape was randomly selected for restoration. They found a substantial delay in recovery of the species.

Species recovery studies/plans have more frequently been incorporating realistic spatial dynamics, whereas those that do not do so have come under increasing fire (Pulliam et al. 1992; Stacey & Taper 1992; Harrison 1993; Harrison et al. 1993; Doak et al. 1994; Dunning et al. 1995; Noon & McKelvey 1996). Additionally, there have been numerous calls for the inclusion of realistic spatial dynamics in the discussion of general conservation issues (Hanski & Gilpin 1991; May 1993; Gilpin & Hanski 1997; Levin et al. 1997; Tilman & Kareiva 1997; Groom & Pascual 1998).

In response to this need, Tilman et al. (1997) used a spatially explicit model to examine habitat destruction and restoration. Their model exhibited a restoration lag that implies a significant number of patches must be restored before a positive effect on population levels is seen. This finding is based upon several key factors, the most important being that the patches in a landscape that are to be restored are randomly selected, and that the target species is not reintroduced into the patch. However, by including spatial processes in restoration management plans, the effects of habitat loss and fragmentation may be offset (Kareiva & Wennergren 1995; Lewis et al. 1996). This is critical because many species face extinction owing to demographic and/or environmental stochasticity given the current rate of habitat loss, fragmentation, and degradation (Hastings 1980; Ehrlich & Ehrlich 1981; Groombridge 1992; Hassell et al. 1993; Tilman et al. 1994; Fahrig 1997; Huxel & Hastings 1998). The decision as to which habitat should be restored may be as important as how much habitat is to be restored. Fahrig (1997) argues that the effect of frag-

mentation is only seen once a given minimum has been reached. Using cellular automata, we test whether incorporating spatial processes in regional management plans can improve the efficacy of restoration efforts.

Methods

The underlying deterministic model on which we base our stochastic, spatially explicit cellular automata is the Levins metapopulation model (Levins 1969). Patches may support either populations as in the original model (Levins 1969), or individuals (Tilman et al. 1994). Patches that are not "destroyed" are assumed identical, as described by the simple model in the following equation:

$$\frac{dp}{dt} = mp(1 - p - h) - ep, \quad (1)$$

where p is the fraction of occupied patches or habitat, h is the fraction of uninhabitable (destroyed) patches or habitat, m is the migration or colonization rate, and e is the extinction rate. We assume m (0.20 in all simulations) and e (0.025 in all simulations) are constant and colonization can occur only in empty but habitable sites, as in Tilman et al. (1994). The values were chosen for demonstration purposes to ensure that the species persisted at the minimum number of patches (i.e., when the number of destroyed patches was at its maximum). These are simplifications in that both colonization and extinction may be dependent on local density (either within a patch or within a set of adjacent patches) and on patch quality. Therefore, within-patch dynamics and the rescue effect are ignored in this model. In the non-spatially explicit Levins model, there is no temporal lag between when habitat is lost and when extinction occurs due to dispersal being global as opposed to local. In the spatially explicit cellular automata, colonization is local and limited to the four cardinal direction patches adjacent to an occupied patch (von Neumann rule; Durrett & Levin 1994).

In spatially explicit model studies of habitat fragmentation, two important results have been demonstrated and hypotheses concerning these results have been made for natural systems. The two results are: (1) less mobile species may become extinct first (Tilman et al. 1994; Huxel & Hastings 1998); and (2) there is an extinction lag or hysteresis that occurs when the amount of habitable area of a landscape drops below the equilibrium threshold level of suitable habitat for a species to persist (Tilman et al. 1994). The first result depends upon the manner and pattern in which habitat is lost (Adler & Nuernberger 1994; Dytham 1995a, 1995b; Moilanen & Hanski 1995; Loehle & Li 1996) and upon the dispersal being modeled as random and local (Tilman et al. 1994, 1997; Dytham 1994, 1995a, 1995b; Huxel & Hastings 1998).

For the second result, the length of the extinction lag depends upon the ratio of colonization to extinction and the random instead of directed dispersal of individuals (Loehle & Li 1996). Colonization rules that allow for increased dispersal distances may totally negate the lag by allowing individuals to cross lethal areas (see below). This model is, therefore, more appropriate for species that have dispersal distances/rates that are small compared to the distance between patches.

Thus, the major results of spatially explicit models of habitat destruction, fragmentation and restoration, greatly rely on model structure and assumptions. Here we are only interested in the restoration aspect of these models. Thus, we follow the Tilman et al. model (1994, 1997) in that we use a cellular automaton in which patches are linked by dispersal. Tilman et al. (1997) randomly selected patches to be destroyed until a set proportion of the habitat was left and then patches were restored. We followed the same pattern of destroying habitat at the rate of 1% per time step (one hundred patches) until 25% of the habitat was still suitable, then restoring 1% of the habitat per time step until all patches were again suitable habitat (Fig. 1). Our spatially explicit model simulated a landscape that was divided into a square grid of 10,000 patches (100 × 100). Dispersal was limited to the four-cardinal-direction-adjacent patches and random so that individuals that dispersed to uninhabitable sites or off the grid were lost (i.e., absorbing boundary). Because of an expected extinction lag (Tilman et al. 1994), we allowed for the system to approach an equilibrium over a hundred time steps between habitat loss or restoration events. We performed ten replicates of each scenario.

Because we are interested in the efficacy of various management strategies, we restored patches by using four strategies: (1) patches to be restored are randomly selected (this is our null management strategy); (2) we randomly select patches to be restored, but we reintroduce the species into the restored patch; (3) only patches that are adjacent to occupied patches are restored; and (4) patches are restored in the reverse order in which they were destroyed (the last patches destroyed are the first to be restored).

The four restoration strategies were chosen to represent the variety of choices that are available to restoration managers and biologists given the various situations in which restoration projects occur. Managers of individual projects usually do not have all of these choices; however, we are more concerned with regional strategies. The first strategy (Random) can evolve in situations where an overall management plan is lacking, such that restoration efforts are done independently and typically involve only one or a few patches. The second strategy (Species Restored) requires necessary resources for the species to persist within the restored

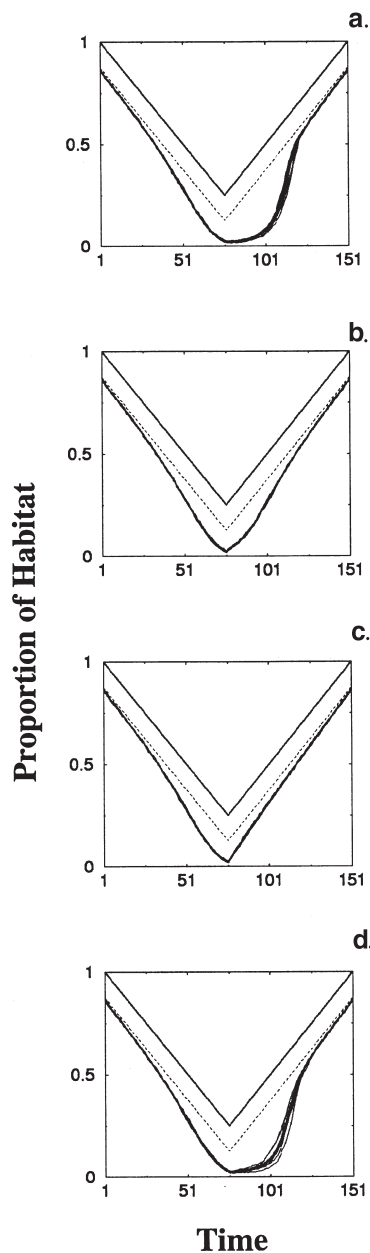


Figure 1. The four parts of this figure (a–d) represent results from simulations of different management/recovery scenarios, in which the method used to select which sites are to be restored differed: (a) patches to be restored are randomly selected (Random—this is our null strategy); (b) last, we randomly select patches to be restored, but we “reintroduce” the species into the restored patch (Species Restored); (c) only patches that are adjacent to occupied patches are restored (Adjacent); and (d) patches are restored in the reverse order in which they were destroyed (Reverse Order—the last patches destroyed are the first to be restored). Ten simulations for each scenario were performed. In each part, the thick solid line is the amount of habitat that is suitable; the dashed line is the deterministic metapopulation model result; and each replicate simulation is shown as solid lines.

habitat over early phases of restoration. The lack of monitoring and maintenance over a sufficient time may result in the target (or any other) species not being restored within the patch. This may also occur in landscapes in which habitat is created, but species are not seeded/reintroduced into the restored areas (as in our first strategy). Restoring habitat adjacent to occupied habitat results in clumped habitat distributions that can increase local patch size and therefore density (Adjacent). However, historical records rarely exist as to the extent of suitable habitat and we only know which sites have been recently destroyed. Thus, restoration efforts focus on these known sites (Reverse Order).

Results

In Figure 1a, we see that when habitat is randomly restored (Random), there is a long restoration lag. This is because when habitat loss is at a maximum, few patches are occupied and the probability that a restored patch will be adjacent to an occupied patch is relatively low. Thus, a number of restoration events may have no effect on patch occupancy. However, when patches are restored and we reintroduce the species into those patches (Species Restored, Fig. 1b), the restoration lag all but disappears. Most restoration attempts will involve reintroduction of a target species, but this may not always be successful for several reasons. One such reason is that habitat structure must be fully developed (assembled) for the restoration of some target species and may require long-term commitments (Lewis et al. 1996; Zedler 1996a, 1996b). Examples are the requirement of red-cockaded woodpeckers for live yellow pine trees with sufficient heartwood for cavities (Walters 1991). When restoration management plans call for restoring only those patches adjacent to occupied patches (Adjacent, Fig. 1c), the recovery is rapid and the species reaches a higher frequency of occupancy during the restoration phase than a corresponding level of habitable patches during the destruction phase. This rapid recovery and higher occupancy are because of the transformation of the habitat from randomly distributed habitable patches to highly clumped distribution. Notice that during the restoration phase, by placing restored sites adjacent to occupied patches versus randomly placing the sites results in up to a six-fold increase in patch occupancy and a two-fold increase during a significant portion of the early restoration phase in general (Fig. 2). Restoring the patches in the reverse order (so that last patches destroyed are the first to be restored) exhibits similar results as the random restoration (Fig. 1d). The restoration lag occurs in this lag strategy because of decreased connectivity and size of continuous habitat. Between when the habitat was destroyed and when it was

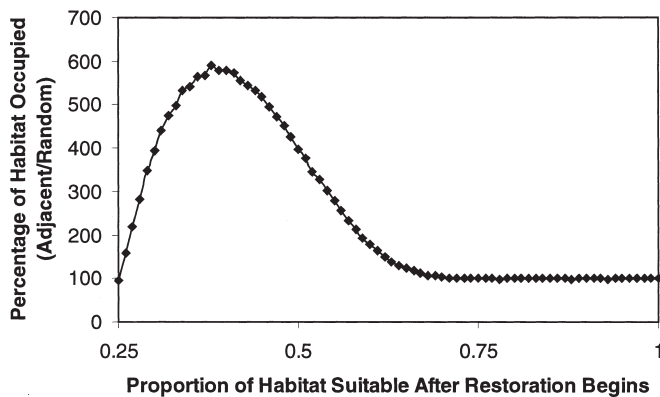


Figure 2. Here we plot the average (of 10 simulations) adjacent:random site occupancy ratio during the restoration phase of each scenario. Notice that after only two sites have been restored, there is a greater than two-fold increase in patch occupancy and that this gain in patch occupancy increases to a point where the benefit is approximately a six-fold increase in patch occupancy in favor of the adjacent scenario. This benefit remains until about 60–65% of the habitat is once again suitable.

restored, at least 100 time steps have occurred and, in that time, the target species may have become extinct in surrounding patches as local patch area decreased and/or larger habitat patches became isolated.

Discussion

Our results demonstrate that either restoring patches adjacent to occupied patches or reintroducing the species into restored patches increases the efficacy of the recovery effort. The former of these two scenarios reduced the amount of fragmentation as compared to the random scenario resulting in a six-fold increase in patch occupancy during the early phase in restoration (Fig. 2). However, as Fahrig (1997) suggested, this resulted in a difference between the adjacent and random scenarios only below a threshold of habitat loss (our threshold (~60–65%) is much greater than the 20% of the landscape that Fahrig suggested) (Figs. 1 & 2). The latter of the two scenarios worked in one of two ways. A single patch either was increased in size so that it became larger than a threshold, or connected two smaller patches, both below the threshold size but together greater than the threshold. Therefore, in the restoration with reintroduction case, dispersal ability, specifically the inability to cross the matrix, played a key role as in the random case. Even if patches were connected or sufficiently enlarged, they remained isolated below a habitat-loss threshold.

A few caveats concerning these results need to be discussed. First, the fairly simplistic cellular automaton

used was chosen for demonstration purposes. We view this model as a caricature of real systems; however, here we are mainly concerned with arguing for a more integrated, regional approach to restoration. Factors such as corridors and landscapes that have patches embedded in matrices of lesser suitable habitat rather than completely hostile habitat may be more realistic for some, but not all, species. Aquatic species that persist in isolated, spatially distributed habitat (e.g., fairy shrimp in vernal pools) and plant species that have narrow ranges of tolerance for environmental conditions or specialized habitats (e.g., salt marsh plants) may not have corridors that connect isolated patches (Mann & Plummer 1995; Rosenberg et al. 1997).

Yet, many systems will have corridors and more vagile species will be able to use these to disperse long distances, thereby negating any restoration lag dependent upon a species' vagility (Noss 1983; Fahrig & Merriam 1985; Wilcove et al. 1986; Saunders & Hobbs 1991; Rosenberg et al. 1997). However, geometrical and ecological features of corridors such as width, length, funneling, bends, habitat type, and any barriers will influence the ability of species to safely negotiate these corridors (Simberloff & Cox 1987; Soulé & Gilpin 1991). Furthermore, many species do not use corridors; instead they encounter patches by chance (Fahrig & Paloheimo 1987; Grevstad & Herzig 1997). Regardless of whether species use corridors or not, many habitats are population sinks or remain uncolonized for a number of years after being restored (Zedler 1996a, 1996b; G. R. Huxel & S. K. Collinge, unpublished manuscript). Therefore, immigration will be a key to species' successful colonization and restoration, and the positioning of restored habitat will influence the efficacy of any restoration efforts (G. R. Huxel & S. K. Collinge, unpublished manuscript).

One could further envision a scenario where the habitable patches are embedded into a matrix, without corridors, in which a species can survive but cannot maintain itself (Holt 1997; Fahrig 1997). This, again, would require that suitable patches are still not too distant and that placement of restored patches could be arranged so that restored habitat can better link suitable habitat.

Second, our results do not imply that the practice by regulatory agencies to allow a less than 1 to 1 ratio of restored/mitigated habitat to original habitat is sustainable (Zedler 1996b), even if the restored patches are selected optimally and corridors are present. As many researchers have noted, habitat loss can threaten many species through stochastic demographic processes as well as genetic impacts (Levins 1969; Hastings 1980; Tilman et al. 1994; Loehle & Li 1996). Further, fewer larger patches may not be appropriate in areas that have large correlated environmental perturbations or for species that experience frequent disease epidemics.

Finally, our results suggest that proper management plans for restoration can have significant effects on the efficacy of a species recovery. This is especially important when funds are limited and relatively few sites can be restored (Fig. 2). We expect similar results for management plans involving multiple species that have dispersal/competition tradeoffs. As extinction occurs first for less vagile species, management rules could increase the patch area of these species by placing restored patches adjacent to those of higher emigration. For less-competitive but more vagile species, restored patches could be placed such that they maximize connections between patches. Thus, while the relative influence of habitat loss and habitat fragmentation is being debated (Dytham 1995b; Moilanen & Hanski 1995; Kareiva & Wennergren 1995; Wennergren et al. 1995; Fahrig 1997; Huxel & Hastings 1998), we find that both are important aspects of species management/recovery plans. The placement of restored patches can increase the area of continuous patches, thereby increasing the local population size and decreasing chances of extinction owing to deterministic and stochastic demographic effects.

The model and results presented here represent a general concept of spatial concerns in restoration and mitigation. Individual project managers are generally concerned with the specifics of restoration or mitigation at individual sites and are usually interested only in the success at a given site. This generally occurs because regional management plans for many species are lacking. Given that funds for restoration are limited, management plans need to make informed decisions on which habitat is to be restored to improve species recoveries (Zedler 1996a). We believe that the successful restoration/conservation of endangered species requires a regional plan. This is especially important for species that have patchy distributions of habitat and experience local extinctions in these patches. These species require habitats that are close enough for effective dispersal to take place between habitats. The placement of restored or mitigated habitat then can be crucial to the long-term persistence of the species. How might this be accomplished? Many species recovery plans allow for mitigation banking. Landowners in some case may pay into a mitigation pool that is used to fund purchases of suitable habitat. Agencies or individuals that create or enhance property for mitigation banking purposes could select habitat in areas that link currently uninhabited but suitable habitat to occupied habitats. G. R. Huxel and S. K. Collinge (unpublished manuscript) have examined such ideas for the recovery of the *Desmocerus californicus dimorphus* Cerambycidae, (Valley Elderberry Longhorn Beetle), a threatened California Central Valley endemic. The riparian habitat of the beetle has been severely depleted (> 90% loss) and fragmented since the 1840s (Smith 1980; Barbour et al. 1993; Kucera &

Barrett 1995) so that riparian habitat in differing drainages has been isolated. Using a spatially explicit model, Huxel and Collinge found that by haphazardly placing mitigation patches within 5 km of naturally occurring sites, occupancy of the naturally occurring sites increased (G. R. Huxel & S. K. Collinge, unpublished data). One would expect that selection of mitigation banking sites in a stepping stone manner, between inhabited, non-isolated sites and isolated, uninhabited sites, would better allow for colonization and of persistence of populations in isolated habitats.

Conclusion

We recognize that regional thinking requires better information on basic biological parameters of species such as local population size, dispersal ability, and fecundity. Regrettably, for many of the species that require mitigation this information is rarely known. Given these limitations, we believe that modeling of these types of systems may provide some valuable information on the spatial aspects of the restoration of endangered species. Finally, we stress that the recovery and conservation of rare species will require proactive management on a landscape scale.

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LITERATURE CITED

- Adler, F. R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. *Theoretical Population Biology* 45:41-75.
- Barbour, M., B. Pavlik, F. Drysdale, and S. Linstrom. 1993. California's changing landscapes. California Native Plant Society, Sacramento.
- Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications* 4:446-460.
- Dunning, Jr., J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L.

- Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5:3–11.
- Durrett, R., and S. A. Levin. 1994. Stochastic spatial models—a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London B* 343:329–350.
- Dytham, C. 1994. Habitat destruction and competitive coexistence: a cellular model. *Journal of Animal Ecology* 63:490–491.
- Dytham, C. 1995a. The effect of habitat destruction pattern on species persistence: a cellular model. *Oikos* 74:340–344.
- Dytham, C. 1995b. Competitive coexistence and empty patches in spatially explicit metapopulation models. *Journal of Animal Ecology* 64:145–146.
- Ehrlich, P., and A. Ehrlich. 1981. *Extinction*. Ballantine Books, New York.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61:603–610.
- Fahrig, L., and H. G. Merriam. 1985. Habitat patch connectivity and population survival. *Ecology* 66:1762–1768.
- Fahrig, L., and J. E. Paloheimo. 1987. Inter-patch dispersal in the cabbage butterfly. *Canadian Journal of Zoology* 65:616–622.
- Gilpin, M. E., and I. Hanski, editors. 1997. *Metapopulation dynamics*. Academic Press, San Diego, California.
- Grevstad, F. S., and A. L. Herzog. 1997. Quantifying the effects of distance and conspecifics on colonization: experiments and models using the looper leaf beetle, *Galerucella calmarensis*. *Oecologia* 110:60–68.
- Groom, M. J., and M. A. Pascual. 1998. The analysis of population persistence: an outlook on the practice of viability analysis. Pages 4–27 in P. L. Fielder and P. M. Kareiva, editors. *Conservation biology: for the coming decade*. 2nd edition. Chapman & Hall, New York.
- Groombridge, B., editor. 1992. *Global biodiversity: state of the earth's living resources*. Chapman & Hall, New York.
- Hanski, I., and M. E. Gilpin, editors. 1991. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California.
- Harrison, S. 1993. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific, Oxford.
- Harrison, S., A. M. Stahl, and D. Doak. 1993. Spotted owl update: U.S. judge rejects Forest Service plan. *Conservation Biology* 7:1–4.
- Hassell, M. P., H. C. J. Godfray, and H. N. Comins. 1993. Effects of global change on the dynamics of insect host-parasitoid interactions. Pages 402–423 in P. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer, Sunderland, Massachusetts.
- Hastings, A. 1980. Disturbance, coexistence, history, and the competition for space. *Theoretical Population Biology* 18:363–373.
- Holt, R. D. 1997. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. Pages 149–164 in M. E. Gilpin and I. Hanski, editors. *Metapopulation dynamics*. Academic Press, San Diego, California.
- Huxel, G. R., and A. Hastings. 1998. Population size dependence, competitive coexistence, and habitat destruction. *Journal of Animal Ecology* 67:446–453.
- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373:299–302.
- Kucera, T. E., and R. H. Barrett. 1995. California wildlife faces uncertain future. *California Agriculture* 49:23–27.
- Levin, S. A., B. Grenfell, A. Hastings, and A. S. Perelson. 1997. Mathematical and computational challenges in population biology and ecosystems science. *Science* 275:334–343.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Lewis, C. A., N. P. Lester, A. D. Bradshaw, J. E. Fitzgibbon, K. Fuller, L. Hakanson, and C. Richards. 1996. Considerations of scale in habitat conservation and restoration. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Supplement 1):440–445.
- Loehle, C., and B.-L. Li. 1996. Habitat destruction and the extinction debt revisited. *Ecological Applications* 6:784–789.
- Mann, C. C., and M. L. Plummer. 1995. Are wildlife corridors the right path? *Science* 270:1428–1430.
- May, R. M. 1993. The effects of spatial scale on ecological questions and answers. Pages 1–18 in P. J. Edwards, R. M. May, and N. R. Webb, editors. *Large-scale ecology and conservation biology*. Blackwell Scientific, Oxford.
- Moilanen, A., and Hanski, I. 1995. Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model. *Journal of Animal Ecology* 64:141–144.
- Noon, B. R., and K. S. McKelvey. 1996. Management of the spotted owl: a case history in conservation biology. *Annual Review of Ecology and Systematics* 27:135–162.
- Noss, R. F. 1983. A regional landscape approach to maintain diversity. *BioScience* 33:700–706.
- Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications* 2:165–177.
- Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors: form, function, and efficacy. *BioScience* 47:677–687.
- Saunders, D. A., and R. J. Hobbs. 1991. The role of corridors in conservation: what do we know and where do we go? Pages 421–427 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.
- Simberloff, D. S., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63–71.
- Smith, F. 1980. A short review of the status of riparian forests in California. Pages 1–2 in A. Sands, editor. *Riparian forests of California*. Division of Agriculture and Natural Resources, University of California Regents, Davis.
- Soulé, M. E., and M. E. Gilpin. 1991. The theory of wildlife corridor capability. Pages 3–8 in D. A. Saunders and R. J. Hobbs, editors. *Nature conservation 2: the role of corridors*. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.
- Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecological Applications* 2:18–29.
- Tilman, D., and P. Kareiva, editors. 1997. *Spatial ecology*. Princeton University Press, Princeton, New Jersey.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature* 371:65–66.
- Tilman, D., C. L. Lehman, and P. Kareiva. 1997. Population dynamics in spatial habitats. Pages 3–20 in D. Tilman and P. Kareiva, editors. *Spatial ecology*. Princeton University Press, Princeton, New Jersey.
- Walters, J. R. 1991. Application of ecological principals to the management of endangered species—the case of the red-cockaded woodpecker. *Annual Review of Ecology and Systematics* 22:505–523.
- Wennergren, U., M. Ruckelhaus, and P. Kareiva. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* 74:349–356.
- Wilcove, D. S., C. H. McLelland, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 in M. E.

- Soulé, editor. Conservation biology. Sinauer Associates, Sunderland, Massachusetts.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**:879–887.
- Zedler, J. 1996a. Ecological issues in wetland migration—an introduction to the forum. *Ecological Applications* **6**:33–37.
- Zedler, J. 1996b. Coastal mitigation in southern California—the need for a regional restoration strategy. *Ecological Applications* **6**:84–93.