Introduction

The correlated processes of habitat loss and fragmentation are probably the most important threats to global biodiversity. Not surprisingly, they are also among the most active fields of inquiry in conservation biology.

Historically, studies of fragmented ecosystems have relied heavily upon the conceptual model of island biogeography theory (MacArthur & Wilson 1967), which emphasizes the effects of fragment area and isolation on species richness. Island biogeography theory is clearly too simplistic, however, and has been superseded by landscape ecology (Forman & Godron 1986), which further emphasizes factors such as fragment shape, spatial configuration of fragments, movement corridors, and structure and composition of the surrounding matrix. Metapopulation theory also has helped lay conceptual groundwork for understanding the responses of subdivided populations to fragmentation (cf. Doak & Mills 1994; Hanski & Gilpin 1996).

Of course, there have also been hundreds if not thousands of empirical studies of fragmented habitats. These range from microcosm experiments, to small-scale landscape manipulations (cf. Debinski & Holt 2000), to field studies of fragmented habitats and land-bridge islands (e.g., Saunders et al. 1991; Laurance & Bierregaard 1997; Laurance & Gascon 1999). These studies have yielded important insights into the responses of various taxa to fragmentation and into the effects of fragment size, shape, connectivity, and other landscape features on species assemblages and ecological processes. Clearly, the study of habitat fragmentation has grown, diversified, and matured.

It could still be argued, however, that many fragmentation studies, and the conceptual models on which they are based, are naive and oversimplified. One of their most striking deficiencies is that fragments in most anthropogenic lands are not merely reduced and isolated; they are also affected by other perturbations that may interact additively or synergistically with fragmentation. Forest fragments in the Amazon, for example, are often selectively logged, degraded by ground fires, and overhunted—changes that dramatically alter fragment ecology (Cochrane et al. 1999; Nepstad et al. 1999; Gascon et al. 2000). In agricultural and urban areas, acid rain, pesticides and herbicides, hydrological changes, livestock grazing, and pressure from invading species can severely degrade fragments (Myers 1987, 1988; Hobbs & Huenneke 1992). In coming decades, anthropogenic climate change may emerge as an increasingly important threat to fragmented communities, especially if droughts, storms, and other rare weather events increase in frequency or severity (Intergovernmental Panel on Climate Change 1996; Timmerman et al. 1999).

It is becoming apparent that the current fragmentation paradigm, which emphasizes changes in landscape configuration while generally ignoring other anthropogenic effects, is dangerously inadequate for conservation purposes (e.g., Curran et al. 1999; Laurance 2000). It is also inadequate from a scientific perspective. What is needed is a more realistic view of fragmented landscapes, one that explicitly recognizes the potential for interacting environmental changes to amplify and alter the ecological effects of habitat fragmentation.

This is a new way of viewing fragmentation research—for which there are as yet few examples. In this special section we present five case studies that explicitly evaluate synergisms between fragmentation and other environmental impacts. The first paper, by Carlos Peres, describes the often-severe effects of hunting and fragmentation on Neotropical wildlife. The second, by Kathleen Weathers and her colleagues, demonstrates that fragmentation increases the vulnerability of deciduous forests in the eastern United States to wind-borne nutrients and pollutants. The third paper, by Mark Cochrane, examines the devastating interactions of fire and fragmentation in eastern Amazonia. In the fourth paper, Richard Hobbs assesses the effects of fragmentation, livestock grazing, and weed invasions in Australian forests. The final study, by William Laurance and Bruce Williamson, describes positive feedbacks among drought, climate change, and fragmentation in the Amazon.

Our hope is that these studies can serve as a springboard to further research on additive and synergistic interactions, especially in fragmented landscapes. Such negative synergisms could potentially be one of the most important—and least understood—aspects of the modern environmental crisis.

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Literature Cited

Cochrane, M. A., A. Alencar, M. D. Schulze, C. M. Souza, D. C. Nepstad, P. Lefebvre, and E. A. Davidson. 1999. Positive feedbacks in the fire dynamics of closed canopy tropical forests. Science **284:** 1832–1835.

Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita, and H. Haeruman. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. Science **286:**2184–2188.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14:**342–355.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology **75:**615–626.

Forman, R. F. F., and M. Godron. 1986. Landscape ecology. Wiley, New York.

Gascon, C., G. B. Williamson, and G. A. B. Fonseca. 2000. Receding edges and vanishing reserves. Science **288:**1356–1358.

Hanski, I., and M. E. Gilpin, editors. 1996. Metapopulation biology: ecology, genetics, and evolution. Academic Press, London.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6:**324–337.

Intergovernmental Panel on Climate Change. 1996. Climate change 1995: impacts, adaptations and mitigation of climate change: scientific technical analyses. Cambridge University Press, Cambridge, United Kingdom.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology and Evolution **15:**134–135.

Laurance, W. F., and R. O. Bierregaard. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Laurance, W. F., and C. Gascon, editors. 1999. Ecology and management of fragmented tropical landscapes. Biological Conservation **91:**101–247.

MacArthur, R. O., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Myers, N. 1987. The extinction spasm impending: synergisms at work. Conservation Biology **1:**14–21.

Myers, N. 1988. Synergistic interactions and environment. BioScience **39:**506.

Nepstad, D. C., A. Verissimo, A. Alencar, C. Nobre, E. Lima, P. Lefebre, P. Schlesinger, C. Potter, P. Moutinho, E. Mendoza, M. Cochrane, and V. Brooks. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. Nature **398:**505–508.

Saunders, D. A., R. J. Hobbs, and C. R. Margules, editors. 1991. Nature conservation: the role of remnants of native vegetation. Surrey Beatty and Sons, Chipping Norton, New South Wales, Australia.

Timmerman, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature **398:**694–697.