

Habitat fragmentation and large-scale conservation: what do we know for sure?

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We review the ecological effects of habitat fragmentation, comparing the theoretical approaches that have been taken to understanding it with the existing evidence from empirical studies. Theory has emphasized the spatial aspects of fragmentation and the role of dispersal among patches, and has generated interesting predictions such as a nonlinear relationship between the amount of remaining habitat and the probability of species persistence. However, while the few available large-scale empirical studies of fragmentation all tend to show that it has major effects, these documented effects tend to be relatively simple ones such as the degradation of habitat quality within fragments. There is good reason to be cautious of any claim that corridors or the spatial configuration of remaining habitat can compensate for the overall loss of habitat.

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Habitat fragmentation has been a central preoccupation in conservation biology since the field began. One reason for this is that fragmentation is occurring to natural habitats throughout the world; the other is that ecologists have felt they had something to offer in terms of understanding and mitigating its effects. MacArthur and Wilson's (1967) theory of island biogeography was the first to offer the prospect that an elegant and general ecological model could lead to a powerful set of conservation prescriptions. Although island biogeography has faded from the scene somewhat, the hope of a general understanding of fragmentation lives on, as evidenced by a continued proliferation of models of fragmented habitats. At the same time, a growing number of empirical studies have examined how ecological processes of all kinds are altered when continuous habitats are turned into sets of isolated remnants. The literature on fragmentation grows ever richer, yet we still lack a synthesis between general principles and consistent field evidence. In this brief and opinionated essay, we will not attempt such a synthesis, but we will

address three related questions: First, what ecological theories are being applied to habitat fragmentation, and how have they contributed to our understanding? Second, what do and don't we know about the ecological effects of habitat fragmentation based on existing empirical evidence? And finally, are we arriving at any general conclusions about fragmentation, and what are our most significant unanswered questions?

Ecological theory and fragmentation

As every ecologist knows, MacArthur and Wilson's (1967) theory asserted that the number of species in insular habitats is set by an equilibrium between distance-dependent colonization and area-dependent extinction, and it predicted that the smaller and more isolated a habitat is the fewer species it will support. This theory changed ecological thinking by identifying the spatial configuration of habitats as an important influence on populations and communities. Island bio-

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geography became one of the founding tenets of the field of conservation biology, and was used to derive principles of reserve design that included maximizing area-to-edge ratios for individual reserves, and connecting reserves with corridors to improve dispersal. Subsequently these principles were avidly promoted by some ecologists and just as enthusiastically contested by others (reviewed by Shaffer 1994).

The attention once given to island biogeography theory by conservation biologists has now largely shifted to metapopulation theory, as recently described by Hanski and Simberloff (1997). Metapopulation theory resembles island biogeography in focusing on patchy habitats, extinction, and colonization, but differs in assuming a network of small patches with no persistent mainland habitat, and in focusing on the dynamics of only one species. Compared with island biogeography theory, metapopulation theory makes an even stronger prediction about the importance of dispersal among habitat fragments: since there is no mainland, inadequate dispersal will lead not only to local but to regional extinction of species. Metapopulation models predict nonlinear effects of habitat loss: as habitats are destroyed in a region, species will become extinct when the amount of remaining habitat falls below a critical threshold set by their dispersal and extinction parameters. Conversely, providing a small amount of additional habitat in the form of corridors can prevent extinction by increasing rates of dispersal. Because of its power to link population dynamics with habitat geometry, and because of its seeming potential to arrive at positive solutions, metapopulation theory has generated great interest among conservation biologists (reviews in Harrison 1994, McCullough 1996, Hanski 1998).

Island biogeography and metapopulation theory both consider non-interacting species. However, a related set of models sometimes called metacommunity theory considers assemblages of interacting species in a metapopulation-like setting of habitat patches with no mainland. Local populations are subject to local extinction and colonization, as well as strong competitive and/or predator-prey interactions. As first shown by Huffaker (1958), a patchy environment can promote coexistence between predators and prey in such circumstances, because temporarily vacant patches provide refuges for the victim species (reviewed in Harrison and Taylor 1997, Nee et al. 1997). Extend this idea to entire assemblages, metacommunity models show that the interplay between patchiness, competition or predation, and limited dispersal can lead to higher regional species diversity (Paine and Levin 1974, Case 1991, Caswell and Cohen 1991, 1993). However, increasing fragmentation can lead to the loss of the dominant species in metacommunity models that assume the best competitors to be the worst dispersers (Tilman et al. 1994).

Other theoretical perspectives that have been applied to fragmentation include source-sink models (Pulliam 1992, Dias 1996), which highlight the importance of the movement of organisms from high to low-quality habitats; and percolation theory, which stresses the role of landscape configuration in controlling patterns of dispersal (Boswell et al. 1998). Though these various theories make predictions that diverge in some respects, they are also unanimous in focusing on dispersal and habitat geometry. Collectively, this body of spatial theory has led to the perspective that spatial strategies, such as corridors to promote dispersal or other ways of configuring conserved habitat, can play an important role in alleviating the effects of habitat fragmentation (Kareiva and Wennergren 1995, Rosenberg et al. 1997).

General theory does not, of course, make exact predictions about how to conserve specific species in real landscapes. Spatially explicit simulation models based on the concepts of metapopulation and source-sink dynamics have enjoyed some popularity as a tool for devising conservation strategies. Such models combine species-specific demographic and dispersal parameters with real or hypothetical configurations of the landscape, and can be used to examine how population viability depends on the size and spacing of habitat fragments (e.g. Lamberson et al. 1992). However, spatially explicit models have been criticized for the excessive sensitivity of their results to the values of parameters many of which are poorly known or unmeasurable (Harrison et al. 1993, Ruckelshaus et al. 1997).

A broader critique of spatial theory in conservation biology was offered by Fahrig (1998). Her generalized simulation model of a population in a fragmented habitat examined a large range of values for the dispersal and other life-history parameters of an organism, as well as for the total amount and configuration (i.e. degree of contagion) of habitat. Not surprisingly, the total amount of habitat proved to have an overwhelming and consistent effect on persistence. However, the spatial configuration of a given amount of habitat affected population persistence in only a tiny fraction of cases (i.e. parameter combinations). Unlike many spatial ecological models, which ask whether it is possible to find interesting effects of spatial configuration, this model asked how often spatial effects are likely to be important. In contrast to the prevailing wisdom, the answer appeared to be "not very often".

In summary, there has been a considerable effort to apply ecological theory to questions about habitat fragmentation. Most of this theory focuses on fragmentation as a spatial problem, emphasizing the central role of dispersal among fragments in determining whether or not populations will persist. In the next sections we evaluate how well such theory matches the existing empirical evidence.

Limitations of the available evidence

Despite the ubiquity of habitat fragmentation throughout the world, and the great interest ecologists have shown in studying it, there are some nearly insurmountable obstacles to answering some of the most interesting and important questions about it. Perhaps the most basic problem is that in habitats undergoing fragmentation, changes in spatial configuration are inevitably confounded with reduction in total habitat area. Documenting the ecological effects of habitat loss, which may indeed be drastic, does not go far toward testing theories about spatial structure.

Another difficulty is that sets of many similar habitat fragments are hard to find, as anyone who has tried to initiate a fragmentation study knows. Not only fragment size and shape, but history, habitat type, proximity to human disturbances, and many other features may vary even within a single region. Moreover, even perfect sets of replicate fragments would only be conducive to asking certain questions about fragmentation, such as how ecological processes vary with the size, shape, or other characteristics of individual fragments. To investigate regional effects, such as how the degree of connectivity among patches affects ecological processes, it would be desirable to examine many replicate sets of patches, varying in the type of matrix habitat, the presence or absence of corridors, or the distance among patches. Likewise, to test whether species diversity or abundance decline nonlinearly with the amount of habitat in the landscape, one would need either many replicate landscapes or a long time series for a single landscape. Given these demanding requirements, it is not surprising that Beier and Noss (1998) recently concluded that no studies provided a completely satisfactory test of the efficacy of corridors.

Beyond the issues of replication and design, there is also the question of how often fragmentation produces spatial pattern similar to that assumed by models. Models often envision a universe of small, discrete, ecologically similar fragments, near enough to exchange dispersing organisms with one another, and far from the overriding influence of a mainland habitat. Whether this caricature captures the essence of many or most real fragmented landscapes is an open question. As always, theory may either be an elegant simplification that allows us to focus on the essential issues, or such an oversimplification that its predictions are never met in real systems because the factors it excludes are too important.

Another basic problem is the extreme difficulty of studying dispersal at a landscape scale. For obvious practical reasons, we have almost no direct evidence on movements of animals or plants among habitat fragments. Even if we did, this would be far from adequate to allow us to assess how movement affects the populations and communities within habitat fragments. To

understand the consequences of a given amount and pattern of movement would require a great deal of information about demography and interactions within patches. To make matters still worse, some spatial ecological models conclude that the most significant aspect of dispersal is the tail of the distribution, i.e. the rare long-distance movements made by a vanishingly small proportion of individuals (e.g. Cain et al. 1998).

Given these daunting obstacles, it is hardly surprising that we lack a solid and conclusive body of evidence about fragmentation, and that instead our knowledge is patched together from a variety of imperfect sources. We next examine some of this evidence.

Evidence from microcosms, mesocosms and mowing

Some of the most elegant tests of spatial ecological theory have come from microcosm studies. For example, the only study to demonstrate experimentally that corridors can enhance population persistence is work by Gilbert et al. (1998) and Gonzalez et al. (1998), who experimentally fragmented patches of moss on rocks; as predicted by metapopulation theory, the invertebrate fauna inhabiting moss persisted longer in sets of fragments connected by corridors than in sets of unconnected fragments. Likewise, the best evidence that a patchy environment can promote the coexistence of predators and prey is a study of protozoans in aquatic microcosms by Holyoak and Lawler (1996); predator and its prey persisted longer in arrays of bottles connected by tubes than in either arrays of unconnected bottles or a single tank of equal total volume.

At a somewhat larger scale, a number of experimental studies have examined fragmentation using patches of either single plant species or of natural grassland communities created by either by planting or by using grazing or mowing to isolate patches. Spatial scale in such studies typically ranges from tens to hundreds of meters between patches and patch size typically varies from tens to hundreds of square meters. Such experiments have shown that the spatial configuration of habitats may affect plant diversity (e.g. Quinn and Robinson 1987, Holt et al. 1995); insect predation (e.g. Kareiva 1987), parasitism (Kruess and Tschamtkke 1994), and pollination (e.g. Kunin 1997, Groom 1998); and the dispersal and demography of small mammals (e.g. Diffendorfer et al. 1995, Dooley and Bowers 1996, 1998).

Micro- and mesocosm experiments have contributed enormously to our ability to evaluate spatial ecological theories. It is less clear how well they pertain to conservation, however, and indeed many of them were not intended to address conservation questions. In the microcosm studies, the dispersal ability of the organisms

was quite limited in relation to the scale of the experimental patches, making these systems reasonable as models for the effects of population subdivision. But microcosms still exclude several key real-world features, such as realistic amounts of spatio-temporal variability in the environment. The mesocosm studies mostly concerned organisms that were relatively mobile and could visit numerous experimental patches in their lifetimes. Thus the effects of patchiness detected in these studies were probably largely behavioral, and would not necessarily translate well to larger spatial scales. While one could debate ad infinitum the meaning and value of model systems for studying fragmentation, the bottom line is that they are still simplifications of natural systems. Just as with mathematical models, further research must still be done to test their applicability to the species and scales of interest to conservation. We next consider studies that have more direct relevance to conservation, although as a result of their larger scale they also have less control and replication.

Evidence from a handful of large-scale studies

The most comprehensive study of forest fragmentation is the Biological Dynamics of Forest Fragments experiment in the Brazilian Amazon, created in 1979 during a period of rapid deforestation (Bierregaard et al. 1992, Laurance and Bierregaard 1997). A series of 1, 10, 100 and 1000-ha plots was established, and a wide range of variables was studied before and after these became isolated. The most conspicuous changes were in the structure of the forest: total biomass decreased, foliage density declined in the overstory and increased in the understory, and for many forest-interior tree species their adult mortality increased and their seedling recruitment declined (Malcolm 1994, Laurance et al. 1997, 1998, Benitez-Malvido 1998). Many other biotic changes were observed. Rates of dung removal decreased as the dung beetle community became impoverished (Klein 1989). An estimated 50% of leaf-litter beetle species were lost from the smallest fragments (Didham et al. 1998). The frog community suffered few extinctions, but "weedy" habitat generalists became more prevalent in small fragments (Tocher et al. 1997). Understory frugivorous birds declined drastically in small fragments, although some species partially recovered as successional vegetation filled the matrix between fragments (Stouffer and Bierregaard 1995).

Underlying many or most of the biotic changes in this study were drastic alterations in the physical environment near forest edges. In particular, higher temperature and wind speeds and lower humidity prevailed at distances up to 60 m into fragment interiors, and led to higher rates of treefall (Kapos 1989, Camargo and

Kapos 1995, Kapos et al. 1997). The overriding importance of physical edge effects has similarly been documented in many other studies of tropical and temperate forest fragmentation (e.g. Saunders et al. 1991, Leigh et al. 1993, Esseen and Renhorn 1998).

Many conservation biologists have speculated that fragmentation could lead to cascades of extinctions and other ecological changes beyond the level of individual species. For example, a number of studies have documented indirect effects of the loss of large-bodied species that cannot maintain populations in small fragments. Since Barro Colorado Island in Panama became isolated by a reservoir, medium-sized nest predators increased enormously in abundance in response to the loss of top predators, and the birds most vulnerable to nest predation became extinct (Sieving and Karr 1997). On smaller islets in the same reservoir, forest composition shifted toward large-seeded tree species following the loss of mammalian seed predators (Leigh et al. 1993). Many of the same islets also lost their army ants (Partridge et al. 1996). On tropical reservoir islands in Venezuela, bird densities increased as rates of nest predation decreased in the absence of capuchin monkeys (Terborgh et al. 1997).

The collapse of plant-pollinator interactions is another possible cause of cascades of extinction in habitat fragments (reviewed by Rathcke and Jules 1993, Bond 1995). In one of the most comprehensive large-scale studies of this question, Aizen and Feinsinger (1994a, b) found that the fragmentation of Argentinian chaco forest led to the replacement of native insect pollinators by feral honey bees, with variable but mainly negative effects on seed set for a number of species. However, the authors concluded that the short-term effects of this change on the plant community were less significant than the direct effects of incursion into forest fragments by cattle. There are surprisingly few examples in which the loss of pollinators has had significant demographic consequences for plants; Bond (1995) argues that long-term studies are needed to address this question, but also that many plant species are buffered by either self-compatibility, generalist pollinators, or vegetative reproduction.

Several studies have suggested that fragmentation could affect interactions between defoliating insects and the insect parasitoids that may control their populations. Parasitism on forest tent caterpillars by tachinid flies declined with increasing forest fragmentation, apparently leading to longer-lasting outbreaks (Roland and Taylor 1997). Similar effects on other defoliators were studied by Cappuccino and Martin (1997) and Cappuccino et al. (1998). The mechanisms for these effects remain unclear, however.

Invasion of fragments by organisms abundant in the matrix is frequently implicated as the cause of ecological change in fragmented habitats. The best known such biological edge effect concerns nest predation on

forest-nesting birds in Scandinavia and the eastern and midwestern U.S.; for a recent review of this extensive literature see Tewksbury et al. (1998). Nests near forest edges may receive higher rates of attack by habitat-generalist nest predators such as cowbirds, crows, and raccoons (e.g. Wilcove 1985), and nest success may increase as a function of the amount of forest in the landscape (e.g. Robinson et al. 1995), although the strength and generality of this effect remain controversial (e.g. Paton 1994, Yahner 1996, Keyser et al. 1998, Tewksbury et al. 1998). Other biological edge effects were observed in a study of fragmented scrubland in southern California, where the invasion of fragments by generalist predators such as cats appears to have contributed to declines in native ground-nesting birds (Soulé et al. 1988) and rodents (Bolger et al. 1997). The same fragments are also invaded by aggressive non-native ants that probably displace native ants through competition (Suarez et al. 1998). Finally, humans may invade fragments and alter ecological processes. Laurance (1998) reviews cases of increased pressure by human hunters in forest remnants.

What do and don't we know?

Although this review is far from comprehensive, we feel it provides a representative selection of studies on the ecological effects of large-scale habitat fragmentation. From existing evidence, we will argue there are several things one can say with some confidence about the ecological effects of fragmentation. First, there is a general pattern of biological impoverishment of fragmented habitats compared with more intact ones. Many studies find that remnant habitat fragments support fewer species of habitat specialists; often, fragments support increased abundances of widespread generalist species. Thus, fragments of habitats such as forests are not simply cookie-cutter pieces of the original habitat; their biotas may be drastically altered. The most important message from fragmentation studies is that we cannot safely assume that conserving small remnant areas will succeed in preserving species diversity.

Second, we can say something about the relative importance of different mechanisms causing the loss of diversity and ecological function within habitat fragments. Physical edge effects appear to be predominant, at least in forests, where increased light and wind penetration, increased treefalls, and decreased humidity have been shown to directly and indirectly affect much of the biotic community. Such effects may render fragments hundreds of hectares in size virtually all edge; Laurance and Yensen (1991) have proposed a simple, data-motivated model that estimates the amount of core area from empirical measurements of edge effects.

Biological edge effects, such as the penetration of remnant habitats by aggressive competitors or predators with deleterious effects on the native fauna, are also common and may exacerbate the effects of physical changes at edges. These often involve exotic species or aggressive natives that attain high abundances near edges because they are subsidized by resources in the matrix. Biological area effects, such as the loss of large-bodied species or top predators that require large amounts of habitat, are also important; however, these could be regarded as effects of regional habitat loss rather than of fragmentation per se.

Third, there is modest but growing evidence that beyond its direct effects on species diversity and abundance, fragmentation may lead to chains of indirect effects and altered ecological interactions. Higher-order effects have been observed in a number of systems where fragments have lost important predators, seed predators or seed dispersers, leading to drastic changes in abundance at lower trophic levels. Evidence is scarcer, thus far, for indirect effects caused by the collapse of mutualisms, but it remains an issue worth pursuing. Potential ecosystem effects are suggested by several interesting examples, such as the reduction in dung removal by beetles in Amazonian forest, and the weakening of the control of insect outbreaks by parasitoids in fragmented temperate forest.

One common theme among most of these examples is that they are relatively local effects, caused by processes within or immediately around the habitat fragment in question. Few of the large-scale studies showed either direct or indirect evidence for the importance of movement among habitat fragments (although see Stouffer and Bierregaard 1995). Even though dispersal among fragments is the defining feature of most theory on fragmentation, there appears to be little basis from which to evaluate the existence of fragmentation thresholds, the disproportionate loss of top competitors from fragmented habitats, the demographic significance of "sink" habitat, the efficacy of corridors at promoting regional (as opposed to local) persistence, or other ideas that follow from dispersal-based ecological theories.

Conclusions

On present evidence, there appears to be a mismatch between ecological theory and empirical studies of fragmentation. Theory portrays fragmentation as a spatial problem and focuses on dispersal among fragments, while empirical studies tend to suggest that fragmentation is more a matter of habitat degradation in which fragments undergoing changes in species composition for mainly edge-related reasons. Existing evidence suggests that spatial configuration is important mainly because of edge effects. Corridors clearly cannot rem-

edy edge effects, nor most of the other consequences of fragmentation that have been best documented. While corridors might possibly prevent the losses of large-bodied species from fragmented landscapes, it is far from self-evident that they could do so; such losses might be mainly a function of the total amount of habitat in a region, not its configuration or connectivity.

The issues of habitat configuration and large-scale dispersal remain worth pursuing with all our available approaches, even if fully conclusive tests are almost impossible. Our point is not that spatial aspects of fragmentation do not matter, but that the applicability of current spatial theory to real fragmented landscapes remains an open question. As the study of fragmentation develops, it is important to avoid jumping from the growing body of evidence that fragmentation matters to the conclusion that we have an adequate conceptual framework for understanding it. There is sometimes a tendency for scientists and conservationists to be captivated by the theoretically interesting issues such as metapopulations and corridors, at the expense of addressing the less interesting and perhaps more basic ones such as the degradation of habitat within fragments. It is important to stress once again that no evidence supports the proposition that corridors can mitigate the overall loss of habitat (Harrison 1994, Fahrig 1998, Rosenberg et al. 1997).

There remain many important questions for ecologists to study about fragmentation. As the natural world continues to experience the combined impacts of habitat loss and fragmentation, global biotic homogenization, and climate change, there can be few tasks more important for ecologists than determining how diversity can be maintained in remnants of natural habitat. With respect to fragmentation, we believe one of our most useful contributions will be to simply continue seeking facts and patterns in careful observational and experimental studies on ecosystems of direct interest to conservation; useful generalizations may slowly emerge as the number of such studies grows. The potential for new tools such as geographic information systems and molecular methods to help us understand fragmentation has hardly begun to be exploited. Finally, we believe there is certainly a useful role for empirically motivated theory that begins with real fragmentation scenarios as its starting point, and has the explanation of real observations as its goal.

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