

11 Reflections on Landscape Experiments and Ecological Theory: Tools for the Study of Habitat Fragmentation

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11.1 Introduction

Habitat destruction and fragmentation are widely recognized as some of the most serious aspects of global change (Saunders et al. 1991; Fahrig and Merriam 1994). Dealing with the far-flung consequences of habitat fragmentation mandates the fusion of a wide range of scientific perspectives. In the study of habitat fragmentation, as with any scientific endeavor, there are three basic tools: (1) observation and correlation; (2) theory and modeling; (3) experimental manipulation. In recent decades, a huge amount of literature on habitat fragmentation has been generated (e.g., Andren 1994; Leach and Givnish 1996; Laurance and Bierregaard 1997). There are hundreds of descriptive studies of fragmentation (e.g., Blake 1991; Aizen and Feinsinger 1994; Hanski et al. 1995) and a large and growing body of relevant theory (e.g., Hess 1996; Wahlberg et al. 1996). Yet, to date, there are barely over a score of fragmentation experiments, past and present, across all biomes worldwide (Margules 1996; Debinski and Holt 2000). Many experiments are quite recent in their initiation, with publications just starting to appear. In contrast to other areas of ecology, such as interspecific interactions like predation and competition (e.g., Hairston 1989), it seems fair to say that our understanding of habitat fragmentation has developed largely apart from the standard scientific method of experimentation. Indeed, authoritative syntheses of ecological experimentation barely even mention habitat fragmentation (Scheiner and Gurevitch 1993; Underwood 1997).

Manipulations of entire landscapes are necessarily large in scale, laborious, and costly (Steinberg and Kareiva 1997). Yet such experiments do exist, and encouragingly, in increasing numbers. This paper is motivated by several issues. First, we believe there is much to be gained from carefully designed experimental approaches to habitat fragmentation, but given the expense and logistical difficulties it is essential to synthesize results across studies, and to

explicitly relate them to ecological theory. Second, it is a pity that more investigators do not seize the opportunity to engage in these ongoing experiments. By writing this paper and a companion piece (Debinski and Holt 2000), we hope to make ecologists more aware of these experiments, and to stimulate a wider range of investigators to consider participating in these grand-scale experiments, which potentially provide arenas for addressing a wide range of issues in spatial ecology. Third, we feel it is essential to be conscious of the limitations of experimental approaches to fragmentation. A full understanding of the dynamics of fragmental landscapes requires an intellectual perspective merging the insights of observational studies, experiment, and theory.

Here, we do not attempt a complete review of the fragmentation literature, but rather present with broad brush strokes a more personal assessment of the state of the science. To place fragmentation experiments in a broader conceptual context, we first outline in summary fashion core ecological theories that seem pertinent to habitat fragmentation, and in particular those that have motivated experiments on fragmentation. Then we sketch some potential strengths of experimental approaches to fragmentation. Some are just those of any ecological experiment (Hairston 1989; Underwood 1997), whereas others have particular relevance to the study of fragmentation. We discuss the interaction between empirical studies and ecological theory in the context of feedback towards a better understanding of fragmentation effects. We present a selective summary of a recent survey of fragmentation experiments around the globe (Debinski and Holt 2000), and try to encapsulate which parts of ecological theory were explicitly utilized, either as general motivating factors, or to justify features of experimental design. As a case study, we briefly discuss a long-term study of an experimentally fragmented landscape in eastern Kansas. This study suggests that many important consequences of habitat fragmentation are not apparent in short-term experiments. This leads us to the important topic of articulating limitations in experimental approaches to the study of habitat fragmentation. We conclude by arguing that much value could arise from the deliberate fusion of observation, theory, and experimentation, but that this fusion has rarely, if ever, satisfactorily been carried out. Underwood (1997, p. 22) notes that "biological science in general and ecology in particular would be well-served if the underlying models (world-views, paradigms, biases, constraints, etc.) were explicit." We hope that the ideas we present here will help facilitate a more conscious linking of theory, observation, and experimentation in the study of habitat fragmentation.

11.2 Theoretical Context

It is useful to begin with a consideration of theory. Experimental and observational studies in ecology are (or should be!) motivated either implicitly or explicitly by theoretical constructs. In turn, ecological models should be "checked" by empirical studies. In ecology, there are many sorts of theory. Some theories (e.g., hierarchy theory) are largely verbal. Usually, however, when one refers to "theory", one has in mind mathematical constructs that deliberately simplify the world so as to highlight some of its essential features. In general, the three roles of theory are: (1) to provide a clear conceptual framework for carrying out empirical studies; (2) to suggest concrete hypotheses and experiments; and (3) to clarify the kinds of data needed to address particular questions. In the study of fragmentation, there is another clear role for theory, which is to connect among scales differing radically in magnitude (Levin 1992).

In principle, almost any area of theoretical ecology could be brought to bear, one way or another, on habitat fragmentation. We suggest there are four core areas of ecological theory that directly pertain to habitat fragmentation, and which have helped to motivate and guide the design of field experiments. These can be crudely, but usefully labeled by the specific environmental factors emphasized in the theory, as follows: (1) area effects; (2) dispersal effects; (3) heterogeneous landscape effects; and (4) interspecific interactions and food web effects. The first two have conceptual roots in island biogeography (MacArthur and Wilson 1967; Robinson and Quinn 1992) and metapopulation biology (Levins 1969; Hanski and Gilpin 1997). The third and fourth arise from recent developments in landscape and community ecology. The topics overlap, but also provide useful points of departure.

11.2.1 Area Effects

The most basic effect of fragmentation is to reduce the original area of a particular habitat type, leaving remnants varying greatly in size. There are two distinct ways in which fragment area can directly affect species composition in the remnant community (leaving aside for the moment effects on colonization rates, but see below).

1. Reduced area almost always leads to lower habitat diversity within the fragment, relative to the original landscape. This implies that on smaller fragments, some habitats may be vanishing to the point of becoming rare, or absent altogether (Williamson 1981). If the original community contains habitat specialists needing one of these absent habitats, the remnant community will lack these species. More subtly, some habitat generalists may be absent, if they are obligate habitat generalists. For instance, many species

pass through life stages with genetically hard-wired ontogenetic habitat shifts. Claude Gascon (pers. comm.; Tocher et al. 1997), for instance, suggests that many frog extinctions in small rainforest patches in the Manaus experiment reflect the absence of bodies of water, rather than small size per se. Many "terrestrial" frogs need water for laying eggs and larval development, and so frog populations cannot survive beyond a single generation without a range of habitats that includes aquatic habitats. These observations suggest that the relationship between area and habitat diversity, and therefore species richness, has a strong autecological base. There is some theory development along these lines (e.g., Holt 1997), but on balance surprisingly little, compared to the next topic.

2. If a species has a fixed density (e.g., because of rigid territory size requirements), reduced area implies lower absolute population size. Smaller population sizes face increased extinction risk, even in favorable environments where a species might be expected to persist. There is a huge amount of theoretical literature on extinction dynamics of small populations (e.g., Stacey and Taper 1992; Hanski and Gilpin 1997; Klok and de Roos 1998). These theoretical studies of extinction risk in small populations have helped focus attention on a prime variable in most landscape experiments, which is the size of patches created experimentally. Many experiments mentioned below and discussed in Debinski and Holt (2000) focus on patch size effects.

11.2.2 Dispersal Effects

Fragmentation usually implies altered dispersal patterns, within and among fragments, relative to the original landscape (Doak et al. 1992). There are two distinct ways the dynamics of dispersal can change due to fragmentation:

1. In remnant patches, colonization may replenish losses due to ongoing local population declines and extinctions (Brown and Kodric-Brown 1977; Fahrig and Paloheimo 1988). The more fragmented a landscape is, the greater the average distance among patches will be. All else being equal, this implies lower recolonization rates on freshly empty patches and lower densities on occupied patches, thus reduced occupancy of patches in potentially habitable areas and overall lower abundances in occupied patches. These effects of greatly reduced dispersal can lead to a high regional extinction risk (With and Crist 1995), although this risk may be offset by corridors.

Dispersal may also be greater onto larger patches because they are bigger "targets", facilitating recolonization following extinction (MacArthur and Wilson 1967; Brown and Kodric-Brown 1977). Without very detailed study, it can be difficult to discriminate this effect of habitat area from the more widely studied effect of area upon extinction rates.

2. Most species disperse during their life cycle. Fragmentation disrupts whatever dispersal was ongoing in the original landscape, an effect with many important and distinct consequences. In particular, unfragmented habitats often consist of a mosaic of landscape patches, differing *inter alia* both qualitatively (e.g., presence/absence of predators) and quantitatively (e.g., availability of nest sites). Dispersal permits species to exploit spatiotemporal variability by "averaging" across local conditions (McPeck and Holt 1992; Holt 1993). Fragmentation can strongly disrupt spatial mechanisms essential to persistence (e.g., of fugitive species in a patchy environment; Tilman et al. 1994; Tilman and Lehman 1997).

A large amount of literature pertains to these issues, though there has been much more attention given to the first consequence of fragmentation for dispersal (simple reductions in colonization/movement rates) than to the second (endangering species which exploit spatial heterogeneity in their life histories). Wolff (1999) provides a useful conceptual model that synthesizes how evolutionary history, ecological specialization, and social system bear on how dispersal patterns respond to fragmentation. Many of these ideas provide pointers for future theoretical exploration. In experiments on habitat fragmentation a consideration of position effects or landscape context effects (e.g., Debinski et al. 2002), both of fragments relative to each other as well as to more distant source pools, should be a central design feature.

11.2.3 Heterogeneous Landscape Effects

Habitat fragments are not islands, but instead patches of one general habitat type, embedded in a (possibly complicated) array of alternative habitat types (Saunders et al. 1991; McIntyre and Barrett 1992). Depending upon the scale at which the landscape is perceived, patchiness can be more or less evident to any particular taxon (Wiens 1989; Dunning et al. 1992; Danielson and Anderson 1999). This implies that the design of fragmentation experiments tends to target subsets of focal species rather than entire communities. In addition, investigators often assume that the scale they have chosen is correct, when in reality the choice of correct scale requires trial and error. Finally, because organisms and materials disperse asymmetrically in heterogeneous landscapes (Polis et al. 1997), habitat fragments and the surrounding matrix are coupled. Flows between distinct habitats have two distinct consequences:

1. There can be landscape controls on local dynamics. For instance, in source-sink dynamics, abundance in a sink habitat reflects source productivity (Pulliam 1988; Holt 1993). Habitats high in productivity are likely to export nutrients, materials, and organisms to less productive habitats (Polis et al. 1997). Compared to specialists, habitat generalists may persist at a higher abundance in each habitat patch type they utilize, for several distinct rea-

- sons. A habitat generalist can buffer localized temporal variation in resource or predator abundance in a given habitat. Moreover, habitat generalists may be less likely to lose dispersing individuals as they move through unfavorable habitats. Habitat generalists are less sensitive to fragmentation than are habitat specialists (Hinsley et al. 1996). Moreover, landscape structure influences the rate of dispersal between habitable patches (Peles et al. 1999; Debinski et al. 2002), an effect that has been convincingly documented for a wide variety of taxa in the Biological Dynamics of Forest Fragmentation Project in central Amazonia (Gascon et al. 1999; Mesquita et al. 1999).
2. Following fragmentation, there is increased opportunity for invasions of "exotics." For instance, Harrison (1997) has shown that plant assemblages on small patches of serpentine soil are enriched by "spill-over" from the surrounding community, while losing some distinctive species present on large expanses of serpentine. Some woodland bird species become endangered on small fragments because of an influx of brood parasites and generalist predators, whose numbers are sustained by the surrounding landscape (Fahrig and Merriam 1994).

An additional landscape effect, distinct from spatial flows, arises because "edges" often have distinct properties, reflecting physical boundaries between habitats (Murcia 1995). The "width" of edges may also have important influences on ecological dynamics within a patch. Investigators may assume that edges are sharply defined, but in fact there are often gradients in edge "width" or edge effects perceived by species within patches. The detailed physical structure of plant architecture strongly affects the degree to which edges permit penetration of fragments, versus buffering fragments from the surrounding matrix (e.g., Didham and Lawton 1999).

A limited amount of theory exists addressing these issues (e.g., Wiens 1995), but this area is still quite poorly developed in terms of explicit theory. Fragmentation experiments need to be viewed holistically, including description and analysis of the habitat surrounding experimentally created habitat fragments. Landscape context analyses may be the next, crucial step towards a better mechanistic understanding of how habitat fragmentation affects ecological communities.

11.2.4 Interspecific Interaction and Food Web Effects

The final area of ecological theory relevant to fragmentation consists of analyses of food web dynamics and multispecies interactions. It is a commonplace observation that all species exist embedded in a network of interacting species (Pimm 1982). This implies that any area, dispersal, or landscape-level effect experienced by a given species may indirectly influence

other species that interact with the directly affected species. This is important even when the research focus is on a single species. Batzli et al. (1999) argue that the interplay of multiple limiting factors (food, direct density-dependence, predation) influences the response of rodent species to fragmentation. More broadly, recent theory (e.g., Holt 1993, 1997) and empirical studies (e.g., Kruess and Tscharrntke 1994; Post et al. 2000) suggest that food chains may be constrained in length by habitat area. Spatial dynamics may be crucial to the persistence of strong predator-prey interactions (Wilson et al. 1998; Holyoak 2002). The disappearance of a top trophic level can unleash shifts in interspecific interactions throughout a food web. Ostfeld et al. (1999) show that species-specific impacts of voles and mice on tree recruitment can substantially influence succession in heterogeneous landscapes; changes in rodent mortality regimes due to fragmentation could thus have major cascading effects on plant community dynamics. Likewise, Terborgh et al. (1997) argue that in Neotropical rainforest, top predators have a major indirect impact upon forest dynamics, influencing strongly the abundance and behavior patterns of mid-sized mammalian seed predators (e.g., agoutis) and raiders of bird nests (e.g., coatimundi). Top predators disappear on islands or isolated habitat patches, particularly if there is direct mortality superimposed on them by hunting. Terborgh et al. (1997) suggest that the absence of top predators has led to a systematic increase in seed predation in many areas of rain forest, favoring recruitment of tree species with unpalatable or low profitability seeds. Thus, there could be major shifts in tree community structure emerging over the next century in forest fragments, indirectly driven by the direct effect of fragmentation upon large top predators.

The general message is that all multispecies theory in ecology pertains, at least in principle, to the study of habitat fragmentation. There is a vast amount of literature here, though rather little has been explicitly tied to habitat fragmentation. One serious hurdle is that empirically it may be difficult to assess many community-level effects, except at the crudest level (e.g., presence-absence of species). The likelihood of complex impacts of fragmentation percolating through webs of interacting species makes it essential that fragmentation experiments attempt to focus on more than a few taxa.

In addition to multispecies issues, the understanding in detail of the ecological mechanisms underlying fragmentation effects is a challenging frontier. Most current experiments on habitat fragmentation have been motivated by very general, qualitative ecological theory, largely focused on area effects and colonization dynamics. This means that the existing designs are not explicit relative to many potentially operating mechanisms.

11.3 What Is a Fragmentation Experiment?

For our purposes, we define a “fragmentation experiment” as a deliberately created spatial design of habitat patches in a landscape. In some (but not all) cases, the surrounding matrix is also created or otherwise controlled by the experimenter. A fragmentation experiment is by necessity a “whole system” experiment, where almost any system component can change, because all species present experience the landscape structure created by the experimenter. In practice, some experiments focus on one or a few species (e.g., Kareiva’s 1987 exemplary study of the influence of patchiness on aphid-predatory beetle population dynamics). Single-species approaches are sensible if one is examining short-term effects of fragmentation, for example, on behavior or demography, but may mislead in long-term experiments because of the opportunity for feedback through numerous system components.

11.4 Why Do Experiments on Fragmentation?

When feasible, manipulative field experiments in ecology (whether of fragmentation, or anything else) have many advantages over purely descriptive, correlative studies (Hairston 1989; Underwood 1997). One major advantage should be to provide a feedback or “check” to theoretical models. Here, we briefly discuss some of these advantages with respect to fragmentation; after presenting the experiments, we then address some limitations of fragmentation experiments (these issues are discussed in more detail in Debinski and Holt 2000; Holt and Bowers 1999).

1. *Knowledge of initial conditions.* In observational studies, it may be difficult to know what a landscape looked like prior to creation of habitat fragments, or the original species composition of the fragments. Unlike descriptive studies, which start with fragments already in place, a fragmentation experiment creates an array of patches at a specific time, permitting pre-treatment surveys to determine initial conditions. This can be important, for instance, in designing stratified sampling regimes that take historical preconditions of a site into account.
2. *Controls.* Ideally, experiments have controls, against which one measures treatment effects. In descriptive studies of fragmentation, it is often difficult to identify appropriate controls. Moreover, empirical studies in practice have problems maintaining controls (e.g., Debinski and Holt 2000), because matrix habitats separating fragments have their own dynamics.
3. *Specified treatments.* Unlike descriptive studies, in an experiment, one can define landscape attributes, such as patch size, position or landscape context in a landscape.

4. *Replication.* One advantage of treatment specification is that one can ensure replication. By contrast, in descriptive studies, it may be difficult to find comparable patches (e.g., equal in area or similar in management history).
5. *Synchronicity in patch initiation.* In anthropogenic landscapes, different patches may have been created at different, and unknown, times in the past. In experimental studies, one establishes specific dates of fragmentation effects.
6. *Randomization across the landscape.* A key element of experimental design is the spatial interspersing of different treatments, and of treatments and controls. This problem may be particularly severe in the case of descriptive studies of habitat fragmentation, and so we dwell on it here. The basic issue is that humans utilize landscapes nonrandomly (Turner et al. 1996), so anthropogenic fragmentation is nonrandom (e.g., in patch size and isolation) relative to pre-existing environmental gradients, and often highly so. For instance, for economic and logistic reasons, settlers typically clear areas that are flat, with fertile soils, and near likely transportation routes (e.g., rivers), rather than areas that are hilly, with rocky soils, and isolated from such routes. The effect of nonrandom landscape usage by humans is that small, rather than large, fragments are likely to be those left in the parts of the landscape favored by humans.

As an example of the existence of nonrandom placement of patches across the landscape in a descriptive study of habitat fragmentation, consider the interesting study by Laurance (1990, 1995) of rainforest mammals on fragments in the Atherton Tableland of Australia. Laurance identified ten fragments of forest, ranging in size from 1.4–590 ha, separated by agricultural lands from large contiguous areas that served as controls. As Laurance himself notes, all the fragments are located along streams, in steep canyons, areas where it is presumably more difficult to clear-cut forest; by contrast, the controls were not usually along streams. If in the preexisting landscape, there were characteristic differences in mammal communities between stream and nonstream habitats, this might determine present-day patterns. Moreover, because of the history of human occupation in the Atherton Tableland, if one takes the map in Laurance (1990, 1995), draws a polygon around the forest fragments, and then draws a similar polygon around the controls, the controls collectively span a larger area. One basic fact about the earth's surface is that heterogeneity of all sorts (e.g., in soil types, community composition, etc.) increases with area (Williamson 1981). The controls, taken as a group, are likely to be more heterogeneous than the treatments (fragments), as a group. Given that many species are habitat specialists, it is plausible to expect greater total species richness for controls, than for fragments. A diminution in species richness in the fragments might thus reflect idiosyncrasies in how the fragments were created, rather than fundamental effects of fragmentation, per se.

In an experimentally fragmented landscape, one can minimize this problem by ensuring the random spatial interspersion of patches differing in variables such as size.

11.5 A Global Survey of Fragmentation Experiments

We recently attempted to identify all past and present fragmentation experiments and in Debinski and Holt (2000) describe the design, specific objectives, and major findings of these experiments. Here, we summarize major features of our survey.

We identified 21 studies. Figure 11.1 shows the global distribution of the fragmentation experiments (two studies were both based at essentially the same location in Ohio, and so lumped together for the purpose of mapping). Fragmentation experiments are not randomly distributed across the globe, but instead largely restricted to either North America, or western Europe. This is not surprising, given the current distribution of academic ecologists and their funding agencies. Of the 21 studies, 5 focused at the population level (1–2 species monitored), and 16 at the community level (multiple taxa or functional groups monitored). There is a distinct biome bias. Nine studies were carried out in forest: one in tropical rainforest (the famous Manaus project initiated by Tom Lovejoy), five in temperate forest, and three in boreal forest. The other studies are in grassland or old fields. These habitat biases reflect obvious logistical constraints. For instance, with the notable exception of the Manaus project, the forest projects are integrated with silviculture and forestry and, hence, linked to profit-making activities that facilitate patch creation and maintenance. In like manner, grasslands and old fields are relatively easy to modify by mowing, providing an inexpensive mechanism for manipulating landscape structure.

With respect to temporal scale, as of 1980, there was exactly one study underway (the Manaus project). In 1990, there were 6, and in 1996 17 studies were underway. Our sense of these experiments, generated from the literature, discussions with scientists involved in setting them up, and our own experience (see below), is that it takes some years for these experiments to begin generating interesting results, particularly for systems involving large spatial scales and multiple taxa. Assuming the current set of experiments continues, one might expect a rich fruit of research results to appear in coming decades.

There is a strong negative relationship between patch size and replication in these experiments (Debinski and Holt 2000). Presumably reflecting logistical, fiscal, and other constraints, our survey found considerably more replication at small patch sizes, than at large sizes. Plot sizes larger than 1 ha usually have very little replication. It is obviously much easier to create and maintain small patches, on the order of 0.01 ha in size.

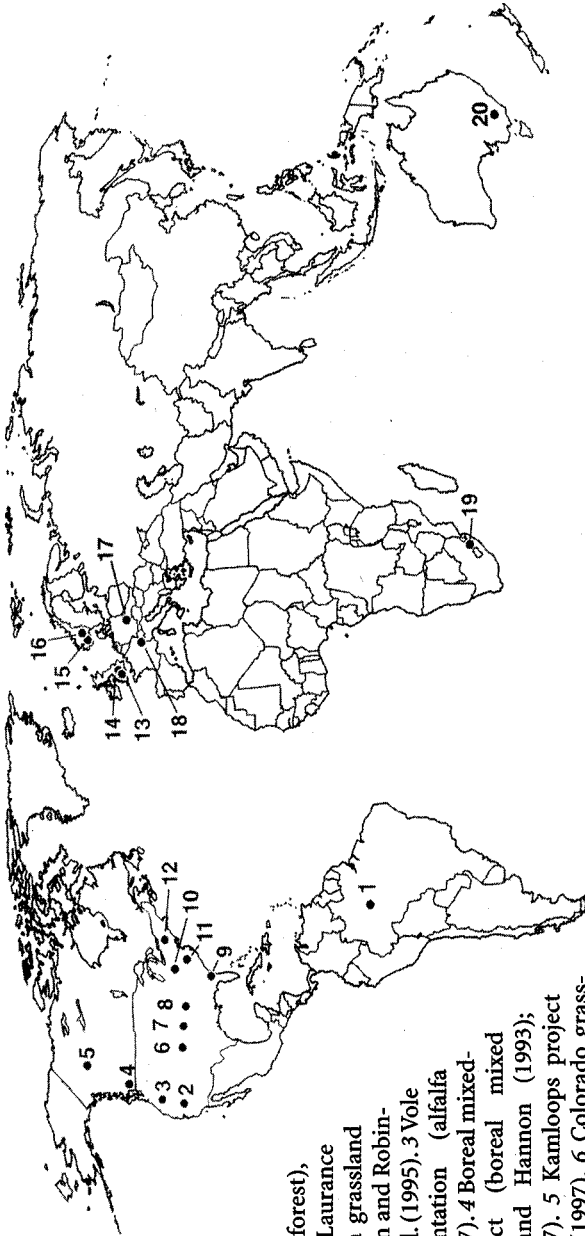


Fig. 11.1. World distribution of fragmentation experiments (with references). The following list gives an informal title to the experiment, the habitat type, and representative publications. 1 Biological dynamics (tropical rainforest), Bierregaard et al. (1992); Laurance et al. (1998). 2 California grassland (annual grassland), Quinn and Robinson (1987); Robinson et al. (1995). 3 Vole behavior and fragmentation (alfalfa patches), Wolff et al. (1997). 4 Boreal mixed-wood dynamics project (boreal mixed woods), Schmiegelow and Hannon (1993); Schmiegelow et al. (1997). 5 Kamloops project (subalpine forest), Vyse (1997). 6 Colorado grassland (short grass prairie), Collinge (1995); Collinge and Forman (1998). 7 Kansas fragmentation study (old field), Holt and Gaines (1993); Holt et al. (1995a,b); Diffendorfer et al. (1999). 8 Missouri Ozark forest ecosystem project (hardwood forest), Kurzejaski et al. (1993). 9 Savanna River site corridor project (forest clear-cuts), Haddad (1997); Haddad and Baum (1999). 10 Miami University fragmentation project (old field), Collins and Barrett (1997); Crist and Golden (pers. comm.). 11 Blandy farm fragmentation study (old field), Bowers and Dooley (1993). 12 Predator-prey interactions and fragmentation (goldenrod monoculture), Kareiva (1987). 13 Long Ashton (croplands), W. Powell (pers. comm.). 14 Moss ecosystem fragments (boulder field), Gonzalez et al. (1998). 15 Evenstedt research station (meadows), Ims et al. (1993). 16 Root vole sex ratio (meadows), Aars et al. (1995). 17 German fragmentation study (clover patches), Kruess and Tschardt (1994). 18 Swiss Jura Mountains (calcareous grassfield), Baur and Erhardt (1995). 19 Groenvaly experiment (grassland), Van Jaarsveld et al. (1998). 20 Wog Wog study (eucalypt forest), Margules (1992); Davies and Margules (1998); Margules et al. (1998)

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How did ecological theory actually bear on the initiation or design of these experiments? Often, it is difficult to find explicit specifications of the theoretical underpinnings for a particular experimental design. However, our overall sense of the literature is that area effects have played a dominant role in guiding the development of fragmentation experiments. For instance, in the case of the Manaus project, the early publications show a strong influence of island biogeography theory and in particular emphasize effects of fragment area on the likely course of community decay or relaxation, following isolation (e.g., Lovejoy et al. 1984; Bierregaard et al. 1992). A similar grounding in island biogeography can be found in other studies as well (e.g., Margules 1992; Margules et al. 1994). Theoretical perspectives on how fragmentation alters the dispersal of demography of focal taxa have been the primary motive of a few studies (e.g., Haddad 1999; Dooley and Bowers 1998). There have been rather few attempts made to explicitly integrate ecological theory with fragmentation experiments. Rather than examine each study one by one, we focus briefly on this issue for a study with which we are personally familiar.

11.6 A Case Study: The Kansas Experimentally Fragmented Landscape

This study, initiated in 1984, is among the longer, continuously running fragmentation experiments. As described in Holt et al. (1995a,b), in contrast to many fragmentation experiments, the basic ecological questions motivating the study were the effect of patch size and position on the rate and pattern of secondary succession. In some respects, this experiment pertains more directly to succession theory and restoration ecology than to conservation biology. Elsewhere (e.g., Foster and Gaines 1991; Robinson et al. 1992; Holt et al. 1995a,b; Diffendorfer et al. 1995, 1996; Schweiger et al. 1999, 2000; Yao et al. 1999) we describe this study in some detail, so here we only sketch key design features and findings pertinent to the issue of the relationship of experimentation and theory in the study of habitat fragmentation.

Patches were created and maintained by intensive mowing in a plot of land formerly used for agriculture. Patches were allowed to undergo succession, based on the community present in the original seed bank and subsequent colonists. Given our interest in succession, our focal organisms naturally include vascular plants, but we have also monitored the small mammal community in detail. The choice of patch sizes and separation were governed by prior knowledge about home ranges, local abundance, and average dispersal distances. The surrounding landscape is heterogeneous, with woods south and west, and brome meadows and cultivated fields north and east. We thus expected gradients in vegetation establishment and so stratified placement of each patch size by distance to the woods. The smaller patches are arranged in

clusters; sample stations in these clusters can be compared with similar grids of sample stations within the large patches.

Our research design was motivated by the ecological theories discussed above, as follows:

Area effects: during secondary succession following field abandonment, plant species absent from the original seed bank, but present nearby can colonize and eventually dominate. We hypothesized that colonization-extinction dynamics might be an important dimension of succession, and that succession might vary with patch size. At the time we initiated this study (1984) an explicit "island biogeographical" interpretation had not been applied to terrestrial plant succession. For small mammals with low densities, or large home range requirements, we expected our small patches to be unfavorable and predicted such species to be differentially missing in these patches.

Dispersal effects: distances among patches and to presumptive sources in the surrounding landscape were based on prior information as to what constituted significant barriers to dispersal for the plants and small mammals at our site. We attempted to choose distances that would hamper dispersal, but not so greatly as to decouple dynamics on different patches.

Interspecific interactions and food web effects: patch size could influence small mammal abundance and/or behavior. In turn, small mammals acting as herbivores and seed predators can severely impact plant numbers (Crawley 1996), so a direct effect of patch size on small mammal abundance could translate into an indirect effect on plant dynamics. Generalist consumers can eliminate preferred or slow-growing species while remaining sustained by less preferred or more productive prey (Holt and Lawton 1994). Depending on how consumer preference correlates with competitive ability, selective herbivory could either facilitate or slow down plant succession (Davidson 1993; Hulme 1996).

Landscape heterogeneity effects: to deal with heterogeneity in the surrounding landscape (viewing broad-scale heterogeneity as a nuisance variable in the experiment), we interspersed patch sizes in a stratified random design. However, our experimental design did not directly assess effects of landscape heterogeneity.

We now summarize core findings from this project, first from the early years of succession (1984–1990), and then more recently (1991–present).

11.6.1 Core Findings, 1985–1990

1. Contrary to our initial hypothesis there was little effect of patch size on overall successional rate or pattern (Robinson et al. 1992; Holt et al. 1995a).
2. Despite the absence of major effects of patch size on the overall trajectory of succession, there were population-level effects for particular plant species, and subtle effects on spatial structuring in the community. For instance, clonal plant species persisted better in our permanent sample quadrats on large, than on small, patches (Robinson et al. 1992; Heisler 1998).
3. There were strong, and at times surprising, effects of patch size on the small mammal community. As expected, some species (e.g., the large-bodied cotton rat *Sigmodon hispidus*) were largely restricted to large patches. However, other species (e.g., the smaller-bodied prairie vole, *Microtus ochrogaster* and deer mouse, *Peromyscus maniculatus*) were actually denser on smaller patches (Foster and Gaines 1991; Diffendorfer et al. 1995; Schweiger et al. 2000). Studies in other patch systems have likewise revealed enhanced densities of small mammals on smaller patches (Bowers and Matter 1997).

11.6.2 Core Findings, 1991–Present

1. There continue to be strong, species-specific effects of patch size on small mammal abundance; some species are more abundant on large patches, others on small patches. Several rodent species characteristic of woody vegetation have invaded, but are largely restricted to those large patches that are near contiguous woodland (Schweiger et al. 1999, 2000). The butterfly community on the site also shows a nested distributional pattern, with some species largely restricted to large patches (Holt et al. 1995b; D. Debinski, unpubl. data). Given the high mobility of butterflies, this likely reflects behavioral responses rather than population dynamics.
2. Woody plant invasion has accelerated and is occurring more rapidly into larger patches (Yao et al. 1999). In contrast to the first phase, there is now a substantial effect of patch size on the rate of succession. There is also a pronounced distance effect, with succession occurring more slowly in patches more distant from the forest (Yao et al. 1999).

As noted above, the original design of the experiment was motivated by theoretical ideas regarding area effects, dispersal effects, and indirect effects. Although ecological theory helped motivate the experimental design and to explain observed patterns, we must admit that to date the relationship between theory and experimentation has been rather loose. Explicit mathe-

mathematical models are always radical simplifications of complex ecological systems, and the "whole-system" nature of fragmentation experiments makes it difficult to use them as "tests" of some particular mathematical model, except in the most general way. We suggest that many fragmentation experiments to date have had a similarly loose relationship between theory and experiment: theory has helped motivate experiments, but the experiments are not truly "tests" of theory. Indeed, it is difficult to see how experiments such as ours, which examine responses by an entire system over long time periods to fragmentation, could even, in principle, be used to "test" simple ecological models. By contrast, a tighter integration with theory is much more feasible when addressing particular mechanisms in short-term experiments focused on one to a few species, such as those of Bowers et al. (1996) and Wolff (1999) aimed at behavioral responses.

11.7 Limitations in Experimental Fragmentation Studies

There are many obvious limitations in experimental studies of fragmentation (Holt and Bowers 1999; W. Laurance, pers. comm.), particularly when one wishes to "scale up" to larger spatial arenas. For instance, there are logistical constraints in the design and execution of fragmentation experiments, including costs of set-up and sampling (which scale linearly with area), the "people power" available to conduct research at a site, constraints on land management, and pre-existing heterogeneities. More important than any of these, there are conceptual limitations that arise because different ecological processes operate at distinct spatial scales.

In the Kansas experiment, there was a particular farmer's field, owned by the University of Kansas Endowment Association, available to researchers to set up the experiment. In an ideal world, we would have exerted control over the surrounding landscape, but in practice for us the landscape was a "given". The predetermined shape and area of the available experimental field automatically set up interlinked constraints among the design desiderata in experimental design. For instance, for fixed patch sizes, increasing distance among patches automatically reduces the degree of feasible replication.

The intellectual scope of the Kansas project has been governed largely by availability of interested researchers and the constraints of spatial scale. For instance, we (RDH and DMD) are personally interested in birds and butterflies and have supervised students carrying out projects examining patch use by these taxa. However, the high mobility of these groups makes it likely that single individuals can use much of the experimental landscape, so these studies necessarily bear more on individual habitat selection and patch utilization, than on population or community-level effects of fragmentation. The spatial scale of our system would have been apt for examining insect popula-

tion dynamics, but by chance our colleagues did not include specialists in this area, and instead included experts on rodent population dynamics. A number of publications thus examine effects of patch size on rodent populations, with an emphasis on how fragmentation disrupts dispersal dynamics. Only recently, Wilson (1998) has shown that variation in vertebrate predator activity may account for some of these patterns. The general point is that fragmentation experiments are "whole system" manipulations, yet person-power and fiscal limitations almost always restrict the range of taxa and processes investigated. These "real world" limitations constrain the range of processes, systems, and landscape features it is feasible to address with experimentation.

Our fragments are maintained by regular mowing in the interstitial habitat. Other possible devices for separating patches suggested at the outset ranged from fanciful (e.g., paving the entire area, except the patches, with AstroTurf) to logistically difficult (e.g., surrounding patches with a coarse-meshed fence, then using sheep to maintain a low turf between patches, as in Quinn and Robinson 1987). Landscape manipulation can introduce artifacts. Mowing is a massive periodic disturbance that can have strong indirect effects on vegetation dynamics within patches. For instance, because of sheet erosion in the interstitial areas, runoff onto patch edges has disproportionately more impact on smaller patches.

In the Kansas study, as in all experimental studies of habitat fragmentation (Debinski and Holt 2000), the spatial scale is limited. This raises the crucial problem of how to scale up from these model systems to "real" landscapes of interest in conservation. Diffendorfer et al. (1996) showed that with small mammals one could successfully extrapolate from patterns of abundance by patch size in our system, to larger patches outside our site. Bowers and Matter (1997) however, show that in broad comparisons, the relationship of small mammal abundance to patch size depends upon the range of patch areas considered. There are thus difficulties in extrapolation, even for a single set of taxa. Furthermore, it is an open question whether or not one can use insights gleaned from the study of one set of taxa, to interpret patterns observed in other, disparate taxa. For instance, mobile organisms may experience a fragmentation experiment largely as minor patchiness. Fragmentation experiments conducted on a "fine" scale may fail to address issues of community or population dynamics adequately, simply because the patches do not support more than a few individuals of select species.

The temporal scale of fragmentation experiments is limited. Most experiments reviewed in Debinski and Holt (2000) have been extant only a few years, and some (e.g., Kruess and Tscharrntke 1994; Bowers et al. 1996) are deliberately short-term. It is likely that effects of fragmentation loom larger at longer time scales (as in community "relaxation"). Successional dynamics in the Kansas study illustrate this effect. As noted above, in the first 6 years of the study there was no evident effect of patch size on plant succession, but in the last few years such effects on woody plant colonization have become pro-

nounced. Moreover, the matrix may have successional dynamics that influence processes in the fragments. A perpetual isolation of patches from a surrounding matrix may not be a good model for "real" systems. For instance, clear-cuts grow back, so in fragmented forest environments the level of fragmentation and the heterogeneity of landscape units will have a temporal dynamic. A challenging task for future experimental work is to devise sensible designs that deliberately incorporate the spatial and temporal heterogeneity of the matrix landscape. Experiments typically create "sharp" edges; in real landscapes, edges are often fuzzy ecotones, and the sharpness of edges is likely to vary over time. Experiments have also focused on simple geometries (e.g., rectangles, linear corridors); in real landscapes, geometries are much more complex (stringy, fractal, etc.; see Adler and Nuernberger 1994 for pertinent theory). No doubt there are other limitations that have not occurred to us. There are many important features of real-world habitat fragmentation that are difficult to simulate in a clean experimental design.

11.8 Conclusions

As in many other areas of ecological science, the theory of fragmentation is much more advanced than are rigorous empirical tests of theory. Over the past few decades, we have witnessed an evolution in the conceptual focus of empirical fragmentation studies from island biogeography, emphasizing area effects, to metapopulation dynamics, which stresses colonization effects, to a landscape ecology perspective, where landscape context, heterogeneity, and interactions with the matrix seem increasingly important. There is also an increasing appreciation of synergistic effects, often mediated by complex food web interactions. No longer are we simply interested in counting the number of species present on a patch; we are now delving into understanding processes that explain such patterns. The landscape context of the patch, the history of the patch, and the behavior of the organisms in the patches are all clearly key determinants of fragmentation effects.

Despite the current urgent need to understand better how fragmentation operates as a driver of species extinction, there are still just a handful of experimentally designed fragmentation studies. The lack of experimental studies is primarily due to logistical constraints, but it may also be explained by sociology, namely, the tendency for most ecologists to work alone or in small groups. Because the costs of establishing and maintaining a fragmentation experiment are high, and the benefits accruing potentially large, it is urgent that ecologists join forces and engage in collaborative research projects, using the habitat fragmentation experiments now scattered around the globe (Fig. 11.1), or designing new experiments that improve on the old ones. These experiments in turn could benefit greatly, we believe, from more

explicit ties to ecological theory, and the results from such experiments can in turn point the direction towards new areas of theoretical development. Experimental landscapes are almost always caricatures of real landscapes, which hardly ever are comprised of habitable patches with geometrically simple shapes embedded in a completely uninhabitable matrix, but instead are complex mosaics of many habitat types with complex shapes and fuzzy edges. However, such caricatures are useful, particularly if one wishes to have a bridge between the abstract "perfect crystals" (May 1973) of ecological theory and the messy reality addressed in purely descriptive studies.

Acknowledgement. We in particular thank all the participants in the Kansas project for our long-term collaborative efforts. We thank the National Science Foundation for its continued support, and the organizers of the IAI-Amigo workshop, Pablo Marquet and Gay Bradshaw, for the opportunity to present this paper. We also thank Mike Bowers for an exceptionally thoughtful review of the manuscript. This is journal paper no. J-19059 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, project 3377, and supported by Hatch and State of Iowa funds.

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