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COMPARATIVE EVALUATION OF EXPERIMENTAL APPROACHES TO THE STUDY OF HABITAT FRAGMENTATION EFFECTS

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Abstract. Ecologists have used a variety of comparative mensurative and manipulative experimental approaches to study the biological consequences of habitat fragmentation. In this paper, we evaluate the merits of the two major approaches and offer guidelines for selecting a design. Manipulative experiments rigorously assess fragmentation effects by comparing pre- and post-treatment conditions. Yet they are often constrained by a number of practical limitations, such as the difficulty in implementing large-scale treatments and the impracticality of measuring the long-term (decades to centuries) responses to the imposed treatments. Comparative mensurative studies generally involve substituting space for time, and without pre-treatment control, can be constrained by variability in ecological characteristics among different landscapes. These confounding effects can seriously limit the strength of inferences. Depending on the scale of the study system and how “landscape” is defined, both approaches may be limited by the difficulty of replicating at the landscape scale. Overall, both mensurative and manipulative approaches have merit and can contribute to the body of knowledge on fragmentation. However, from our review of 134 fragmentation studies published recently in three major ecological journals, it is evident that most manipulative and mensurative fragmentation experiments have not provided clear insights into the ecological mechanisms and effects of habitat fragmentation. We discuss the reasons for this and conclude with recommendations for improving the design and implementation of fragmentation experiments.

Key words: *experimental design; fragmentation; landscape scale; manipulative approach; mensurative approach.*

INTRODUCTION

Habitat fragmentation is a landscape-level process in which a specific habitat is progressively subdivided into smaller and more isolated fragments. It involves changes in landscape composition, structure, and function across scales and occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances (McGarigal and McComb 1999). The process of habitat fragmentation as defined here is distinguished from habitat loss, even though these processes are almost always confounded in the real world (Fahrig 1997). We use the term “fragmentation” to refer specifically to the progressive subdivision of habitat blocks into fragments. Although habitat loss always accompanies fragmentation, they are different phenomena and should be distinguished.

Many scientists believe that the earth is facing the greatest mass extinction in 65×10^6 years (Wilson 1992). Habitat loss and fragmentation are the key drivers of this global biodiversity crisis (Burgess and

Sharpe 1981, Noss 1983, Harris 1984, Wilcox and Murphy 1985, Noss and Cooperrider 1994), and there is a wide consensus that studies of the effects of habitat fragmentation are especially urgent and should receive special priority (Lubchenko et al. 1991). In response, there have been hundreds of theoretical and empirical studies of the ecological effects of habitat fragmentation conducted over the past 15 yr (Saunders et al. 1991, Andrén 1994, Debinski and Holt 2000). The knowledge gained from these studies has come from a variety of approaches, including field observations and experiments as well as mathematical and spatial models. In spite of these efforts, very little is yet known about the mechanisms that link ecosystem responses to changes in habitat patterns that result from fragmentation.

Ultimately, inferences about cause and effect between fragmentation and ecological processes can only be inferred reliably from proper field experiments, i.e., study designs with replicated treatment allocation randomized among an adequate sample of experimental units. Hence, proper experimentation must play a prominent role in the study of fragmentation whenever feasible and ethical. Yet, there are many forms of experimentation and these vary in the reliability of the inferences drawn. In this paper, we focus on the relative

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merits of the two major experimental approaches (meritative and manipulative) used to study the effects of habitat fragmentation in the field. Specifically, we consider the strengths and weaknesses of the two approaches, analyze their use in recently published papers from three major journals, describe situations in which each approach can be profitably applied, and offer guidelines for improving the reliability of inferences drawn from each approach.

CONCEPTUAL FRAMEWORK

Early interest in habitat fragmentation arose from island biogeographic theory (MacArthur and Wilson 1967). Despite the many identified shortcomings of the theory, early empirical data supported these simple predictions. This empirical work has served as a springboard for theoretical work with mathematical and spatial models of fragmentation effects. The latter have led to numerous, often contradictory, theoretical predictions regarding the dynamics of fragmented landscapes and mechanisms of fragmentation effects on organisms (Chesson and Case 1986, Kareiva 1990). These theoretical predictions have important implications for conservation, if true, in real landscapes. For example, many theoretical models predict that the local and regional persistence of some species and the balance of predator-prey and competitive interactions may be sensitive to changes in both the total amount and configuration of habitats in the landscape (Fahrig and Merriam 1985, Kareiva 1987, Fahrig and Paloheimo 1988a, b, Pulliam and Danielson 1991, Nee and May 1992, Pulliam et al. 1992, Ives 1995). Some models indicate that the effects of habitat fragmentation on a population can be nonlinear and appear suddenly and catastrophically after a large portion of the habitat has been removed with little or no observed effect (Kareiva and Wennergren 1995, Fahrig 1997, 1998).

Unfortunately, it is proving very difficult to test any of these theoretical predictions in situ. The effects of habitat fragmentation, it turns out, are exceedingly difficult to isolate experimentally (de Roos and Sabelis 1995, McGarigal and McComb 1995, 1999). Much of this difficulty arises from the fact that fragmentation effects often operate at vast spatial and temporal scales, depend on species-specific behavioral and life-history characteristics (Fahrig and Paloheimo 1988a, b, Kareiva 1990), and result from the nonlinear synergism of patterns and processes operating simultaneously across a range of scales. Consequently, the extent to which the spatial structure of habitats actually affects ecosystem and population processes is still largely unknown (Wennergren et al. 1995). One of our main goals in this paper is to ascertain why recent empirical work has not kept pace with theoretical studies, and to evaluate the effectiveness of empirical studies in isolating particular effects of fragmentation and illuminating the mechanisms driving them.

But before we can determine if we are successfully meeting our objectives in the study of fragmentation, we need to know what the objectives are. In other words, what do we want to know about fragmentation? There is a hierarchy of complexity in the questions that we could pose about fragmentation effects. Using reductionism, we can tease apart some of the key pattern-process linkages from the complex network that forms the whole fragmentation process, and ask relatively simple questions. For example, what are the relationships among patch area, patch shape, patch isolation, edge, the interaction of these factors, and various population (e.g., predation, reproduction, dispersal) and ecosystem (e.g., energy and nutrient flow, disturbance) processes? How do various landscape elements, such as corridors, linear networks, and matrix, affect various ecosystem processes and the connectivity (or isolation) of populations in fragmented landscapes? Experiments designed to tease apart these complex patterns of relationship must address organism- or question-relevant patterns and processes at organism- or question-relevant scales. Answers to these questions will form the building blocks to more complex, high-level questions. For example, how do these pattern-process linkages function in spatially and temporally dynamic landscapes across the range of spatial and temporal scales needed to characterize the dynamics of the landscape? How do interspecific interactions affect various population and ecosystem processes associated with the above linkages? Are there critical threshold effects in any of these linkages? For example, at what levels of habitat loss and fragmentation does population viability decline drastically? How long does it take population and ecosystem processes to respond to physical changes in the landscape associated with fragmentation (i.e., time lags)? Reliable answers to all of these questions are needed in order to fully understand the effects of fragmentation and to be able to use this knowledge confidently in our efforts to conserve biodiversity in fragmented landscapes. Therefore, another major goal in this paper is to ascertain whether or not current empirical studies are providing the answers. If not, how could we more effectively design field experiments to accomplish this goal?

Why empirical field studies are necessary to produce reliable knowledge

The empirical sciences obtain rigor through their use of the accumulative method of inductive inference, which, as normally described, employs three steps: observation/induction, alternative hypothesis formation, and experimentation (Platt 1964, Romesburg 1989). In this method, observation and induction are used to devise alternative hypotheses, and then crucial experiments are carried out, with alternative possible outcomes, each of which will, as nearly as possible, exclude one or more of the hypotheses (Popper 1962,

Platt 1964). The result of this method is a winnowing through many possible explanations, rejecting those that cannot be correct, and being left with a small number of possibilities that could be.

The experimental approach has always been central to this scientific method. It has been largely responsible for the flowering of the medical and biological sciences this century, and figured critically in the development of ecological thought. Who can deny the importance of Gause's bottles or Huffaker's microcosm? Laboratory experiments, of course, are very important in ecology, as are theoretical modeling exercises, in pointing out possible mechanisms. However, they lack generality. They are species, scale, and design specific. It is an open question whether the findings of any ecological laboratory experiment or modeling exercise are extendable to different species and scales, and to the vastly more complicated systems in the real world.

The solution to this, clearly, is to conduct our experiments in the real world: in the field, that is. Field experiments have several decided advantages over laboratory experiments in ecology. In particular, they are applied in situ, to the system and species of question, so no extrapolation to other scales and species is necessary. In general, field experiments gain realism, spatial scale, and scope over laboratory experiments, at the expense of control of independent variables related to manipulations, site differences, and temporal changes (Diamond 1986). In other words, field experiments gain generality at the price of reduced ability to isolate the effects of particular mechanisms.

The ideal field experiment

Experiments may be either *manipulative* or *mensurative* (Hurlbert 1984). In a manipulative experiment, the experimenter physically manipulates some attribute of the system in a controlled manner, while holding all other attributes constant. The control over variation and confounding factors allows the experimenter to attribute observed differences to the imposed treatments. In contrast, in a mensurative study, the "experimenter" simply observes or measures the system at different locations or times. In a mensurative experiment, the treatment is the different conditions in space or time.

In general, manipulative experiments lead to stronger inferences and therefore more reliable knowledge than mensurative experiments. The defining feature of a manipulative experiment is that the different experimental units receive different treatments imposed by the experimenter and that the assignment of treatments to experimental units is, or can be, randomized (Hurlbert 1984). In the study of fragmentation, by applying specific treatments to experimental units, the investigator has direct control over one or more aspects of the fragmentation process (i.e., the independent variables). By randomizing the selection and treatment allocation of experimental units and selecting some to serve as a

control, the investigator can minimize other potentially confounding sources of variation that affect the dependent variables of interest. In this manner, a direct cause and effect relation associated with a specific treatment can be established, resulting in strong inferences.

In the study of fragmentation, an ideal manipulative experiment has the following features:

1) The experimental units represent structurally similar landscapes of the same size drawn from a broader regional landscape; the similarity among landscapes minimizes the experimental error (i.e., the natural variability among experimental units), so that differences among experimental units can be attributed to the treatment effects alone.

2) The sizes of the landscapes are functionally relevant to the process/organism(s) under consideration; i.e., the size is not chosen merely according to its convenience for experimentation, so that the inferences are biologically meaningful.

3) The treatments involve (a) systematically manipulating the areal extent (i.e., area) and configuration (i.e., fragmentation) of habitat for the target organism(s), so that the independent and interactive effects of these two processes can be assessed, or (b) systematically manipulating the configuration of habitat while holding area constant to isolate fragmentation effects *per se*.

4) The treatments are adequately replicated and randomly assigned to the experimental units (i.e., landscapes), so that powerful (in the statistical sense) and unbiased inferences about treatment effects can be distinguished from other potentially confounding sources of variation that affect the dependent variables of interest.

5) The experimental design includes adequate temporal and spatial controls so that treatment effects can be distinguished from any natural variability (i.e., unrelated to the treatment effects) in the dependent variables.

6) The treatments are implemented systematically to experimental units, so that any natural temporal variability in the dependent variables does not bias the comparisons among treatments.

7) The post-treatment sampling period is long enough to ensure that any real treatment effects that may be delayed in time (i.e., time lag) are observed.

Real-world challenges

Unfortunately, researchers are faced with numerous real-world challenges that make manipulative fragmentation experiments exceedingly difficult to implement. Indeed, we are not aware of any published study that has all of the attributes just listed. Fragmentation studies are often unreplicated or pseudoreplicated (Hurlbert 1984). Replication is often impossible be-

cause of the spatial scale of the phenomena and limited resources. Also, in heterogeneous environments, there is likely to be considerable variation among sites in many potentially influential variables. Experimenters typically cannot regulate more than a few independent variables. This lack of control of independent variables, coupled with the difficulty of obtaining independent replication, makes it very hard for field experiments to obtain unbiased, reproducible results, or to identify mechanisms driving the response (Diamond 1986).

In addition to difficulties related to control and replication, there are other important limitations related to issues of scale. There are practical limits to the area that can be manipulated in field experiments. This disqualifies many important large-scale phenomena from manipulative experiments. Furthermore, limited resources truncate the temporal scale of any manipulative experiment, which can have important consequences for the effects observed and conclusions drawn. Also, at large scales there is a decided limit to the range of manipulations and controls that can be utilized.

Here, we focus on three important limitations. First, given that fragmentation is a landscape-level process and that functionally relevant landscapes must be scaled to the organisms or processes under consideration, the study of fragmentation often requires large landscapes. Implementing treatments of any kind across large areas of land is fraught with practical and logistical constraints. These difficulties are exacerbated when the treatments involve manipulating forest vegetation, as is often the case. For example, in most forested systems, it is not practical to harvest thousands of hectares in a short period of time to satisfy the needs of an experimental design. Moreover, most landscapes contain multiple landowners, and the logistics of coordinating treatment implementation across multi-ownership landscapes can challenge even the most astute politician. Second, given the time often required for biological systems to adjust to perturbations (i.e., time lags), it is not unreasonable to expect populations and communities to take many years or even many decades to respond to fragmentation-induced changes in the physical landscape. Moreover, it is quite likely that short-term biological responses to imposed fragmentation treatments may not accurately represent the long-term impacts (Hagan et al. 1996, Schmiegelow et al. 1997), therefore requiring that manipulative experiments be carried out for many years, and perhaps even decades, in order to reveal the ultimate effects of experimental perturbations. Yet, given the current incentive structure of most scientific institutions (e.g., academia), long-term studies are not properly rewarded. Finally, fragmentation research rarely has the luxury of true experimental replication and control because of the difficulty of working at the landscape scale. Given the inherent variability and spatial autocorrelation among large, natural landscapes, it is virtually impos-

sible to eliminate major sources of confounding variation. Thus, pretreatment differences among experimental units may be so great that one must question the validity of treating them as replicates. Moreover, as a result of inherent high variability among experiment units, the statistical power associated with detecting treatment effects can be considerably reduced.

Alternative approaches

Given these real-world complexities, manipulative experimentation in the field is exceedingly difficult, if not impossible, in most circumstances. Because a landscape ecology devoid of proper experiments would weaken our ability to understand and predict the most important ecological implications of habitat fragmentation, various alternative experimental approaches have been advocated. For example, to avoid the limitations associated with studying large-scale landscapes, the use of so-called experimental model systems (EMS) has been advocated (Ims et al. 1993, Lawton 1995). Another approach for overcoming many of the limitations previously discussed has been to combine field studies with spatially explicit population modeling. In this approach, long-term field studies can identify how real populations change over time and space, whereas modeling can be used to explore factors that might be causing the population dynamics (J. B. Dunning, *unpublished manuscript*). However, the most common approach has been to use comparative mensurative field experiments.

Mensurative field experiments

Mensurative experiments offer a means of overcoming some of the important limitations that we have discussed for manipulative experiments. Most importantly, the practical and logistical difficulties of implementing large-scale treatments are avoided altogether. There is no practical limit to the spatial or temporal scale of the study system. In a mensurative experiment, the investigator also has some flexibility in dealing with time lag effects. For example, by selecting landscapes that have been fragmented long enough to let within-fragment dynamics equilibrate, the investigator can reduce the risk of reaching erroneous conclusions based on short-term biological responses.

Unfortunately, the additional sources of variation associated with inconsistent and uncontrolled past perturbations usually more than offset any gains in control over time lags. In addition, because comparative mensurative studies generally involve substituting space for time, and therefore lack pretreatment control, they are hampered by the inherent variability and autocorrelation among landscapes. Consequently, not only is the statistical power associated with detecting "treatment effects" reduced, but also the potential for confounding effects due to this uncontrolled variability can further limit the scope of inferences. In statistical terms, men-

TABLE 1. Total number and percentage by category, of experimental fragmentation studies published in *Landscape Ecology*, *Conservation Biology*, and *Ecological Applications* from January 1995 to January 2000.

Study design	<i>n</i>	Patch	Patch–landscape	Landscape	Edge
Total	54	57.4	14.8	9.3	18.5
Mensurative	41	51.2	19.5	4.9	24.4
Manipulative	13	76.9	0	23.1	0
Replicated	38	55.3	15.8	2.6	26.3
Unreplicated	16	62.5	12.5	25.0	0
Controlled	23	52.2	26.1	17.4	4.3
Uncontrolled	31	61.3	6.5	3.2	29.0
Area and configuration	2	50.0	0	50.0	0
Area or configuration	52	57.6	15.4	7.7	19.3

Notes: Studies are tabulated on the basis of several criteria used to evaluate the experimental design (see *Literature review* section for details). Percentages sum to 100 within each row and represent the percentage of studies conducted at the patch, patch–landscape, landscape, and edge levels, as defined in the text.

surative studies provide correlations between observed differences that discriminate between sets of sites (Diamond 1986). Other evidence must be examined to distinguish cause from effect. As a positive trade-off, however, mensurative experiments have the highest realism and generality, because they are applied to unmanipulated, real-world systems. For many fragmentation questions, due to issues of scale and scope, mensurative experiments are the only feasible approach.

LITERATURE REVIEW

Our task was to review recent fragmentation literature to provide feedback to researchers on the effectiveness of recent fragmentation field research, and to provide suggestions to strengthen it. We reviewed a total of 134 papers on habitat fragmentation published in the journals *Conservation Biology*, *Landscape Ecology*, and *Ecological Applications* from January 1995 through January 2000. We selected these journals because of their representativeness and widespread readership. Although we did not intend this to be a complete review of all published fragmentation studies, we feel that our survey effectively represents the literature on fragmentation. We classified the papers as to whether they were field experiments, modeling-based, or observational studies. We classified a paper as experimental only if it had a priori defined “treatments” assigned (usually randomly) to experimental units and was replicated so as to allow the researchers to test one or more specific hypotheses associated with treatments. Experimental studies allowed for at least some inferences about cause and effect. Studies that looked for patterns among variables or relationships between independent and dependent variables across a number of “samples” using correlational procedures were classified as observational. Studies that used inferential statistical procedures such as ANOVA, but applied them in a post hoc manner after the sample had been collected, were likewise classified as observational. Studies that observed patterns or changes over time in

one or several sites without any explicit hypothesis or clearly defined dependent variable were also classified as observational. Of the 134 papers we reviewed, 41% were experimental, 43% were observational, and 16% were modeling studies (see the Appendix for the complete bibliography). Furthermore, >75% of the experiments were mensurative in design; only 13 studies used manipulative treatments (Table 1). These results indicate that many researchers are using experimental approaches to study fragmentation, but few are using manipulative designs that lead to the strongest inferences, highlighting the difficulties of conducting manipulative experiments as described earlier.

We further classified papers as to whether they were edge, patch, patch–landscape, or landscape studies. We classified the paper as an edge study if, by experimental design, the key independent variable was distance from the edge of a patch. We considered the paper a patch study if individual patches, not landscapes (i.e., patch mosaics), were the experimental units. Independent variables in a patch study usually included patch size or isolation, although other variables such as patch shape, cover type, and within-patch habitat variables were sometimes included. We separated an important class of patch studies, referred to here as patch–landscape studies, in which the patch was still the experimental unit, but the independent variables included landscape structure within a specified “neighborhood” distance surrounding the patch. Landscape studies were those in which individual landscapes (i.e., entire patch mosaics) were the experimental units. Independent variables in a landscape study usually described the composition, diversity, or configuration of the habitat mosaic. Of the 134 papers we reviewed, ~8% were edge studies, 39% were patch studies that did not consider local landscape structure, 19% were patch–landscape studies, and 22% were landscape studies. The remainder were studies that did not fit into these categories.

For experimental studies, the percentage of studies conducted at the landscape level decreased to 9%, in-

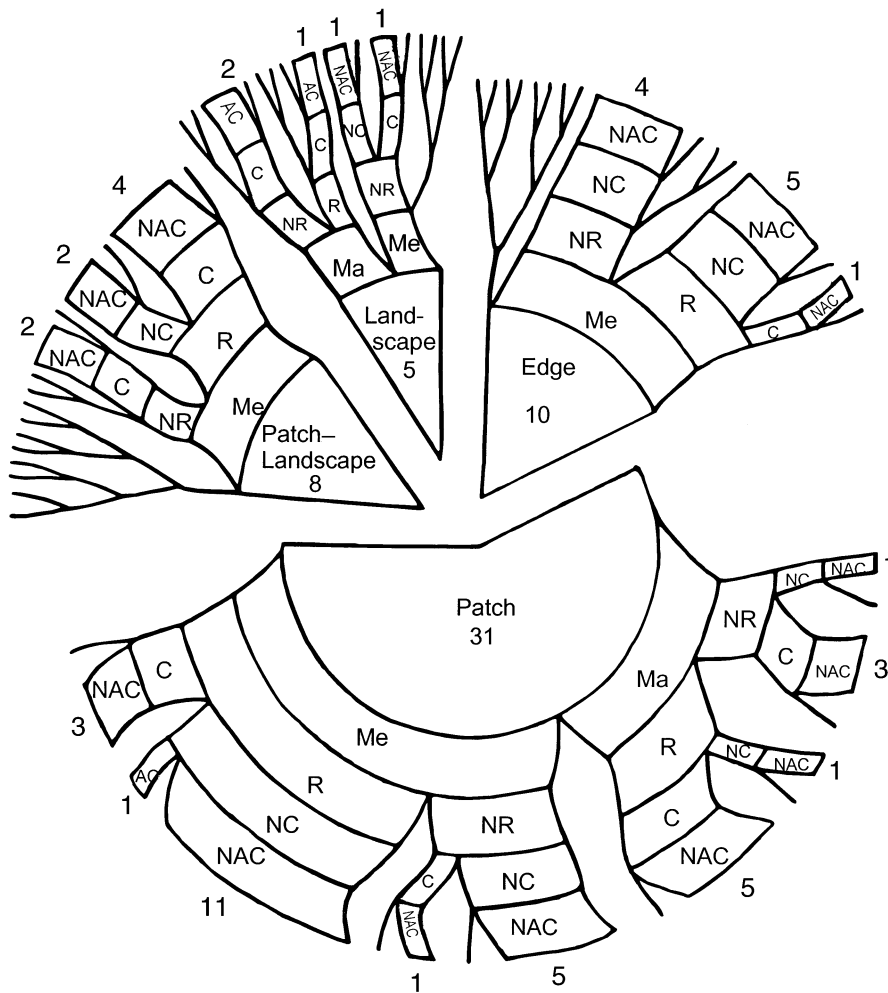


FIG. 1. Hierarchical distribution of 54 experimental studies across the following five criteria (corresponding to the concentric bands in the figure): (1) spatial level (patch, edge, patch-landscape, and landscape); (2) experimental design (Me, mensurative; Ma, manipulative); (3) replication (R, five or more replicates; NR, fewer than five replicates); (4) level of control (C, controlled and NC, uncontrolled); and (5) habitat area vs. habitat configuration (AC, separated area and configuration effects; NAC, did not separate area and configuration effects). The width of the branch represents the number of studies in the corresponding category of experiments. Unlabeled branches represent categories with no studies. See the *Literature review section* for details on evaluation criteria. Studies were published in *Landscape Ecology*, *Conservation Biology*, and *Ecological Applications* from January 1995 to January 2000.

dicating that few experiments were designed to elucidate cause and effect relationships at the landscape level (Fig. 1). In all other experiments, individual patches or edges were the experimental units. Patch- and edge-based studies can effectively elucidate certain kinds of phenomena, but they are entirely incapable of answering many of the most important questions that we have about fragmentation. Patch-landscape studies can provide a great deal more information about the effects of habitat fragmentation than can purely patch-based studies. However, they are still limited because they are not true landscape studies; patches are still the experimental unit. Fragmentation is fundamentally a landscape-level process. An individual patch can be progressively reduced in size and, as a consequence,

can become more isolated over time; the biological consequences of these changes are the subject of island biogeography, not fragmentation research. Fragmentation occurs when a contiguous habitat is broken into several pieces (patches); the biological consequences of the fragmented (subdivided) distribution of habitat patches are the subject of fragmentation research. This does not imply that studying patch-level processes has no utility in the study of fragmentation. Quite the contrary. Understanding these patch-level processes allows us to understand some of the mechanisms contributing to fragmentation effects. However, knowledge gained from patch-level studies alone is inadequate to understand fragmentation at the landscape level. It is analogous to trying to understand metapopulation dynamics

(landscape-level process) by studying only one of the subpopulations (patch-level). Indeed, it is widely recognized that extrapolating findings across spatial scales, especially patch-level to landscape-level scales, can lead to erroneous conclusions (Wiens et al. 1987, 1993, Wiens 1989a, b, McGarigal and McComb 1995, 1999, Villard et al. 1999). Based on the literature that we reviewed, it seems that there is a mismatch between scale of the process (landscape) and scale of investigation (patch) in the vast majority of fragmentation studies (Fig. 1).

On a more positive note, most studies did explicitly associate fragmentation pattern with some level of process. Over 90% of experimental studies associated changes in habitat area or configuration with a process-oriented dependent variable. However, there was great variability in the strength of inferences about process that could be obtained from these studies. First, patch-based studies are fundamentally limited in their inferences about the relationship between fragmentation pattern and process, as previously discussed, because the only measure of pattern that they make is the characteristics of a single focal patch; they disregard the influences of neighborhood and landscape structure. Patch-landscape studies have less crippling limitations, but are still limited because the landscape pattern-process relationships are correlative in nature. Second, the nature of the process studied varied greatly. Only 36% of experimental studies associated fragmentation with actual demographic responses, such as predation rate, mortality, brood parasitism rate, or reproduction. In the remainder of the studies, the process was either strict presence/absence of an organism, the diversity of a certain group of organisms, or the abundance of one or more organisms. There is a fundamental limit to what inferences can be drawn from this kind of study. Associating presence/absence and abundance with levels of fragmentation is, in essence, a correlative design, even when tested with ANOVA, because we are merely describing differences between habitat types or levels of fragmentation and are not ascribing the causes of these differences.

None of the studies that we reviewed addressed any of the interesting high-level questions previously listed (see *So what is the best approach?*), such as the causes of extinction thresholds, time lags, and synergisms between habitat area and configuration. Most of the studies merely quantified differences in a "process" between fragmented and unfragmented experimental units. None of the experimental studies was designed to isolate the characteristics of fragmentation that cause these effects. Thus, these inferences are also correlative, as they describe differences between fragmented and unfragmented habitats without identifying the mechanisms causing the differences.

There was considerable inequity in the organismal focus of fragmentation studies that we reviewed. Birds

were the experimental organism in over half of the studies, and of these, songbirds accounted for the vast majority. Mammals and plants were the second most common organism types, with ~18% of studies based on each of them. Invertebrates and reptiles and amphibians were the most understudied groups, with only 9% and 4% of studies, respectively. There was also a strong imbalance in the representation of ecological systems. Overall, temperate forest was the study system in 37% of studies and in 45% of all experimental studies. Tropical forest was the second most represented system, with 13% of all studies and 22% of experimental studies. All other systems were poorly represented. Desert, steppe, and grassland were especially understudied, together accounting for only 5% of experimental studies. These results reflect the high interest in birds and mammals in temperate forests, but are somewhat surprising because less vagile organisms and simpler ecological systems are perhaps the best suited for experimental study at the landscape level. Less vagile organisms, such as many invertebrates, reptiles, and amphibians, perceive and respond to the environment at finer scales, and therefore require much smaller experimental landscapes than do most wide-ranging birds and mammals. In addition, the relatively simple environments in desert, steppe, and grassland systems make experimental manipulations much more practical than in tropical and temperate forests.

The spatial scale of fragmentation studies imposes severe limits on the patterns observed and the processes involved. For patch studies, spatial scale is simply the size of the experimental patches. In the 134 studies that we analyzed, patches varied greatly in size, from <0.04 ha to >1000 ha. The spatial scale in patch studies is important only to patch-level processes, as previously discussed. The scale reported for patch-landscape studies ranged from 16 to 1256 ha; for landscape studies, it ranged from 25 m² to >62 000 ha. The small number of experimental landscape and patch-landscape studies, however, makes any generalization tenuous. Importantly, only 16% of experimental studies measured the pattern and considered the effects of fragmentation at multiple scales. Most of these were patch-landscape studies that analyzed landscape composition or structure within one or more "distance neighborhoods" around the focal experimental patches. Only 5% of experimental studies considered fragmentation from an explicitly organism-relevant scale. These studies analyzed fragmentation at the scale of the home range of a particular bird or forest mammal. In all other cases, the scale was either arbitrary or simply assumed to be relevant for the organisms under investigation. In many cases, the focus was on a group of organisms (e.g., breeding birds) and therefore it was impossible to select a single scale that would be relevant to all species. Nevertheless, the relatively poor effort made to adopt

organism-centered scales for investigation is cause for concern.

It is often very difficult to obtain independent replication in fragmentation studies. This was confirmed in our review by the fact that most experiments were poorly replicated. The median number of replicates in the experimental studies that we reviewed was five. Of the experimental studies, 30% had fewer than five replicates and 62% had fewer than nine replicates. This pattern was even more pronounced in manipulative studies, in which the median replication was four replicates and 75% of all studies had fewer than nine replicates. In addition, there was considerable doubt as to the independence of the experimental units in many studies, and in others, a high degree of uncontrolled, natural variability among replicate experimental units probably heavily masked treatment effects. Importantly, no experimental studies explicitly addressed the effects of spatial autocorrelation among experimental units.

On average, the fragmentation studies that we reviewed were also poorly controlled. Only 42% of experiments included controls in which the same dependent variables were measured in the absence of the experimental perturbation. However, on a positive note, >75% of landscape and patch–landscape experiments included controls. Unfortunately, in many cases, the controls were insufficient and unreplicated. The combined effect of these shortcomings is reduction in the power to detect differences among treatments and reliably ascribe those differences to the treatment.

Although many papers included separate variables for habitat area and habitat configuration, only 6% of all studies had designs that allowed for explicit separation of these effects. Only 3% of the experimental studies separated the effects of area and configuration (Table 1). Only one landscape study was designed to separate the effects of these two different factors, and only one of the experiments that separated area and configuration was manipulative in design (Fig. 1). This is discouraging because robust and effective conservation biology requires the distinction between the effects of habitat area and configuration. Recent simulation results suggest that habitat loss may have a much larger effect than habitat fragmentation (configuration) on population extinction (Fahrig 1997, 1998, 2002). If this is so, current emphasis on habitat spatial pattern may be misguided (Kareiva and Wennergren 1995). However, some recent empirical work has indicated that, under certain circumstances, habitat configuration can be as influential as habitat area (Villard et al. 1999). Clearly there is need for clarification of this important question. It is surprising, therefore, that so few studies attempted to separate area and configuration effects.

Clearly, sample size, replicate independence, and uncontrolled variation in confounding variables remain critical problems in fragmentation studies. Earlier, we

described the adequacy of studies in each of these criteria independently. It is equally important for us to consider the performance of studies on several of these factors simultaneously. When these calculations are made, we see that most recent experimental studies of habitat fragmentation are seriously limited. For example, <25% of experimental studies had both at least five replicates and one rigorous control. Importantly, most of these studies were at the patch level (Fig. 1). Few landscape and patch–landscape studies were both replicated and controlled. This has serious implications for their ability to rigorously quantify fragmentation effects at the landscape level, and should be a cause of great concern. Furthermore, only one study that was designed to explicitly separate area and configuration included rigorous controls (Fig. 1). Until a number of carefully controlled and well replicated studies are undertaken to explicitly separate the effects of habitat area and configuration on the population and behavioral ecology of a range of organisms, we will remain uncertain about the importance and relative influence of these distinct landscape characteristics.

Although many of the studies that we reviewed effectively dealt with one or a few of the issues discussed here, there were few exemplary studies to point to as models that effectively integrated all, or even most, of our concerns. One of the better examples of a manipulative experiment from our review was that of Wolff et al. (1997). This manipulative experiment involved monitoring the short-term behavioral and demographic responses of gray-tailed voles (*Microtus canicaudus*) to the reduction and fragmentation of their grassland habitat. The experiment was conducted in 12 0.2-ha enclosures planted with alfalfa, with four replicates for each of two manipulated treatments and a control. The treatments allowed for explicit separation of habitat area and habitat configuration effects. Of course, this type of manipulative experiment at the landscape level was practical because of the relatively small landscapes perceived by this species and the relative ease of conducting vegetation manipulations in grassland systems. This type of small-scale field experiment is often referred to as an Experimental Model System.

Similarly, there were few good examples of comparative mensurative experiments to point to as models. One of the better examples from our review was that of Trzcinski et al. (1999). This mensurative experiment involved measuring the relative importance of the independent and interactive effects of forest cover (i.e., habitat area) and fragmentation on the distribution of forest breeding birds. The experiment was conducted using 94 landscapes, each 10 × 10 km, selected to represent a two-dimensional gradient in forest cover and fragmentation. The a priori assignment of treatments allowed for the explicit separation of habitat area and habitat configuration effects. Although the study did not attempt to evaluate demographic processes, and

therefore cannot elucidate the mechanisms behind the observed effects, it did address important theoretical predictions regarding the interaction of habitat area and fragmentation on species occurrence.

CONCLUSIONS

In light of our conceptual framework, what can we conclude from our review of the recent fragmentation literature? Are our empirical studies providing the answers to our most interesting fragmentation questions? Are empirical studies keeping pace with the rapid advances in fragmentation theory? Overall, it seems that, although we have learned a great deal about patch-level processes related to island biogeography, we have yet to address many of the most interesting and relevant questions about fragmentation at the landscape level. Clearly, there is a paucity of experimental studies at the landscape level, yet fragmentation is a landscape-level process and ultimately can be understood only by investigating landscapes, not patches. Moreover, there has been only a handful of manipulative experiments at the landscape level, yet this experimental approach provides the strongest inferences on cause and effect. Furthermore, there have been few attempts to separate the effects of habitat loss from fragmentation by experimental design. Although typically confounded in the real world, these processes and their biological consequences are distinct. If we hope to gain a reliable understanding of fragmentation *per se*, we must separate and isolate fragmentation effects from habitat loss. In addition, few studies have been designed to measure actual demographic responses, such as predation rate, mortality, brood parasitism rate, or reproduction. Much recent fragmentation research has focused on merely correlating patch size or landscape pattern with some pattern or biological response, without considering the processes or mechanisms that are responsible for the changes. Yet, explicit experimental tests of cause–effect linkages are essential if we are to understand what causes fragmentation effects and to predict the effects of future landscape changes. Finally, sample size, replicate independence, and uncontrolled variation in confounding variables remain critical problems in fragmentation studies, leading to low power to detect treatment effects. Hence, it does not appear that empirical studies, in general, are providing reliable answers to many of the important fragmentation questions.

How can we more effectively design field experiments to better understand the biological consequences of fragmentation? We believe that more emphasis should be given to landscape-level experiments designed to explicitly separate the effects of habitat area and habitat fragmentation on demographic or ecosystem responses. Moreover, these experiments should be adequately replicated and controlled. Particular care should be given to the selection of experimental units

to minimize the confounding effects of uncontrolled variation. Overall, experiments should be designed to answer some of the most important high-level questions posed by recent theoretical work; for example, how demographic processes such as dispersal, mortality, and reproduction are affected independently and interactively by habitat area and habitat fragmentation, and whether threshold effects exist in any of these relationships. Finally, additional attention should be given to conducting experiments at organism-relevant scales (Wiens 1989*a*). The approach for doing so will vary depending on the biological parameter of interest, but will undoubtedly involve autecological information (Goodwin and Fahrig 1998). If, for example, the study aims to investigate how habitat fragmentation affects individual behavior and fitness, then the appropriate spatial scale is the range over which the organism moves during usual (nondispersal) activities. If the focus is the population (local or regional), then the appropriate spatial scale is the intrinsic scale(s) determined by the actual spatial structure of the population. Determining this population structure is fraught with difficulties because of the large spatial scales over which most populations operate. Knowledge of dispersal rates and patterns (i.e., distance) is needed to insure that the scale of observation (landscape) exceeds that over which this critical population process operates. In many cases, the appropriate scale of study will be too large to investigate realistically. Sometimes this problem can be overcome through the judicious use of simulation or theoretical models in combination with empirical study (Kareiva and Andersen 1986). The latter can provide critical information (e.g., habitat use, reproductive rates, movement patterns) needed to parameterize the models, which can then be used to conduct habitat fragmentation experiments.

What is the best experimental approach to accomplish the goal of gaining more reliable knowledge about the consequences of fragmentation? Unfortunately, there is no simple dichotomy of the right and wrong approach. The appropriate approach will be dictated by the question and the system being studied, as well as socioeconomic constraints. Both manipulative or mensurative approaches can be appropriate, given suitable questions. Certainly, manipulative experiments provide the strongest inferences about cause and effect and therefore produce the most reliable knowledge. Unfortunately, the difficulties associated with implementing large-scale manipulations, the inability to account effectively for certain time lag effects, and inherent variability among natural landscapes make manipulative studies exceedingly difficult to implement. Nevertheless, manipulative studies at the landscape scale can, and should, be conducted when practical.

Because of real-world complexities, manipulative experiments are often not practical or feasible for the study of more vagile species in more complex ecolog-

ical systems. Comparative mensurative experiments provide an alternative means of gaining reliable knowledge in these circumstances, if designed properly. One of the greatest difficulties in conducting a comparative mensurative experiment in the field is finding and choosing experimental units that meet all of the experimental design criteria. In addition to selecting landscapes that vary precisely in the independent variables under investigation (typically habitat area and configuration), there is usually a need to carefully control for potentially confounding sources of variation. This may involve, for example, controlling for physiographic variation associated with geomorphological substrates, the composition and pattern of the matrix, and the time since the target habitats were initially fragmented. Given the number of variables to consider, this can be an overwhelming source of difficulty in conducting a study, and ultimately can lead to shortcomings in the experimental design. Although there is no single solution for handling this problem, we can recommend a general approach. Specifically, geographic information systems (GIS) can be used to screen potential experimental units for their suitability, given the specific concerns of the study. Many of the variables used to screen experiment units are readily available as extant digital spatial data layers. Indeed, many states maintain a GIS database with comprehensive ecological and socioeconomic information. These data layers can be clipped to the study area extent and then subsequently subdivided into arbitrary (e.g., fixed area) or natural (e.g., watersheds) units. This set of potential experimental units forms a universal population from which to sample. Using simple GIS queries and existing landscape analysis software (e.g., FRAGSTATS; McGarigal and Marks 1995), each landscape can be measured and filtered with respect to the variables of concern. Landscapes passing through this filter form a final population from which to select sample experimental units for study. This approach allows the researcher a priori control over multiple sources of variation and has an added benefit as well. By comparing the filtered population of potential experimental units to the universal population, the researcher can gain quantitative insight into the representativeness of the final sample. This allows for an explicit representation of the scope of inferences associated with the test hypotheses.

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APPENDIX

A complete bibliography of the 134 papers reviewed is available in ESA's Electronic Data Archive: *Ecological Archives* A012-002-A1.