Review

A Survey and Overview of Habitat Fragmentation Experiments

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Abstract: *Habitat destruction and fragmentation are the root causes of many conservation problems. We conducted a literature survey and canvassed the ecological community to identify experimental studies of terrestrial habitat fragmentation and to determine whether consistent themes were emerging from these studies. Our survey revealed 20 fragmentation experiments worldwide. Most studies focused on effects of fragmentation on species richness or on the abundance(s) of particular species. Other important themes were the effect of fragmentation in interspecific interactions, the role of corridors and landscape connectivity in individual movements and species richness, and the influences of edge effects on ecosystem services. Our comparisons showed a remarkable lack of consistency in results across studies, especially with regard to species richness and abundance relative to fragment size. Experiments with arthropods showed the best fit with theoretical expectations of greater species richness on larger fragments. Highly mobile taxa such as birds and mammals, early-successional plant species, long-lived species, and generalist predators did not respond in the "expected" manner. Reasons for these discrepancies included edge effects, competitive release in the habitat fragments, and the spatial scale of the experiments. One of the more consistently supported hypotheses was that movement and species richness are positively affected by corridors and connectivity, respectively. Transient effects dominated many systems; for example, crowding of individuals on fragments commonly was observed after fragmentation, followed by a relaxation toward lower abundance in subsequent years. The three long-term studies (≥14 years) revealed strong patterns that would have been missed in short-term investigations. Our results emphasize the wide range of species-specific responses to fragmentation, the need for elucidation of behavioral mechanisms affecting these responses, and the potential for changing responses to fragmentation over time.*

Sondeo y Revisión de Experimentos de Fragmentación de Hábitat

Resumen: *La destrucción y la fragmentación del hábitat son las causas fundamentales de muchos problemas de conservación. Realizamos un sondeo de la literatura y examinamos de cerca la comunidad ecológica para identificar estudios experimentales sobre la fragmentación de hábitats terrestres y para determinar si emergen temas homogéneos de estos estudios. Nuestro sondeo revela que existen 20 estudios experimentales de fragmentación en el ámbito mundial. La mayoría de los estudios enfocan en los efectos de la fragmentación sobre la riqueza de especies, o en la(s) abundancia(s) de ciertas especies en particular. Otros temas importantes fueron el efecto de la fragmentación sobre las interacciones interespecíficas, el papel de los corredores y la conectividad del paisaje en los movimientos individuales y la riqueza de especies y la influencia de los efectos de bordes sobre los servicios proporcionados por el ecosistema. Nuestras comparaciones muestran una carencia notable de homogeneidad en los resultados de los estudios, especialmente en lo referente a la riqueza y a la abundancia de especies, y su relación con el tamaño de los fragmentos. Experimentos con artrópodos demostraron que existía un mejor ajuste entre los valores teóricos esperados y los valores reales de aumentos en la riqueza de especies en fragmentos grandes. Los taxones altamente móviles (por ejemplo, aves y mamíferos), las especies de plantas en sucesión temprana, las especies de gran longevidad y los depredadores generalistas no respondieron de la manera "esperada". Entre las razones que explican estas diver-*

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gencias se incluyen los efectos de bordes, la liberación competitiva en los fragmentos de hábitat y la escala es-
pacial del experimento. Una de las hipótesis más aceptadas establece que el movimiento y la riqueza de
especies son afectadas positivamente por los corredores y la conectividad, respectivamente. Algunos efectos
pasajeros dominaron muchos sistemas; por ejemplo, el hacinamiento de individuos en fragmentos se ob-
servó a menudo después de la fragmentación, seguido de un disminución de la abundancia en los años pos-
teriores. Los tres estudios a largo plazo (=14 años) revelaron fuertes patrones que hubieran sido ignorados
en investigaciones a corto plazo. Nuestros resultados señalan el amplio rango de respuestas especie-especifi-
cas, la necesidad de elucidar mecanismos de comportamiento que afectan las respuestas a la fragmentación
y el potencial de respuestas cambiantes a la fragmentación a lo largo del tiempo.

Introduction

Given the importance of habitat fragmentation in con-
servation, it is not surprising that there exists a burgeon-
ing literature based on observational studies of frag-
mented landscapes (e.g., Wilcove et al. 1986; Quinn &
Harrison 1987; Gibbs & Faaborg 1990; Blake 1991; Mc-
Coy & Mushinsky 1994) and a substantial theoretical lit-
erature on the population and community effects of frag-
mentation (e.g., Fahrig & Paloheimo 1988; Doak et al.
1992; Nee & May 1992; Adler & Nuernberger 1994; Til-
man et al. 1994; With & Crist 1995). In contrast, fewer
researchers have deliberately created an experimentally
fragmented landscape and then assessed the ecological
consequences of the fragmentation (Margules 1996). It
is easy to see why. Manipulation of entire landscapes
tends to be large in scale, laborious, and costly. Yet the
difficulty and expense of large-scale spatial experiments
makes it particularly important that whatever data they
generate be used to address general issues in ecology. In
principle, fragmentation experiments could provide a
rich testing ground for theories and methodologies deal-
ing with spatiotemporal dynamics (Tilman & Kareiva
1997). Moreover, because of the logistical difficulty of
such experiments, synthesis across studies may help
provide guidelines and cautionary lessons for the design
of future landscape experiments.

We present the results from a survey of studies con-
ducted worldwide in experimentally fragmented habi-
tats. By our definition, an experiment involves a delib-
erate manipulation of the landscape, usually with an eye
toward assessing a particular hypothesis. In many de-
scriptive fragmentation studies, researchers cannot con-
trol attributes such as patch size, degree of replication,
site initiation, and position on the landscape because
they are investigating the effects of landscape manipu-
lation (e.g., clearcutting in logging or plowing in ag-
riculture) conducted by others. Thus, we excluded such
studies from our review. We concentrated on terrestrial
systems because of the major differences in the dy-
namics of colonization between terrestrial and aquatic
systems.

Methods

We conducted a literature survey of the major ecological
journals (*American Naturalist, Biological Conservation,
BioScience, Canadian Journal of Zoology, Conservation
Biology, Ecography, Ecological Applications, Ecological
Modeling, Ecological Monographs, Ecology, Evolution-
ary Ecology, Forest Science, Heredity, Journal of Animal
Ecology, Journal of Biogeography, Journal of Mammal-
ogy, Landscape Ecology, Nature, Oecologia, Oikos, Theo-
retical Population Biology,* and *Trends in Ecology and
Evolution*) since 1984 using the keyword *fragmentation.*
We also canvassed the ecological community using the In-
ternet (CONSBIO listserver) and made informal contact
with many colleagues. After compiling a list of candidate
studies, we sent out a survey to the authors of the studies
which asked questions about experimental design, focal
organisms of study, hypotheses being tested, study length,
and practical issues such as how the integrity of the exper-
iment was maintained. We summarized the results in the
form of a vote count tally of the number of times the hy-
pothesis was supported. We believe that a more formal
meta-analysis (e.g., Gurevitch & Hedges 1993) of these ex-
periments is not yet warranted because of the relatively
small number of studies and because of the heterogeneity
among study designs, spatial and temporal scales, and
methodological protocols.

Results

Replication and Temporal Span

Based on our criteria for fragmentation experiments, we
identified 20 experimental studies; 6 were conducted in
forests and 14 were conducted in grasslands or old fields.
The experimental studies clustered into evaluations of
five broad focal issues: species richness, the interplay of
connectivity versus isolation, individual species behavior,
demography, and genetics. They tested six major hypoth-
eses: (1) species richness increases with area, (2) species
abundance or density increases with area, (3) interspe-

cific interactions are modified by fragmentation, (4) edge effects influence ecosystem services, (5) corridors enhance movement between fragments, and (6) connectivity between fragments increases species richness. For ease in following the discussion of the experiments included in our review (compiled in Table 1), we include within the text a number in brackets corresponding to the experiment number in Table 1.

The number of fragmentation experiments and the length of time for which they have been conducted have increased substantially in recent years (Table 1). A decade ago there were just 3 studies extant; at present 14 studies are ongoing. The geographic distribution of the 20 studies was primarily North America and Europe. The spatial scale (Fig. 1) ranged from grassland patches of <1 m² (Quinn & Robinson 1987 [2]) to Amazonian rainforest fragments of 1000 ha (Bierregaard et al. 1992 [1]). Replication (Fig. 1) varied from 1 to 160 per category of patch size. Patch sizes were chosen relative to the questions being addressed and the organism(s) of study. Generally, as the landscape scale increased, there were fewer replicates at larger fragment sizes. There was a threshold of decrease in degree of replication at roughly 0.2 ha; above this size, the number of replicates was usually <10. This weakens the statistical power of conclusions about the effects of large fragment size. The temporal spans for these studies ranged from 1 to 19 years, with a mean of just over 6 years (Table 1). Little experimental data exist on the long-term consequences of habitat fragmentation. Three experiments have been in progress for over a decade, and eight have been in progress for 5–10 years. The remaining projects were run for 3 years or less.

These experiments contain taxonomic and habitat biases. Only a few studies explicitly focused on plant population and community dynamics (Table 2). Among animals, there was a heavy emphasis on songbirds and small mammals. A number of studies focused closely on particular species, but few analyzed in detail the effects of fragmentation on pairwise or multispecies interactions (Kareiva 1987 [17] is a notable exception). Several of these projects examined responses across a variety of taxonomic groups simultaneously (Bierregaard et al. 1992 [1]; Margules 1992 [4]; Robinson et al. 1992 [3]; Baur & Erhardt 1995 [19]; D. Huggard, personal communication [6]). There also were habitat biases in that most studies were conducted in either forest, grassland, or old fields. This may reflect the economics and mechanics of creating and maintaining experimental patches, such as using mowing in old fields or grassland and relying upon forestry practices or clearcutting in forested biomes.

Predictions that Work

Numerous studies reported results that supported theoretical expectations; but many revealed effects contrary to initial theoretical expectations. Here we summarize results relative to the hypotheses tested (Table 2).

SPECIES RICHNESS

Following from the theory of island biogeography (MacArthur & Wilson 1967), species richness in habitat fragments is expected to be a function of island size and degree of isolation. Smaller, more isolated fragments are expected to retain fewer species than larger, less isolated habitat tracts (Diamond 1975; Wilson & Willis 1975; Terborg 1976). A major focus of these studies has been the relationship among habitat size, species richness, and individual species' abundances.

Initial theoretical expectations regarding increased species richness with increasing area were supported in only 6 out of 14 examples (not including 3 taxa that exhibited changing patterns over time). In cases in which the hypotheses were upheld, the effects were often striking. For example, even in a 100-ha tropical forest fragment, a beetle community was recognizably different in composition and lower in species richness than those on control sites in continuous forest (Laurance & Bierregaard 1996 [1]). Collinge (1995 [8]) found that insect species diversity was lowest in the smallest fragments and highest in the largest fragments. In a comparison of several types of fragmented landscapes, Collinge and Forman (1998 [8]) found that large-bodied, initially rare species were concentrated in the remaining larger core habitats, as opposed to areas where a central portion of habitat was removed. T. Crist (personal communication [11]) found a similar decrease in arthropod species richness with increasing fragmentation of an old field and determined that the pattern was driven primarily by the loss of rare species. In an old-field study [3] in Kansas, larger patches had higher species richness of butterflies, but small mammals and plants tended to show less consistent differences in species richness among patch sizes (Robinson et al. 1992; Holt et al. 1995a, 1995b). Baur and Erhardt (1995 [19]) found that, after 2 years, isolated grassland fragments were less frequently occupied by various gastropod species than were control patches, leading to lower species richness in the fragments. This set of studies provides a reasonable match with theoretical expectations.

Comparable to the effect of area on species richness, one might expect to observe area effects on genetic diversity within species; smaller fragments should have lower effective population sizes, higher rates of genetic drift, and fewer immigrants (Jaenike 1973). In the experimental studies in our survey, the effect of fragmentation on genetic variation was studied infrequently. Baur and Erhardt (1995 [19]), however, found reduced fecundity and genetic diversity among herbaceous plant species in isolated patches. Interactions between plants and pollinators also exhibited modifications, with potential

Table 1.   A summary of fragmentation experiments with contact persons, references, biomes, dates of initiation and conclusion, patch sizes and replication, and other pertinent data.

Experiment no. and project name or biome	Patch habitat	Matrix habitat	Institutional affiliation	Time span	Fragment sizes (replication)	Preexisting matrix	Community focus	Reference or contact
1. Biological dynamics	tropical rainforest	clearcut	National Museum of History, Smithsonian Institution	1980–present (19 years)	1 ha (8), 10 ha (8),100 ha (5), 200 ha (1), 1000 ha (3)	yes	yes	Bierregaard et al. 1992; Bierregaard & Stouffer 1997
2. California grassland	California annual grassland	mowed grass	University of California, Davis	1983–1987 (4 years)	2 m^2 (32), 8 m^2 (8), 32 m^2 (2)	yes	yes	Quinn & Robinson 1987; Robinson et al. 1995
3. Kansas fragmentation study	Kansas old field	mowed grass	University of Kansas	1983–present (16 years)	50 × 100 m (6), 12 × 24 m (18), 4 × 8 m (82)	no	yes	Holt et al. 1995a, 1995b; Robinson et al. 1992
4. Wog Wog study	eucalypt forest	pine plantation	CSIRO Division of Wildlife and Ecology	1985–present (14 years)	0.25 ha (6), 0.875 ha (6), 3.062 ha (6)	yes	yes	Margules 1992; Margules 1996
5. Groenvaly experiment	South African grassland	pine plantation	University of Pretoria, South Africa	1994–present (5 years)	0.25 ha (6), 0.875 ha (6), 3.062 ha (6)	yes	yes	Jaarsveld, personal communication
6. Kamloops project	Canadian subalpine forest	clearcut	British Columbia Ministry of Forests	1995–present (3 years)	0.1 ha (160), 1 ha (27), 10 ha (3)	yes	yes	Vyse 1997; Klenner & Huggard 1997
7. Missouri Ozark forest ecosystem project	Missouri Ozark hardwood forest	clearcut	Missouri Department of Conservation, University of Missouri	1990–present (9 years)	300 ha (2), 800 ha (1)	yes	yes	Kurzejaski et al. 1993
8. Colorado grassland	Colorado short grass prairie	mowed grass	University of Colorado	1992–1994 (2 years)	1 m^2 (18), 10 m^2 (18), 100 m^2 (18)	yes	yes	Collinge 1995
9. Boreal mixed-wood dynamics project	Canadian boreal mixed-woods	clearcut	University of British Columbia, University of Alberta, Edmonton	1993–present (6 years)	1, 10, 40, 100 ha (3 each)	yes	yes	Schmiegelow & Hannon 1993; Schmiegelow et al. 1997
10. Savannah River Site corridor project	clearcut	pine forest	University of Georgia, Iowa State University, U.S. Forest Service	1994–present (5 years)	128 × 128 m (27) with differing corridor lengths	yes	yes	Haddad 1997; Danielson and Hubbard (2000)
11. Miami University fragmentation project	Ohio old field	mowed grass	Miami University	1995–present (5 years)	2 × 2 m (36), 9 × 9 m (36), 13 × 13 m (36)	yes	yes	Crist & Golden, personal communication
12. German fragmentation study	Bavarian clover patches	crop fields and meadows	Gottingen University	1992–present (7 years)	1.2 m^2 (18) with separation varying	yes	yes	Kruess & Tscharntke 1994
13. Blandy farm fragmentation study	Virginia old field	mowed grass	University of Virginia	1990–present (9 years)	1 ha (4), 0.25 ha (4), 0.63 ha (4)	no	no	Bowers & Dooley 1993
14. Vole behavior and fragmentation	alfalfa patches	mowed grass	Oregon State University	1994 (ongoing 4-month experiments)	25 × 25 m (4), 12.5 × 12.5 m (32), 5 × 5 m (100)	no	no	Wolff et al. 1997
15. Evensted research station	Norwegian meadows	mowed grass	University of Oslo, Norwegian Forest Research Institute, Agricultural University of Norway	1982–1989 (6 years)	15 × 20 m (4), 15 × 45 m (4), 0.5 ha (2)	no	no	Ims et al. 1993

Table 1.   (continued)

Experiment no. and project name or biome	Patch habitat	Matrix habitat	Institutional affiliation	Time span	Fragment sizes (replication)	Preexisting matrix	Community focus	Reference or contact
16. Long Ashton	British croplands	mowed grass	Institute of Arable Crops Research	1995–present (4 years)	9 × 9 m (36), 27 × 27 m (5)	no	yes	Powell
17. Predator-prey interactions and fragmentation	New York goldenrod monoculture	mowed grass	Cornell University	1982–1985 (3 years)	20 m² (3), 6 m² (30)	no	no	Kareiva 1987
18. Ohio old-field project	Ohio old field	mowed grass	Miami University	annual	160 m² (4), 40 m² (16)	no	no	Barrett et al. 1995
19. Swiss Jura mountains	European calcareous grassland	mowed grass	University of Basel, Switzerland	1993–present (6 years)	4.5 × 4.5 m (24), 1.5 × 1.5 m (24), 0.5 × 0.5 m (48)	yes	yes	Baur & Erhardt 1995
20. Root vole sex ratio	Norwegian grassland	mowed grass	University of Oslo	1990–1995 (5 years)	0.0225 ha (12), 0.675 ha (4)	yes	no	Aars et al. 1995

ramifications for genetic diversity. For example, butterflies visited flowers less frequently in isolated patches, thus leading to reduced fecundity and possibly lower plant genetic diversity.

DENSITY AND ABUNDANCE OF SPECIES

The negative effects of fragmentation on species richness arise in part because of lower-level effects on population abundance and so should be evident even in those species that do not become extinct. The simplest a priori expectation is that, for habitat specialists restricted to the fragments and unable to use the matrix habitat, fragmentation reduces density. The mechanism for this reduced density could be increased demographic stochasticity or the disruption of metapopulation dynamics. The alternative hypothesis, however, is that species move from the matrix habitat to the remaining habitat patches after a disturbance, such that "crowding" ensues in the patches (Whitcomb et al. 1981; Fahrig & Paloheimo 1988; Fahrig 1991). Our summary refers to density and abundance because some authors presented their results as density, whereas others presented results as abundance or trapping success per unit time.

Species abundance decreased with fragmentation in 6 out of 13 examples. For instance, Margules and Milkovits (1994 [4]) found that the abundance of amphipods (family Talltridae) decreased markedly in remnant forest patches relative to controls and that this effect was more dramatic on smaller remnants than on larger ones. In the Kansas project [3], the cotton rat (*Sigmodon hispidus*) and the white-footed mouse (*Peromyscus leucopus*) were differentially more abundant in larger patches (Foster & Gaines 1991; Robinson et al. 1992; Schweiger et al. 1999). H. Norowi (personal communication [16]) similarly found that weevil and parasitoid densities were consistently greater in contiguous habitat patches than in fragmented patches of equivalent area.

The density of tree seedlings declined significantly from continuous forest to forest fragments in the Amazonian Biological Dynamics Project [1] (Benitez-Malvido 1998). These results demonstrate the effect of fragmentation on key life-history stages in trees. In the Kansas study [3], which involves old-field succession, colonization by woody plant species is proceeding more rapidly in larger patches (Holt et al. 1995b; Yao et al. 1999). Thus, changes at the level of individual species can often be discerned, even when coarser, whole-community effects of fragmentation are not apparent (Robinson et al. 1992).

INTERSPECIFIC INTERACTIONS AND ECOLOGICAL PROCESSES

Spatial dynamics can have profound effects on individual behavior (e.g., Hanski et al. 1995; Redpath 1995) and interspecific interactions such as predation (Aizen & Feinsinger 1994; Tilman & Kareiva 1997), so it is sensi-
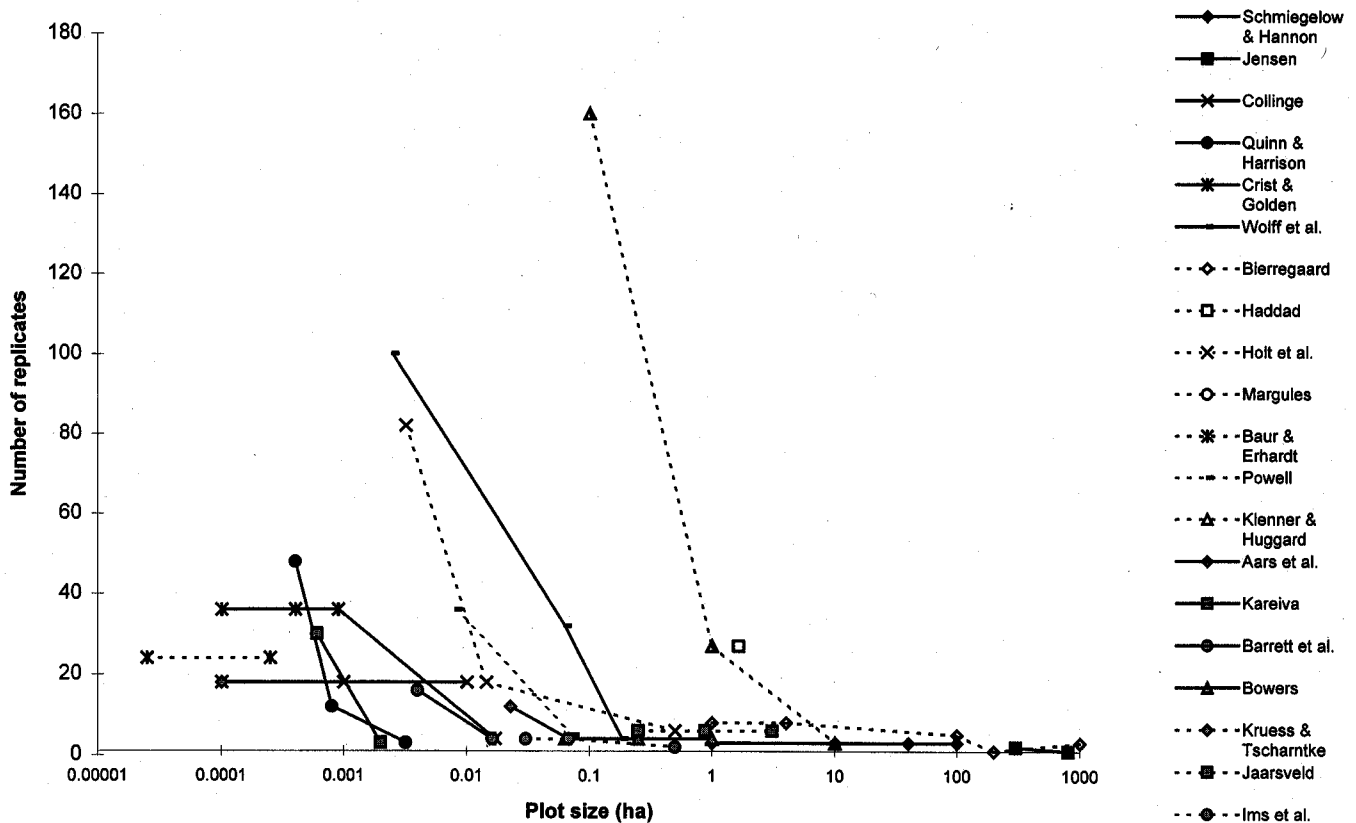
Figure 1. Frequency distribution of fragmentation studies relative to plot size.

ble to expect that the effects of habitat fragmentation may be mediated or exacerbated through shifts in such interactions. Kareiva (1987 [17]) demonstrated this effect by performing experiments on a predator-prey interaction between an aphid and a coccinellid predator in monocultures of *Solidago*. The fragmented treatment had more frequent aphid outbreaks, apparently because fragmentation disrupted the ability of the predator to aggregate rapidly at localized clusters of the aphid in early phases of an outbreak. H. Norowi (personal communication [16]) found that the rate of weevil parasitism varied with parasitoid species and the spatial scale of analysis. W. Powell (personal communication [16]) similarly found that carabid beetle assemblages in experimentally fragmented agroecosystems revealed significant spatial and temporal effects arising from altered predator-prey interactions within grassland patches.

EDGE EFFECTS

Another rule derived from the theory of island biogeography is that reserves should minimize the edge-to-area ratio to maximize the effective core area of the reserve. Increasing the amount of edge can make a reserve more vulnerable to invasion by exotic species and subject it to more extreme abiotic influences such as wind and tem-

perature (Saunders et al. 1991). Physical changes associated with creating an edge can have profound effects on ecological processes. For instance, R. Bierregaard (personal communication [1]) documented that edge effects penetrate 300 m or more into a tropical forest remnant, and Didham (1997 [1]) showed that isolated patches have leaf-litter insect fauna substantially different than that of continuous forest.

In principle, the altered abiotic conditions associated with fragmentation can also influence ecosystem services such as nutrient cycling (Saunders et al. 1991). Three projects have addressed ecosystem consequences of fragmentation with varying results. Two forest projects found effects on nutrient cycling (Bierregaard et al. 1992 [1]; Klenner & Huggard 1997 [6]), whereas the Kansas old-field study [3] did not (Robinson et al. 1992). In the Biological Dynamics Project [1] and other forest studies, the contrast in abiotic conditions between fragments (e.g., tall forest) and the surrounding matrix (e.g., pasture) is dramatic. In other systems, there are less dramatic differences between the matrix and fragments, so one might expect ecosystem effects to be less noticeable.

Because fragmentation inevitably leads to the juxtaposition of qualitatively different habitats, flows of materials and individuals between them can indirectly exert profound influences on within-fragment communities

(Polis et al. 1997). In the Kansas study [3], for instance, generalist arthropod predators such as web-building spiders are more abundant in the fragments, particularly along edges, where they can profit from the aerial "drift" of insects from the surrounding productive, mown interstitial turf (T. Jackson et al., unpublished data). Smaller forest fragments similarly had greater community invasibility for successional tree species in the Biological Dynamics Project [1] (Benitez-Malvido 1998). Laurence et al. (1998) found that recruitment rates were markedly higher near forest edges and highest within 100 m of forest edges.

CORRIDORS AND MOVEMENT/CONNECTIVITY

Fragmentation creates barriers to dispersal (e.g., Mader 1984), and behavioral responses to fragmentation may underlie many observed effects at higher organizational levels such as populations and communities. Even narrow breaks (50–100 m) in continuous forest habitat produce substantial barriers to the movement of many species of birds and some insects. Of the five fragmentation experiments that directly tested the effects of corridors, all but one found that corridors enhanced movement for some of the species examined (Collinge 1995 [8]; Haddad 1997 [10]; Schmiegelow et al. 1997 [9]; Wolff et al. 1997 [14]). Collinge (1995 [8]) found that corridors slightly decreased the rate of species loss and that this effect was greatest in medium-sized fragments. In another experiment (Haddad 1999; Haddad & Baum 1999 [10]), three open-habitat butterfly species (*Juononia coenia, Phoebis sennae*, and *Euptoieta claudia*) reached higher densities in patches connected by corridors than in isolated patches. But the abundance of a fourth, generalist species, *Papilio troilus*, was insensitive to forest corridors.

Related to corridors is the effect of landscape pattern on movement, as expressed for instance in rates of colonization and dispersal. H. Norowi (personal communication [16]) found that the presence of a hedgerow on one side of an experimental patch affected the pattern of colonization of newly created habitat patches by one species of weevil (*Gymnetron pascuorum*). Kruess and Tscharntke (1994 [12]) found substantial distance effects on colonization by parasitoids in a clover field but only minor effects on colonization by herbivores. This led to release from parasitism on the isolated patches, analogous to the effects of fragmentation in the predator-prey interaction studied by Kareiva (1987 [17]). Parasitoid species that failed to establish tended to be those with low and variable populations. These patterns have persisted over several years (T. Tscharntke, personal communication).

There is a growing literature on small mammals focusing on the effects of experimental fragmentation on dispersal and home-range size. Diffendorfer et al. (1995*a,b* [3]) showed that fragmentation reduced the movement rates and altered spatial patterning of distances moved in several small-mammal species. Wolff et al. (1997 [14])

found that fragmentation reduced vole (*Microtus canicaudus*) movements considerably. Ims et al. (1993 [15]) found decreased home-range size and more home range overlap in small mammals on smaller patches. Harper et al. (1993 [18]) found that the shape of habitat patches affected the number of voles that dispersed when population densities were low but not when densities were high. Furthermore, the shape of the habitat patches affected the space-use behavior of resident voles. Bowers et al. (1995 [13]) examined the space-use behavior of voles (*Microtus pennsylvanicus*) and found that adult females at edges tended to have larger home ranges, body sizes, residence times, and reproductive rates than individuals in the interior of a patch. Bowers et al. (1995 [13]) suggest that this edge effect could account for the inverse patch-size effects on abundance for small mammals noted in several studies (e.g., Foster & Gaines 1991 [3]). Finally, Ims et al. (1993 [15]) studied the effects of fragmentation on aggressive and docile strains of voles (*Microtus oeconomus*) and found that different sex and age groups are likely to exhibit different spatial responses to fragmentation.

Predictions that Do Not Work

SPECIES RICHNESS

In a number of experiments, species richness either increased with or was unaffected by fragmentation. In most cases, these effects could be attributed to an increase in early-successional species, transient species, or edge effects (community "spillover" from surrounding habitats; Holt 1997). For instance, Schmiegelow et al. (1997 [9]) examined passerine data gathered before fragmentation and during the 2 years thereafter. Despite effects on turnover rates, they found no significant change in species richness as a result of harvesting, except in the 1-ha connected fragment treatment, where the number of species actually increased 2 years after isolation. This increase reflected transient species rather than species breeding in the patches, suggesting that buffer strips were being used as corridors.

In the Biological Dynamics Project [1], frog diversity increased after fragmentation because of unpredicted immigration by generalist species that flourished in the matrix of pasture surrounding the forest fragments (Laurance & Bierregaard 1996). The Wog Wog Study [4] in southeast Australia (Margules 1996; Davies & Margules 1998; Margules et al. 1998) revealed that different taxa had highly disparate responses to fragmentation, including a lack of response. Plant communities in several experiments have exhibited species-richness patterns contrary to the expectations of island biogeography models. Quinn and Robinson (1987 [2]) found increased flowering-plant and insect species richness with increasing habitat subdivision. They hypothesized that these patterns might reflect the effect of fragmentation on competition

Table 2.   A vote-count summary of fragmentation-experiment results, separated by hypothesis tested.*

Project name	Taxonomic group	Hypothesis supported	Reference or contact
Species richness increases with area			
1. Biological dynamics	birds	yes	Bierregaard et al. 1992; Stouffer & Bierregaard 1995
	beetles	no	Laurance & Bierregaard 1996
	frogs	no	Laurance & Bierregaard 1996
	primates	yes	Bierregaard et al. 1992
2. California grassland	plants	no	Quinn & Robinson 1987; Robinson et al. 1995
	insects	no	Quinn & Robinson 1987; Robinson et al. 1995
3. Kansas fragmentation study	small mammals	no	Holt et al. 1995a, 1995b; Robinson et al. 1992
	plants	no	Robinson et al. 1992; Holt et al. 1995a, 1995b
	butterflies	yes	Holt et al. 1995a
4. Wog Wog study	millipedes	no, years 1–7; yes, years 7–present	Margules 1992
	frogs	yes, years 0–5; no, years 5–present	Margules 1996
	beetles	no	Davies & Margules 1998
8. Colorado grassland	insects	yes	Collinge 1995; Collinge & Forman 1998
9. Boreal mixed-wood dynamics project	birds	no, treatments and controls; yes, isolated fragments	Schmiegelow et al. 1997
11. Miami University fragmentation project	insects	yes	Crist & Golden, personal communication
19. Swiss Jura mountains	gastropods	yes	Baur & Erhardt 1995
Species abundance or density increases with area			
1. Biological dynamics	trees (woody)	yes	Benitez-Malvido 1998
	trees (seedling recruitment)	no	Benitez-Malvido 1998
	beetles	yes	Bierregaard et al. 1992
	birds	no (short term); yes later	Bierregaard & Lovejoy 1989
3. Kansas fragmentation study	trees	yes	Holt et al. 1995b; Yao et al. 1999
	small mammals	mixed	Foster & Gaines 1991; Schweiger et al. 1999
4. Wog Wog study	amphipod density	yes	Margules & Milkovits 1994
	scorpions	no	Margules & Milkovits 1994
8. Colorado grassland	insects	no	Collinge & Forman 1998
9. Boreal mixed-wood dynamics project	birds	no, treatments and controls; yes, isolated fragments	Schmiegelow et al. 1997; Schmiegelow et al. 1997
13. Blandy farm fragmentation study	small mammals	no	Bowers & Matter 1997; Dooley & Bowers 1998
14. Vole behavior and fragmentation	small mammals	no	Wolff et al. 1997
15. Evensted research station	small mammals	no	Ims et al. 1993
16. Long Ashton	weevils and parasitoids	yes	W. Powell, personal communication
17. Predator-prey interactions and fragmentation	insects	yes	Kareiva 1987
18. Ohio old-field project	small mammals	no	Barrett et al. 1995; Collins & Barrett 1997
Interspecific interactions are modified by fragmentation			
12. German fragmentation study	parasitoids	yes (less parasitism on far patches)	Kruess & Tscharntke 1994

continued

Table 2.   (continued)

Project name	Taxonomic group	Hypothesis supported	Reference or contact
16. Long Ashton	beetles	yes	W. Powell, personal communication
17. Predator-prey interactions and fragmentation	insects	yes	Kareiva 1987
Edge effects influence ecosystem services			
1. Biological dynamics	nutrient cycling	yes	Bierregaard et al. 1992
6. Kamloops project	nutrient cycling	yes	Klenner & Huggard 1997
3. Kansas fragmentation study	nutrient pools	no	Robinson et al. 1992
Corridors enhance movement between fragments			
8. Colorado grassland	insects	yes	Collinge 1995
9. Boreal mixed-wood dynamics project	birds	no for Neotropical migrants	Schmiegelow et al. 1997
		yes for transient species	
10. Savannah river site corridor project	butterflies	yes for some; no for others	Haddad 1997
	small mammals	no	Danielson & Hubbard 2000
14. Vole behavior and fragmentation	small mammals	yes	Wolff et al. 1997
Connectivity between fragments increases species richness			
8. Colorado grassland	insects	yes	Collinge 1995
9. Boreal mixed-wood dynamics project	birds	no for Neotropical migrants	Schmiegelow et al. 1997
		yes for transient species	Schmiegelow et al. 1997

* Where multiple taxa were examined in a single study, there are multiple entries for the same experimental site.

among plants. In small patches, for instance, short-statured plant species could persist in edges and priority effects could permit local dominance not possible in a single large patch. Robinson et al. (1995 [2]) also examined invasibility by a native California poppy (*Eschscholzia californica*) in these same plots and found the species-rich plots more invasible. Contributing factors included a positive effect of small-mammal disturbance and a negative effect of *Bromus diadrus* coverage.

Invasion by species from the surrounding matrix could lead to a temporary increase in species richness within patches, at least if extinction rates are slow. If smaller fragments experience higher disturbance rates, this could shift competitive regimes such that in some situations species richness is enhanced. During the first 8 years of the Kansas [3] old-field experiment, patch size had little effect on successional replacement of major plant functional groups. Rather, the main influence of patch size was on the spatial autocorrelation of herbaceous community structure and on local persistence of some rare or clonal plant species (Robinson et al. 1992; Holt et al. 1995a, 1995b; Heisler 1998). In contrast, patch size had substantial effects on the colonization and growth rate of woody species (Yao et al. 1999).

DENSITY AND ABUNDANCE OF SPECIES

In several fragmentation experiments, population densities increased on the smaller fragments, perhaps be-

cause of the crowding effects of fragmentation. This was especially prevalent in small-mammal studies but was also observed in birds and insects. Barrett et al. (1995 [18]) found vole densities to be greater in a more fragmented landscape. In a review of patch-size effects on small-mammal communities, Bowers and Matter (1997 [13]) noted that inverse relations between density and patch size are frequently observed, particularly at the smaller patch sizes used in experimental landscape studies.

In some cases, the unexpected effect of fragmentation on density seems to reflect the ability of a focal species to utilize both the matrix habitat and the fragment. For instance, Foster and Gaines (1991 [3]) observed a high density of deer mice on small fragments and substantial numbers in the intervening matrix. They interpreted this pattern as simply a reflection of habitat generalization, but more recent work (Schweiger et al. 1999) suggests that a combination of habitat generalization and competitive release on small patches may explain this density relationship.

There appears to be a complex relationship between patch fragmentation and social structure that may underlie some of the inverse-density relationships. For instance, Collins and Barrett (1997 [18]) found that fragmented patches of grassland support greater densities of female voles than unfragmented sites. Aars et al. (1995 [20]) found differences in sex ratios among some litters of root voles and speculated that resource conditions (as affected by fragmentation) could lead to such biases.

Dooley and Bowers (1998 [13]) found weak fragment-size effects on the density and recruitment of *Microtus pennsylvanicus* in a grassland fragmentation experiment. They postulate that higher recruitment rates on fragmented patches result from diminished social costs and enhanced food resources on fragments. Andreassen et al. (1998 [15]) also found complex behavioral responses of voles to habitat fragmentation. Wolff et al. (1997 [14]) found that habitat loss did not decrease adult survival, reproductive rate, juvenile recruitment, or population size in the gray-tailed vole (*Microtus canicaudus*); surviving voles simply moved into remaining fragments. An influx of unrelated females into habitat fragments, however, resulted in decreased juvenile recruitment in those fragments.

Crowding effects have also been observed after fragmentation in bird and insect communities. Schmiegelow et al. (1997 [9]) noted that this crowding effect disappeared for birds after the second year of their study. Margules and Milkovits (1994 [4]) found that two millipede species experienced population explosions after treatment in both the remnants and the intervening cleared area, but they returned to pretreatment levels after 7 years. Collinge and Forman (1998 [8]) found crowding effects on fragments in an insect community but did not collect data long enough to test for a temporal effect.

CORRIDORS AND MOVEMENT/CONNECTIVITY

A few studies showed movement patterns contrary to what are generally expected to be the effects of habitat fragmentation, patch shape, and corridors. Barrett et al. (1995 [18]) showed that patch shape does not markedly affect dispersal or demographic variables of the meadow vole (*Microtus pennsylvanicus*). Andreassen et al. (1998 [15]) found that the rate of interfragment movements of small mammals actually increases with habitat fragmentation. Even more surprisingly, Danielson and Hubbard (2000 [10]) found that the presence of corridors reduces the probability that old-field mice (*Peromyscus polionotus*) will leave a patch in a forest fragment. In this same landscape Haddad (1997 [10]) found one butterfly species that does not respond to corridors. Schmiegelow et al. (1997 [9]) showed that Neotropical migrants declined in all fragmented areas, regardless of connectivity. As one might imagine, the use of corridors and the effect of fragmentation on movement patterns seems to be highly species-specific. These results suggest a need for further study of the potentially complex interactions between fragmentation and individual behavior.

Logistical Problems and Considerations

We concentrated on the fruits of experimentation in the study of habitat fragmentation. But our survey did reveal recurrent problems with such experiments, which future workers attempting to conduct fragmentation experiments need to be aware of and consider in designing their experiments. These considerations are important in that they define the likely scope of the applicability of results from fragmentation experiments.

Common problems in orchestrating fragmentation experiments mentioned to us by a number of investigators in our survey included the costs and difficulty of adequate replication of large patches, the struggle to maintain patches, and the problems of identification of specimens in many species-rich taxa. Patches carved out of preexisting vegetation are likely to be heterogeneous in many respects; careful thought must be given to overlaying fragmentation treatments on preexisting heterogenous landscapes, especially with a low degree of replication. In cases in which patch sizes are large, costs and other problems with establishing the largest patches often result in low replication. In any system operating within a fixed area, there is a necessary trade-off among interpatch distance, patch size, and replication. Because of such constraints, out of the full domain of potential landscape configurations, experiments are likely to focus on only a modest swath of parameter space (Holt & Bowers 1999).

Maintenance of the experimental area also can be expensive, time-consuming, and uncertain. Collaboration between government agencies and/or private landowners and researchers is often key to establishing and maintaining a landscape for experimental purposes. In highly productive habitat such as tropical rainforest, the rate of secondary succession can be so high that it is difficult to keep patches "isolated" (e.g., Bierregaard et al. 1992). If the surrounding sea of vegetation is not completely inhospitable, this could skew results in experiments testing for the effects of isolation.

In small experimental fragments, the effects of sampling can be problematic, especially if multiple investigators are collecting data on several taxonomic groups. For example, to sample small patches without trampling the vegetation, G. Robinson (personal communication [2]) had to build portable scaffolds over the patches. Finally, taxonomic problems were noted by many investigators working on plants and insects (Holt et al. 1995*a* [3]; S. Collinge, personal communication [8]; C. Margules, personal communication [4]). This mundane problem is important if species-rich groups tend to have stronger responses to fragmentation.

Discussion

There was a considerable lack of consistency in results across taxa and across experiments. The two most frequently tested hypotheses, that species richness increases with fragment area and that species abundance

or density increase with fragment area, showed entirely mixed results. Some of these discrepancies may be explained by differential relaxation times (Brown 1971) and rates of responses to fragmentation by different taxa. Most of the studies that fit initial theoretical expectations about the effects of fragmentation upon species richness involved arthropod assemblages. The species in these assemblages were typically small in body size (relative to the fragment sizes) and short in generation length (relative to the length of the fragmentation experiments). These assemblages might be expected to show responses over time scales commensurate with the time frame of typical field experiments. One of the more consistently supported hypotheses was that corridors supported connectivity between fragments. In four out of five cases, the presence of corridors enhanced movement for at least some of the species examined, and in two out of two examples the presence of corridors increased species richness in fragments.

Taxonomic groups that did not respond in the expected manner displayed a range of responses to fragmentation. Some examples include highly mobile taxa whose population-level responses may integrate over spatial domains much larger than that of a single fragment. At short time scales, behavioral responses by mobile organisms can generate idiosyncratic patterns. Crowding of individuals was commonly observed after fragmentation, followed by a relaxation in subsequent years. Other groups that responded differently than expected include long-lived species unlikely to show dramatic population responses in short-term experiments and taxa with generalized habitat requirements. Predicting fragmentation effects depends on a basic knowledge of the range of habitats that different taxa can utilize and on the factors limiting and regulating population abundance in unfragmented landscapes. The plethora of contradictory results for small mammals in fragmentation experiments seems to be caused by several factors, including habitat generalization, disparate responses among species to edges and corridors, and social interactions that may be modified by landscape changes.

Many of the "contrary" results we report may reflect the relatively short time span of the experiments. A number of studies used patches that lasted only one season or an annual cycle to examine changes in the behavior or demography of particular species. The advantage of this approach is that it permits a clearer evaluation of potential mechanisms underlying landscape effects. A disadvantage is that such experiments cannot evaluate the multiplicity of indirect feedbacks that occur in anthropogenically disturbed landscapes. Long-term experiments are vital because they reveal processes that are obscured at shorter time scales. The three long-term studies [1, 3, 4] each revealed strong phenomena that would have been missed in short-term investigations.

Some key findings of experimental habitat fragmentation studies might be difficult to achieve in purely obser-

vational studies, reflecting in part the value of good experimental controls and properly randomized designs. We do not imply that experimental fragmentation projects are more rigorous than observational studies. Experimental fragmentation studies often suffer from the intellectual costs of focusing on small spatial and temporal scales and the use of species that may not serve as good models for the effects of fragmentation on species of conservation concern. Although observational studies pay a price by lacking "controls," they nonetheless provide more realism with respect to landscape scale and species of concern. The value of having real controls, however, should not be underestimated; controls proved vital in interpreting results in many of these experiments (e.g., Robinson et al. 1995 [2]; Collins & Barrett 1997 [18]; Davies & Margules 1998 [4]; Laurance et al. 1998 [1]; Danielson & Hubbard 2000 [10]).

Future fragmentation studies should focus on understanding the mechanisms behind observed community- and population-level patterns. For example, a critical issue is how fragmentation affects dispersal and movement. Similarly, a better understanding of species interactions, such as plant-pollinator interactions or competition in fragmented landscapes, is essential. Analysis of the matrix habitat may be crucial for understanding the dynamics of remnant fragments. The most important determinant of which species are retained in isolated patches appears to be the interaction of patches with the surrounding habitat matrix (Bierregaard & Stouffer 1997 [1]; Tocher et al. 1997 [1]). There is a growing recognition that connection among habitats that differ in productivity and structure is often a crucial determinant of community dynamics (Holt 1996; Polis et al. 1997), and fragmentation experiments provide a natural forum for analyzing such dynamics. Finally, more analysis of how fragmentation influences genetic variation for both neutral alleles and traits related to fitness would be particularly valuable.

Choosing an appropriate landscape scale for the taxonomic group(s) of interest can have major implications for the findings of fragmentation studies. Communities are composed of species that experience the world on a vast range of spatial scales (Kareiva 1990; Holt 1993). In all the studies we reviewed, there were some mobile and/or large-bodied organisms for which the patches were small pieces of a fine-grained environment much smaller than a home range. Usually, however, some species will be present that experience the patches in a coarse-grained manner. An important challenge is to map out an intellectual protocol for applying these fine-scale experimental studies to scales that are more directly pertinent to conservation problems.

The studies described in our review provide a first step in understanding the effects of fragmentation. Our results, however, emphasize the wide range of species-specific responses and the potential for changing results

over time. Fragmentation effects cascade through the community, modifying interspecific interactions, providing predator or competitive release, altering social relationships and movements of individuals, exacerbating edge effects, modifying nutrient flows, and potentially even affecting the genetic composition of local populations. Perhaps it is not surprising then that fragmentation shows inconsistent effects across the experimental studies of fragmentation to date.

Acknowledgments

Note added in proof: Since this paper was written, we have become aware of an additional experimental study of fragmentation involving microinvertebrate species assemblages on moss patches on boulders. Gonzalez et al. showed strong effects of fragmentation on species diversity and population size (A. Gonzalez, J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045-2047.).

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