A Survey and Overview of Habitat Fragmentation Experiments

DIANE M. DEBINSKI* AND ROBERT D. HOLT†
*Department of Animal Ecology, 124 Science II, Iowa State University, Ames, IA 50011, U.S.A., email debinski@iastate.edu
†Natural History Museum and Center for Biodiversity Research, Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, U.S.A., email predator@kuhub.cc.ukans.edu

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 interspecíficas, 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-
gencias se incluyen los efectos de bordes, la liberación competitiva en los fragmentos de hábitat y la escala espacial 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 observó a menudo después de la fragmentación, seguido de un disminución de la abundancia en los años posteriores. 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-específicas, 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 conservation, it is not surprising that there exists a burgeoning literature based on observational studies of fragmented landscapes (e.g., Wilcove et al. 1986; Quinn & Harrison 1987; Gibbs & Faaborg 1990; Blake 1991; McCoy & Mushinsky 1994) and a substantial theoretical literature on the population and community effects of fragmentation (e.g., Fahrig & Paloheimo 1988; Doak et al. 1992; Nee & May 1992; Adler & Nuernberger 1994; Tilman 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 dealing 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 conducted worldwide in experimentally fragmented habitats. By our definition, an experiment involves a deliberate manipulation of the landscape, usually with an eye toward assessing a particular hypothesis. In many descriptive fragmentation studies, researchers cannot control attributes such as patch size, degree of replication, site initiation, and position on the landscape because they are investigating the effects of landscape manipulation (e.g., clearcutting in logging or plowing in agriculture) conducted by others. Thus, we excluded such studies from our review. We concentrated on terrestrial systems because of the major differences in the dynamics 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, Evolutionary Ecology, Forest Science, Heredity, Journal of Animal Ecology, Journal of Biogeography, Journal of Mammalogy, Landscape Ecology, Nature, Oecologia, Oikos, Theoretical Population Biology, and Trends in Ecology and Evolution) since 1984 using the keyword fragmentation. We also canvassed the ecological community using the Internet (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 experiment was maintained. We summarized the results in the form of a vote count tally of the number of times the hypothesis was supported. We believe that a more formal meta-analysis (e.g., Gurevitch & Hedges 1993) of these experiments 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 hypotheses: (1) species richness increases with area, (2) species abundance or density increases with area, (3) interspe-
Specific 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.

<table>
<thead>
<tr>
<th>Experiment no. and project name or biome</th>
<th>Patch habitat</th>
<th>Matrix habitat</th>
<th>Institutional affiliation</th>
<th>Time span</th>
<th>Fragment sizes (replication)</th>
<th>Preexisting matrix</th>
<th>Community focus</th>
<th>Reference or contact</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Biological dynamics tropical rainforest</td>
<td>clearcut</td>
<td>National Museum of History, Smithsonian Institution</td>
<td>1980–present (19 years)</td>
<td>1 ha (8), 10 ha (8), 100 ha (5), 200 ha (1), 1000 ha (3)</td>
<td>yes</td>
<td>yes</td>
<td>Bierregaard et al. 1992, Bierregaard &amp; Stouffer 1997</td>
<td></td>
</tr>
<tr>
<td>2. California grassland California annual grassland</td>
<td>mowed grass</td>
<td>University of California, Davis</td>
<td>1983–1987 (4 years)</td>
<td>2 m² (32), 8 m² (8), 52 m² (2)</td>
<td>yes</td>
<td>yes</td>
<td>Quinn &amp; Robinson 1987; Robinson et al. 1995</td>
<td></td>
</tr>
<tr>
<td>3. Kansas fragmentation study Kansas old field</td>
<td>mowed grass</td>
<td>University of Kansas</td>
<td>1983–present (16 years)</td>
<td>50 × 100 m (6), 12 × 24 m (18), 4 × 8 m (82)</td>
<td>no</td>
<td>yes</td>
<td>Holt et al. 1995a, 1995b; Robinson et al. 1992</td>
<td></td>
</tr>
<tr>
<td>4. Wog Wog study eucalypt forest pine plantation</td>
<td>CSIRO Division of Wildlife and Ecology</td>
<td>1985–present (14 years)</td>
<td>0.25 ha (6), 0.875 ha (6), 3.062 ha (6)</td>
<td>yes</td>
<td>yes</td>
<td>Margules 1992; Margules 1996</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Groenveld experiment South African grassland</td>
<td>pine plantation</td>
<td>University of Pretoria, South Africa</td>
<td>1994–1997 (5 years)</td>
<td>0.25 ha (6), 0.875 ha (6), 3.062 ha (6)</td>
<td>yes</td>
<td>yes</td>
<td>Jaarsveld, personal communication</td>
<td></td>
</tr>
<tr>
<td>6. Kamloops project Canadian subalpine forest clearcut</td>
<td>British Columbia Ministry of Forests</td>
<td>1995–present (3 years)</td>
<td>0.1 ha (160), 1 ha (27), 10 ha (3)</td>
<td>yes</td>
<td>yes</td>
<td>Vyse 1997; Klenner &amp; Huggard 1997</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Missouri Ozark forest ecosystem project Missouri Ozark hardwood forest</td>
<td>clearcut</td>
<td>Missouri Department of Conservation, University of Missouri</td>
<td>1990–present (9 years)</td>
<td>300 ha (2), 800 ha (1)</td>
<td>yes</td>
<td>yes</td>
<td>Kurzejski et al. 1993</td>
<td></td>
</tr>
<tr>
<td>8. Colorado grassland Colorado short grass prairie</td>
<td>mowed grass</td>
<td>University of Colorado</td>
<td>1992–1994 (2 years)</td>
<td>1 m² (18), 10 m² (18), 100 m² (18)</td>
<td>yes</td>
<td>yes</td>
<td>Collinge 1995</td>
<td></td>
</tr>
<tr>
<td>9. Boreal mixed-wood dynamics project Canadian boreal mixed-woods</td>
<td>clearcut</td>
<td>University of British Columbia, University of Alberta, Edmonton</td>
<td>1993–present (6 years)</td>
<td>1, 10, 40, 100 ha (3 each)</td>
<td>yes</td>
<td>yes</td>
<td>Schmiegelow &amp; Hannon 1993; Schmiegelow et al. 1997</td>
<td></td>
</tr>
<tr>
<td>10. Savannah River Site corridor project clearcut</td>
<td>pine forest</td>
<td>University of Georgia, Iowa State University, U.S. Forest Service</td>
<td>1994–present (5 years)</td>
<td>128 × 128 m (27) with differing corridor lengths</td>
<td>yes</td>
<td>yes</td>
<td>Haddad 1997; Danielson and Hubbard (2000)</td>
<td></td>
</tr>
<tr>
<td>11. Miami University fragmentation project Ohio old field</td>
<td>mowed grass</td>
<td>Miami University</td>
<td>1995–present (5 years)</td>
<td>2 × 2 m (36), 9 × 9 m (36), 15 × 15 m (36)</td>
<td>yes</td>
<td>yes</td>
<td>Crist &amp; Golden, personal communication</td>
<td></td>
</tr>
<tr>
<td>12. German fragmentation study Bavarian clover patches crop fields and meadows</td>
<td>Gottingen University</td>
<td>1992–present (7 years)</td>
<td>1.2 m² (18) with separation varying</td>
<td>yes</td>
<td>yes</td>
<td>Krueez &amp; Tschamtke 1994</td>
<td></td>
<td></td>
</tr>
<tr>
<td>13. Blandy farm fragmentation study Virginia old field</td>
<td>mowed grass</td>
<td>University of Virginia</td>
<td>1990–present (9 years)</td>
<td>1 ha (4), 0.25 ha (4), 0.63 ha (4)</td>
<td>no</td>
<td>no</td>
<td>Bowers &amp; Dooley 1995</td>
<td></td>
</tr>
<tr>
<td>14. Vole behavior and fragmentation alfalfa patches</td>
<td>mowed grass</td>
<td>Oregon State University</td>
<td>1994 (ongoing 4-month experiments)</td>
<td>25 × 25 m (4), 12.5 × 12.5 m (32), 5 × 5 m (100)</td>
<td>no</td>
<td>no</td>
<td>Wolff et al. 1997</td>
<td></td>
</tr>
<tr>
<td>15. Evensted research station Norwegian meadows</td>
<td>mowed grass</td>
<td>University of Oslo, Norwegian Forest Research Institute, Agricultural University of Norway</td>
<td>1982–1989 (6 years)</td>
<td>15 × 20 m (4), 15 × 45 m (4), 0.5 ha (2)</td>
<td>no</td>
<td>no</td>
<td>Ims et al. 1993</td>
<td></td>
</tr>
</tbody>
</table>

continued
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 & Palohéimo 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-
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 temperature (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.

---

**Figure 1. Frequency distribution of fragmentation studies relative to plot size.**

![Diagram showing frequency distribution of fragmentation studies relative to plot size.](image)
(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 invisibility for successional tree species in the Biological Dynamics Project [1] (Benítez-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*, *Phoebris sennae*, and *Lupitoleta 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*). Kruesz 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. (1995a,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 canicau- dius*) movements considerably. Ims et al. (1995 [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 (Laurence & 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 flower-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.\(^{a}\)

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

\(^{a}\) Continued
among plants. In small patches, for instance, short-stat-tered plant species could persist in edges and priority ef-
ficts could permit local dominance not possible in a sin-
gle 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 nega-
tive 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 herba-
ceous 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 densi-
ties 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 frag-
mented 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 compet-
titive release on small patches may explain this density
relationship.

There appears to be a complex relationship between
patch fragmentation and social structure that may under-
lie some of the inverse-density relationships. For in-
stance, Collins and Barrett (1997 [18]) found that frag-
mented 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.

### Table 2. (continued)

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

* Where multiple taxa were examined in a single study, there are multiple entries for the same experimental site.*
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 canicau dus); 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 heterogeneous 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. 1995a [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 observational 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]; Laurence 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, exacerbat- ing 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

We thank all those investigators who provided insights into their experiences with fragmentation studies. This manuscript benefited from the comments of G. Belovsky and two anonymous reviewers. The research was sup- ported by grant 93-08065 from the Long-Term Research in Environmental Biology program of the National Science Foundation. This is journal paper J-17802 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa (project 3377).

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. Meta-population dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047).

Literature Cited


Schweiger, E. W., J. E. Diffendorfer, R. Pierotti, and R. D. Holt. 1999. The relative importance of small scale and landscape-level hetero-


