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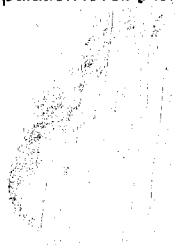

A study of habitat fragmentation in a successional field at the University of Kansas's Nelson Environmental Study Area has monitored population, community, and ecosystem responses to fragmentation since 1984. The different sizes of the patches in the field were used to investigate the effect of different levels of fragmentation. See page 524. Negligible ecosystem and aggregate community responses may mask profound effects of fragmentation at the population level. [Aerial infrared photo: James E. Busse]

Diverse and Contrasting Effects of Habitat Fragmentation

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Different components of an ecosystem can respond in very different ways to habitat fragmentation. An archipelago of patches, representing different levels of fragmentation, was arrayed within a successional field and studied over a period of 6 years. Ecosystem processes (soil mineralization and plant succession) did not vary with the degree of subdivision, nor did most measures of plant and animal community diversity. However, fragmentation affected vertebrate population dynamics and distributional patterns as well as the population persistence of clonal plant species. The results highlight the dangers of relying on broad community measures in lieu of detailed population analyses in studies of fragmented habitats.

It is becoming increasingly necessary to understand the consequences of the destruction and fragmentation of natural habitats (*1*). Habitat fragmentation can influence the entire suite of processes studied by ecologists, from individual behavior through population dynamics to ecosystem fluxes (*2*). However, experimental research has largely focused on single levels of ecological organization (*3*). We report on the first 6 years of results from an experimental model system (*4*) in which we examined the population, community, and ecosystem effects of habitat fragmentation.

In the fall of 1984 we created an array of patches of three sizes in an agricultural field (Fig. 1). The interstitial area separating the patches has been maintained at a low turf by regular mowing, and the patches themselves have undergone secondary succession without further disturbance. The small and medium patches are arrayed in clusters that (within the constraints of our field) spanned the same area as a large patch (50 by 100 m). Comparing samples from large patches to samples from clusters of successively smaller patches, we can examine two levels of fragmentation (at a 0.5-ha level of resolution). Our initial hypothesis was that fragmentation would conspicuously alter a range of ecological variables, including abiotic soil resources, local species richness, and population dynamics, and that these effects would be most prevalent in the most fragmented treatment.

However, the degree of habitat fragmentation had no effect on ecosystem and community measures such as soil properties, rates of plant succession, and local community diversity at several trophic levels. For example, monthly soil moisture readings averaged approximately 20% (by weight) in all treatments; pools of available ammonium were similar across patch sizes (from 1.9 ± 0.2 to 1.7 ± 0.15 mg/kg in small and large patches, respectively), and rates of in situ total nitrogen mineralization were also similar (from 2.2 ± 0.4 to 2.4 ± 0.5 mg/kg in small and large patches, respectively) (*5*). Over time, a substantial difference developed between the plant communities in the mowed turf and those in the successional patches. However, patch size did not affect the overall course of plant succession within patches (*6*). For example, the average percentage cover of perennial plants increased from 18 to 71% in small patches and from 17 to 70% in large patches. Local species diversity was also independent of patch size. For vascular plants (*7*) and foliar arthropods (*8*), an average large patch contained no more species than an average cluster of medium or small patches (about 38 plant species and 72 arthropod species per census). In addition, species evenness, an index of average relative species abundance (*9*), was similar among fragmentation treatments for plants (from 0.44 in combined small patches to 0.45 in combined large patches) and arthropods (from 0.30 in combined small patches to 0.34 in combined large patches). Finally, the five small mammal species (*10*) were captured in every patch type, as were the six snake species that were captured more than once (*11*).

Using aggregate, whole-community measures such as species richness, one might conclude that the plant and animal communities were insensitive to the degree of fragmentation imposed in our design. This interpretation would belie the effects that we observed at the level of individual species and populations. Of the 206 vascular plant species found over the period of 6 years, 40 occurred in only one patch type. The cumulative proportion of these unique species varied significantly with the level of fragmentation: 10/146 in small patches, 7/130 in medium patches, and 20/164 in large patches ($G_{2df} = 7.13$, $P < 0.03$). Results for foliar arthropods (461 total species) were more pronounced. Cumulative species counts, as well as proportions unique to each patch size, were higher in the least fragmented treatment: 78/367 in large patches versus 42/315 in small patches and 39/303 in medium patches ($G_{2df} = 7.88$, $P <$

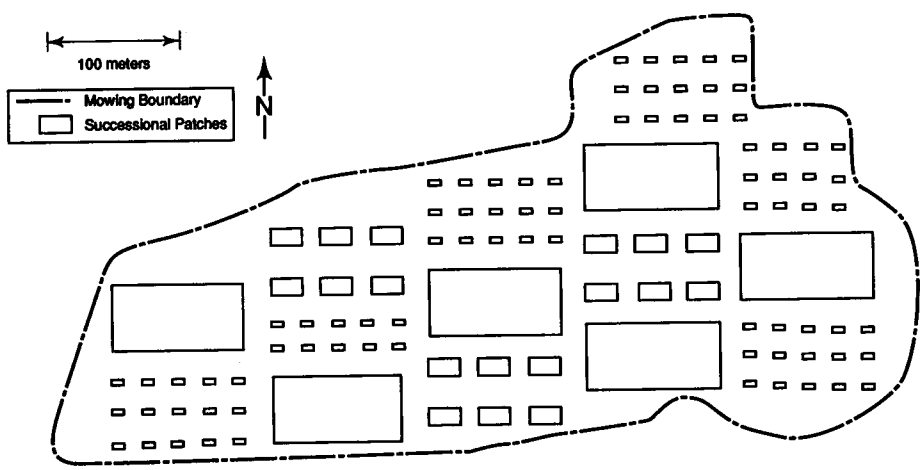

Fig. 1. Diagram of the experimental design (*16*). The three replicated treatments are single large (50 by 100 m) patches and clusters of six medium (12 × 24 m) or 15 small (4 × 8 m) patches. The amount of intact habitat per 0.5 ha is decreased by roughly one-third with each decrease in patch size; a minimum distance of 15 m was retained between patches. The choice of patch dimensions and distances represents a compromise between field dimensions and expected minimum habitable areas for small mammals.

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0.02). For vertebrates, we observed particularly strong effects of patch size on population densities. For the three most abundant small mammal species, there was a rank-order relation between body size and the patch size at which density peaked (Fig. 2A). For snakes, the rate of total captures per trap increased with patch size (Fig. 2B).

Population effects were evident at even small spatial scales. Our sequential census data were sufficiently detailed to allow us to test for relations between patch size and the persistence of local populations or individuals. We separated vascular plants into two broad functional groups: clonal species, which reproduce largely by vegetative growth over short spatial scales, and nonclonal species, which reproduce only by seeds dispersed more broadly. Over a period of 5 years, persistence of nonclonal plants did not vary systematically with patch size, whereas clonal plant populations were much less likely to persist in the smallest patch size (Fig. 3A). Although unexpected, this result is consistent with theoretical studies of internal spatial dynamics on islands (*12*). Over time, clonal plants resemble amoebae moving across the landscape and are at greater risk in highly fragmented habitats because fragmentation reduces the opportunity for re-invasion by vegetative growth. Among small mammals, individual persistence of the two larger bodied species increased with patch size (Fig. 3B), and the age structure on small patches was biased toward nonreproductive subadults (*13*). By contrast, the smallest species persisted equally well in all patch sizes, and their age structure on large patches was biased toward subadults. The data on persistence and age structure suggest a hypothesis to explain the observed density distribution patterns (Fig. 2A): Individual spatial requirements of the two larger bodied species lower their abundances on small patches; interspecific competition from larger species reduces the abundance of smaller, subordinate species on larger patches; all species are found in all habitats because subordinate individuals are forced out of their respective optimal habitats. That is, the small mammal distribution pattern reflects a source-sink population structure (*14*).

Our results show that different components of an ecosystem can respond in different ways to habitat fragmentation and that the effects seen among populations can be hidden at the level of aggregated community variables. Certain ecosystem and community variables, such as the overall rates of replacement of annual plants by perennials or the local species richness, were not affected by habitat fragmentation. Understanding the consequences of habitat fragmentation requires documenting the system attributes that do not change as well as those that do.

Most studies of fragmented landscapes concentrate on the long-term, gradual loss of species after habitat subdivision (*15*), whereas we have documented the effect of fragmentation on community development during secondary succession. The species losses and gains that occur during the normal course of succession may obscure patch size effects that are likely to be more apparent in systems near dynamic equilibrium. We would hesitate to extrapolate from our experimental model system to all spatial and temporal scales. Nevertheless, this study revealed effects of habitat fragmentation at the population level that were missed at higher levels of ecological organization. Two novel findings are the partial segregation of small mammal species according to body size and the subtle role of clonal versus nonclonal reproduction in determining the sensitivity of local plant populations to patch size. Our experimental results highlight the need for detailed population analyses to interpret observational data from fragmented habitats.

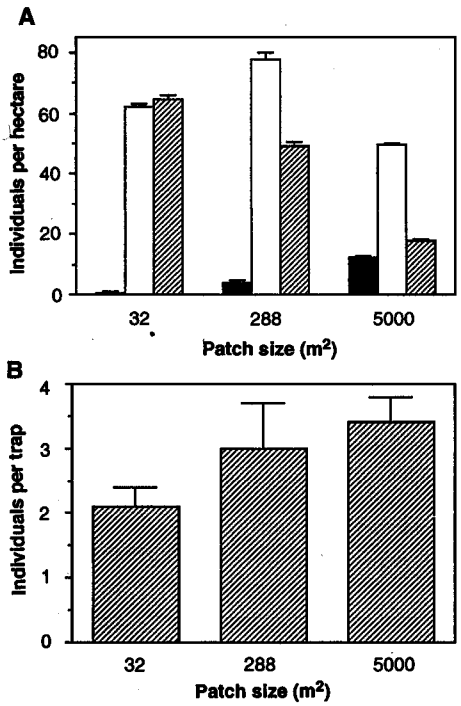

Fig. 2. (**A**) Mean population densities (*17*) for the three common small mammal species in order of average adult body mass, grouped by patch size. *Sigmodon hispidus* (black bars, 135 g), *Microtus ochrogaster* (white bars, 43 g), and *Peromyscus maniculatus* (ruled bars, 22 g). Densities are estimates from 67 semimonthly censuses, from the winter of 1987 to the spring of 1990. Animals were captured in Sherman live traps set in a 7-m grid superimposed on two replicates of each fragmentation treatment. Further details of methods are reported elsewhere (*18*). ANOVA tests indicated that mean densities vary significantly with patch size for all three species. (**B**) Density of snakes, expressed as the cumulative mean of captures (all species included) per trap, grouped by patch size. Traps (44 total) were artificial shelters (0.6 by 1.2 m), monitored at 6-day intervals, from the spring of 1987 through the fall of 1989. Regression slope (±95% confidence interval) of counts per trap on patch size is positive and significant [$y = (0.25 \pm 0.21) \log x + 1.24$]. Error bars in (A) and (B) represent single standard errors.

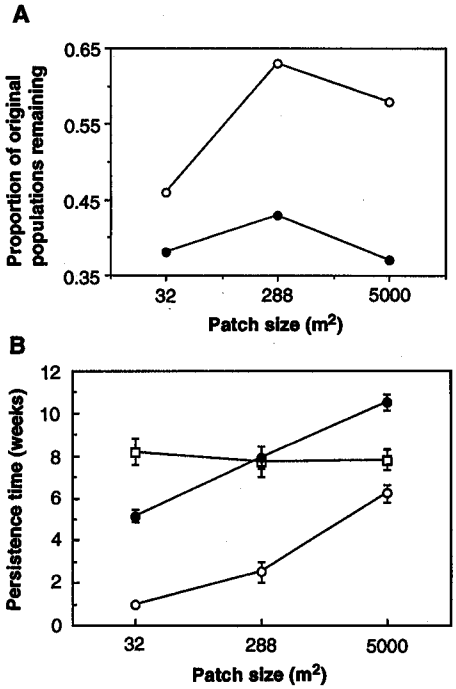

Fig. 3. (**A**) Proportion of local plant populations persisting over 6 years, grouped by patch size. A local population was considered persistent if a given species was observed during the first and last year in the same permanent sampling quadrat. Persistence of clonal plant populations (open circles, $n = 1659$) was significantly lower in small patches ($G_{2df} = 30.65$, $P < 0.0001$), but the persistence of nonclonal populations (closed circles, $n = 3482$), although lower overall, did not vary significantly with patch size. (**B**) Mean individual persistence times for three species of small mammals, grouped by patch size. Persistence time was the duration (in weeks) between the first and last periods trapped, plus one. Regression slopes (with 95% confidence intervals) of persistence time on the logarithm of patch size are positive and significant for *S. hispidus* (open circles) [$y = (1.16 \pm 0.67) \log x - 3.71$; $R^2 = 0.03$; $n = 1425$] and *M. ochrogaster* (filled circles) [$y = (1.03 \pm 0.25) \log x + 1.76$; $R^2 = 0.04$; $n = 375$], but not for *P. maniculatus* (open squares) [$y = -(0.08 \pm 0.33) \log x + 8.39$; $n = 751$]. Error bars represent single standard errors.

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4. We attribute the term "experimental model system" to J. A. Wiens and B. T. Milne, *Landscape Ecol.* **3**, 87 (1989); R. A. Ims and N. C. Stenseth, *Nature* **342**, 21 (1989).
5. We collected 20-cm-deep soil cores every 28 days, from the spring of 1988 through the summer of 1989. Cores were taken in pairs from each of three sites in large, medium, and small patches as well as in the mowed area between patches. We homogenized and separated each core into three parts and immediately analyzed one of these for H_2O, nitrate, and ammonium concentrations by running the sample with 2 M KCl extracts through an autoanalyzer and using cadmium reduction and indophenol methods. The remaining portions were incubated in sealed polybags in their original field locations or in open cups in an optimal (20°C at field water capacity) environment according to established protocols [J. Pastor, J. D. Aber, C. A. McClaugherty, J. M. Melillo, *Ecology* **65**, 256 (1984); P. M. Vitousek and P. A. Matson, *ibid.* **66**, 1360 (1985)]. After 1 month, the incubated samples were reexamined for changes in inorganic nitrogen concentrations. Differences in the cumulative values among fragmentation treatments were insignificant as measured by analysis of variance (ANOVA) tests.
6. R. D. Holt, G. R. Robinson, M. S. Gaines, in preparation. At each census, the principal dominant species occurred at similar densities in patches of all sizes.
7. Plant data are from 13 censuses, from the fall of 1984 through the fall of 1989. All plants were identified, and the percent cover was measured by means of a modified point-frame method [D. W. Goodall, *Aust. J. Sci. Res. Ser. B* **5**, 1 (1952)] in permanently positioned 1-m^2 quadrats. Thirty quadrats were sampled in each large patch, four in each medium patch, and two in each small patch. Patch size differences in cumulative species counts were not significant as measured by ANOVA tests.
8. Foliar arthropods were sampled in 30 censuses, from the summer of 1985 through the winter of 1987. At each census, sweep nets were used to sample 600 m of linear transects inside patches of each size. As with the plant data, cumulative species counts did not vary significantly with patch size as measured by ANOVA tests.
9. Species evenness was calculated as

$$[(1/\Sigma p_i^2) - 1] \div [(e^{-\Sigma p_i \log p_i}) - 1]$$

where p_i is the proportional representation (relative percent cover of plants or number of individuals for arthropods) of each species. Higher values indicate more even representation of multiple species; lower values indicate dominance by fewer species [R. V. Alatalo, *Oikos* **37**, 199 (1981)].
10. Mammal species censused (total captures in parentheses) were the prairie vole, *Microtus ochrogaster* (6391); deer mouse, *Peromyscus maniculatus* (2385); cotton rat, *Sigmodon hispidus* (945); white-footed mouse, *Peromyscus leucopus* (185); and western harvest mouse, *Reithrodontomys megalotis* (46).
11. Snake species censused (total captures in parentheses) were the western yellow-bellied racer, *Coluber constrictor flaviventris* (65); osage copperhead, *Agkistrodon contortix phaeogaster* (18); red-sided garter snake, *Thamnophis sirtalis parietalis* (16); black rat snake, *Elaphe obsoleta obsoleta* (12); prairie ringneck snake, *Diadophis punctatus arnyi* (6); red milk snake, *Lampropeltis triangulum syspila* (5); timber rattlesnake, *Crotalus horridus* (1); and lined snake, *Tropidoclonium lineatum* (1).
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15. J. M. Diamond, in *Extinctions*, M. H. Nitecki, Ed. (Univ. of Chicago Press, Chicago, 1984), pp. 191–246; B. D. Patterson and W. Atmar, *Biol. J. Linn. Soc.* **28**, 65 (1986); C. R. Dickman, *J. Appl. Ecol.* **24**, 337 (1987); D. T. Bolger, A. C. Alberts, M. E. Soulé, *Am. Nat.* **137**, 155 (1991).
16. The 12-ha field is a section of the Nelson Environmental Study Area of the University of Kansas, in Leavenworth County (39°N, 94°W) [H. S. Fitch and W. D. Kettle, *Trans. Kans. Acad. Sci.* **9**, 30 (1988)]. The site had been in a wheat-soybean rotation before the initiation of the experiment. The patch array was created immediately after a final winter wheat harvest. Natural vegetation of the region is a mosaic of open prairie, successional woodlands, and mature deciduous forest [A. W. Kuchler, *Ecology* **55**, 586 (1974)]. In the absence of fire, abandoned farmland in this region typically undergoes successive invasions of annual herbs, perennial herbs, and woody species [S. T. A. Pickett, *Vegetatio* **49**, 15 (1982); F. A. Bazzaz, in *Perspectives on Plant Competition*, J. B. Grace and D. Tilman, Eds. (Academic Press, New York, 1990), pp. 239–263].
17. Density estimates are minimum number known alive [C. J. Krebs, *Ecological Methodology* (Harper and Row, New York, 1989)]. Estimates of mammal densities in small patches were reduced by 45% to compensate for differences in sampling effort per unit area.
18. J. Foster and M. S. Gaines, *Ecology* **72**, 1358 (1991).
19. We thank K. Armitage, J. Hamrick, B. Johanning, D. Kettle, and G. Pittman for assisting in the implementation of the experiment. Field and other assistance was provided by R. Albano, L. Andrews, A. Busby, J. Danoff-Burg, J. Diffendorfer, J. Foster, K. Kindscher, A. Kovach, A. McMillen, K. O'Brien, K. Parker, J. Pascarella, S. Reyes, J. Roth, W. Sera, T. Shistar, E. Teravainen, and J. Volestcy. We thank S. Handel, J. F. Quinn, and three anonymous reviewers for comments on the manuscript. Support was provided by the National Science Foundation (grant BSR-8718088 to R.D.H., M.S.G., and S.P.H.), the University of Kansas General Research Fund, the Nelson Environmental Study Area, the Kansas Museum of Natural History, and the Bureau of Biological Research, Rutgers University.

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