10 Perspectives from an Experimental Study of Habitat Fragmentation in an Agroecosystem

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10.1 INTRODUCTION AND CONCEPTUAL BACKGROUND

From the perspective of an entire landscape, agroecosystems are patches of a particular habitat type created or modified by humans, embedded within a spatially complex patchwork of many distinct habitat patches—some anthropogenic, and some natural. Because organisms disperse and materials are physically transported, ecological phenomena at any given site will usually reflect processes occurring over a broader array of sites (though to differing degrees for different populations or phenomena (Holt, 1993; Holt & Gaines, 1993). In particular, understanding and mitigating the effects of mobile pests such as insects, rodents, and fungal blights in a given arable ecosystem will often require a consideration of the spatial dimension of population and community dynamics in complex landscapes.

Current ecological theory emphasizes spatial processes and scaling as central themes for basic research (Ricklefs, 1987; Kareiva & Anderson, 1988; Roughgarden et al., 1991; Levin, 1992). Understanding the spatial attributes of natural communities is of particular relevance in the applied science of conservation biology, because the preservation of endangered species often requires the analysis of spatial dynamics in fragmented landscapes. Unfortunately, an increasingly pervasive effect of humans on the earth is the destruction and fragmentation of natural habitats. Habitat fragmentation potentially influences all the processes studied by ecologists, at levels of organization from the individual to the ecosystem (Saunders et al., 1991).

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Ameliorating the effects of habitat fragmentation will require an enhanced understanding of the role of spatial processes in population and community dynamics, given that a primary effect of fragmentation is to disrupt or modify spatial fluxes of individuals, materials, and energy (Wiens, 1989; Lord & Norton, 1992). To achieve such understanding will require a melding of observational, theoretical, and experimental approaches.

A burgeoning body of observational (e.g. Dickman, 1987; Quinn & Harrison, 1987; Gibbs & Faaborg, 1990; Blake, 1991) and theoretical (e.g. Wilcove *et al.*, 1986; Fahrig & Paloheimo, 1988; Temple & Cary, 1988) analyses of habitat fragmentation now exists. However, for obvious logistical reasons, experimental studies of habitat fragmentation are still rather scarce. Examples include annual grassland in California (Robinson & Quinn, 1988), Amazonian forest fragments (Lovejoy *et al.*, 1984), Norwegian meadows (Ims *et al.*, 1993), Australian eucalyptus woodland (C. Margules, personal communication), and English arable ecosystems (W. Powell *et al.*, personal communication; see also Chapter 10). This chapter presents the principal findings to date for one such experiment in a successional ecosystem in eastern Kansas.

It is useful to consider briefly some general aspects of experimental studies of habitat fragmentation. Different species are likely to respond to fragmentation over different time-scales (e.g. Holt, 1992), and some critical effects may not be evident in short-term studies. Longer-term studies than are typical in ecological research are, thus, needed to analyse the consequences of fragmentation. Moreover, an experimentally fragmented landscape is automatically a 'whole-system' experiment (Schindler, 1991), in which a suite of simultaneous system responses is to be expected. Effects of fragmentation at one organizational level (e.g. plant community dynamics) may be driven, magnified, or dampened by shifts at another (e.g. herbivores and their own natural enemies), and the net effect of fragmentation may reflect the interplay of direct and indirect interactions among numerous system components. Only through long-term studies can we understand the potential, cumulative magnitude of indirect feedbacks in communities and ecosystems (Pickett, 1991), including those filtered through the constraints of habitat fragmentation.

10.2   AN EXPERIMENTALLY FRAGMENTED LANDSCAPE

For the past 9 years, researchers at the University of Kansas have been examining population and community dynamics in an experimentally created archipelago of patches undergoing secondary succession (Figure 10.1), surrounded by a 'sea' of low turf maintained by regular mowing (Robinson *et al.*, 1992). The natural, pre-settlement landscape was a mixture of woodland and prairie; eastern Kansas is a transitional ecotone between the eastern deciduous biome and the tall-grass prairie biome (Fitch, 1965).
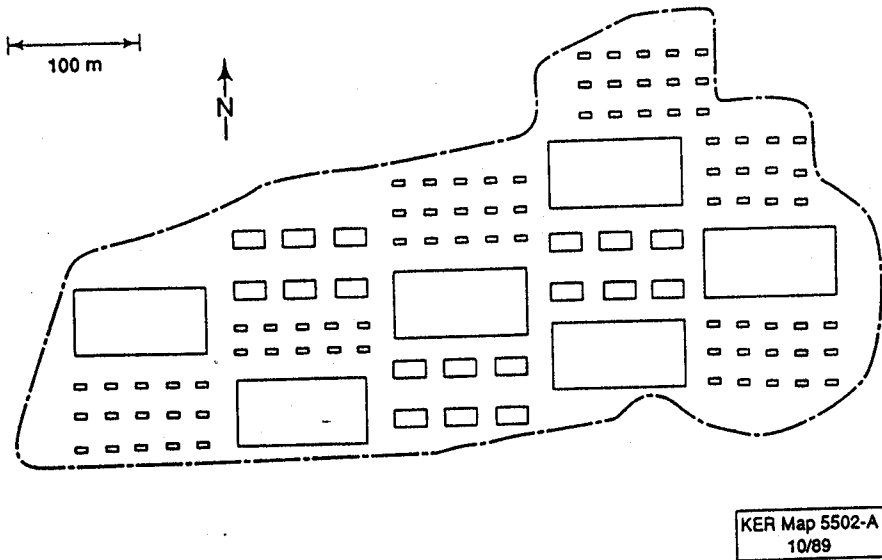
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Figure 10.1. Map of the Kansas Biotic Succession Facility, University of Kansas, on the Nelson Environmental Study Area of the Kansas Ecological Reserves. The experimental design includes three treatments: large (50 × 100 m) patches and clusters of six medium (12 × 24 m) patches or fifteen 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 landscape to the south is predominantly woodland; the landscape to the north is predominantly open fields, abutting an experimental pond facility. Mowing boundary — ·; successional patches □

This study was originally set up to test a conceptual model about how the rate and pattern of secondary succession might be influenced by the spatial scale and context of the community undergoing succession (Holt & Gaines, 1993). In particular, it was reasoned that if long-distance colonization was important in the early stages of succession, then succession might be accelerated on larger patches (e.g. because they experience higher initial colonization rates, or lower rates of extinction, post-colonization).

Successional dynamics may be substantially modified by herbivores (Louda et al., 1990; Huntly, 1991; Bowers, 1993), so it is sensible to examine the interlinked responses of multiple trophic levels during succession. Because the degree of herbivory might be expected to vary with patch size, patch size effects observed in the plant community might be indirectly due to spatially variable impacts of herbivores.

Irrespective of interest in the potential effect of patch size on the rate of succession, early and mid-successional systems have many pragmatic advantages as experimental model systems (Wiens & Milne, 1989) for the study of

the ecological consequences of habitat fragmentation: (1) there are few ethical quandries in creating fragments of agricultural fields, compared to experimental fragmentation of pristine forests or virgin prairies; (2) the size of individual organisms is typically small, and their generations relatively short, compared with late succession. This makes it logistically feasible to design studies with reasonable spatial replication and time horizons (decades versus centuries).

10.3 STUDY SITE

The study site is a 12 ha field on the University of Kansas' Nelson Environmental Study Area (NESA), 16 km north-east of Lawrence, Kansas. It is a small part of a larger tract of land owned and protected by the University. The archipelago of habitat islands shown in Figure 10.1 was created from an agricultural field in the autumn of 1984 and has been maintained ever since by intensive mowing of the interstitial areas between patches. Secondary succession within the patches has been allowed to proceed unhindered.

Choices of patch sizes, of separations, and of spatial arrangement were guided by: (1) a knowledge of the dispersal biology of plants and small mammals; (2) a consideration of local landscape patterns; and (3) pragmatic concerns (e.g. size of available experimental field). The largest patches (0.5 ha) are comparable with standard-sized enclosures in experimental studies of small mammal dynamics (e.g. Johnson & Gaines, 1987). The smallest patch size (0.0032 ha) can potentially harbour many hundred individuals of herbaceous species and five to 20 or more stems of woody species (at least in the sapling phase). The minimum distance between patches was determined from prior data on plant and small mammal dispersal (e.g. Gaines *et al.*, 1979); the interstitial habitat created by mowing constitutes a dispersal barrier for many organisms (Foster & Gaines, 1991; Gaines *et al.*, 1994). Small and medium patches were clustered so that the total area spanned by a cluster perimeter equalled the area of a large patch (with two exceptions imposed by the irregular shape of the field). This design permitted the comparison of grids of sampling units (e.g. quadrats or traps) in large patches with comparably spaced sample grids in clusters of small or medium patches. In effect, the system compares large contiguous patches with clusters of smaller patches in two size classes, representing two levels of habitat fragmentation.

The institutional objective of the Kansas fragmentation experiment is to provide a forum for multiple investigators to pursue their own research interests in a manner that is intellectually mutually reinforcing and focused on a significant long-term ecological problem—the interplay of successional dynamics and fragmentation—that is difficult for any single investigator to address alone. The authors hereby invite investigators from other institutions with complementary interests to work with them.

Reflecting the research expertise in the group, plant (Robinson *et al.*, 1992; Holt *et al.*, unpublished data) and small mammal (Foster & Gaines, 1991; Gaines *et al.*, 1992a,b, 1994) community dynamics have been monitored in detail. Also, data are available for some to many years on soil water and nitrogen, on arthropod species richness, on snake and butterfly abundance, and on breeding bird utilization patterns (Robinson *et al.*, 1992; Teravainen, in press; Roth, 1991, and unpublished data; Fitch, unpublished data; Martinko, unpublished data). With respect to consumers, the most detailed data set to date is for the rodent community (Foster & Gaines, 1991; Gaines *et al.*, 1992a,b, 1994). A survey of the arthropod community has been conducted from 1985 to the present by E. Martinko and S. Reyes. This past summer, a more detailed study on the distribution of butterflies in the fragmented field was initiated by D. Debinski. In this chapter, the authors briefly review their results to date for most of these functional groups, emphasizing new and unpublished findings. In this chapter, a broad picture of results is painted, but for those aspects which have already published (plant and small mammal communities) the reader is referred to other papers for more details about methods (e.g. Foster & Gaines, 1991; Robinson *et al.*, 1992). The authors' general procedures are merely sketched below, although somewhat more details are provided for their recent woody plant and butterfly work.

10.4   SUMMARY OF RESULTS TO DATE

10.4.1   PLANT RESOURCES

To ascertain how fragmentation influences the abiotic environment, soil nitrogen and water relationships have been documented. During 1989–90, nitrogen pool sizes and mineralization rates were measured in soil samples taken from patches of each size and from the mowed, interstitial area, using laboratory and *in situ* incubations. Large significant differences were found between the successional patches and the mowed interstitial areas. The mineralization potential tended to be higher in smaller patches, but, in general, among-patch differences were statistically non-significant and small relative to the magnitude of overall temporal variation (Robinson *et al.*, 1992). In 1990–91, water availability was assessed in a sampling grid of permanently implanted probes using time-domain-reflectometry (TDR) (Herkelrath *et al.*, 1991). Slight differences among patch sizes were observed, but these were insignificant relative to background variation. This technique was calibrated in a parallel study initiated at the Konza Prairie near Manhattan, Kansas. Measurements along known moisture gradients in this virgin prairie verified the suitability of the TDR technique for documenting spatial variation in water availability and highlighted the relatively small differences in

water availability observed among patch sizes in the reported fragmentation
project (Knapp *et al.*, 1993; S. Hamburg, personal communication). The
conclusion from this work is that physical differences among patches differ-
ent in size were unlikely to account for any observed differences in commu-
nity or population dynamics.

10.4.2 PLANT DYNAMICS

Here, the overall long-term objective is to elucidate the effect of fragmenta-
tion on plant community composition, on population persistence and spatial
patterning, and on plant architecture. The principal sampling units are per-
manent 1 m^2 quadrats, positioned at regular intervals within each patch and
patch cluster (a total of 416 quadrats). In each sampling period, all species
present are recorded and percentage cover estimated using a modified point-
intercept quadrat method.

10.4.2.1 Patch size and succession

Old-field succession in the authors' system has followed patterns common
throughout central North America in fire-free habitats (e.g. Bazzaz, 1968).
Substantial changes in species' relative abundances occurred in the first 3
years, but the rate of change in the plant community slowed thereafter as
perennial forbs began to replace annuals (Foster & Gaines, 1991; Holt &
Gaines, 1993).

The authors initially hypothesized that the rate of succession would be
slower on smaller patches, but after 7 years of secondary succession there
was no strong patch-size effect on the rate of succession or on local species
richness (Foster & Gaines, 1991; Robinson *et al.*, 1992). Standard ordination
techniques (reciprocal averaging, canonical correlation analysis) did not gen-
erate aggregate axes clearly separating the communities on different-sized
patches. In contrast, the same data analysis techniques revealed that sub-
stantial differences had developed between the mowed interstitial turf and
the patches undergoing succession (G. Robinson, unpublished results).
Moreover, although the system of patches does show the usual species–area
relationship, so that large patches have a greater total number of species
than do small patches, species richness per quadrat does not increase with
increasing patch size (Holt, 1992).

In short, 'It is fair to conclude that habitat fragmentation at the [spatial
and temporal] scales imposed in this experiment, did *not* have a marked
effect on the overall rate or pattern of secondary succession. The usual
explanations for succession—life history differences, interspecific interac-
tions, [etc.]—thus seem to be of overriding importance [compared to patch
size effects]' (Holt *et al.*, manuscript).

The authors believe that this absence of a marked patch-size effect occur-

red because the dominant species during this period were present even in the first year across all patch sizes, and so presumably were in the pretreatment seed bank. Much of the successional change observed in the first 6 years was, in effect, an unfolding of a community structure latent in this initial community; species have waxed and waned in their relative abundances, but without substantial input (as measured by per cent cover) of new species colonizing from external sources. It is interesting that, on average, changes in dominance relationships played out in a similar fashion, among the same suite of species, irrespective of patch size.

10.4.2.2   Patch size and spatial pattern

However, patch size does influence spatial patterning, and the way such patterns change during succession (Holt & Gaines, 1993). Nearby sample quadrats within large patches became more similar, compared with similarly spaced quadrats among smaller patches (Figure 10.2). This pattern was reversed at large distances; there was less variability among widely spaced quadrats on small patches than among similarly separated quadrats on large patches.

The authors' working hypothesis is that fragmentation breaks up spatial coupling (i.e. metapopulation effects, Hanski, 1991) that can act as a homogenizing influence over relatively short distances in large patches (Holt, 1992; Holt & Gaines, 1993). However, small patches, taken collectively, experience a more homogeneous physical environment than do large patches, essentially
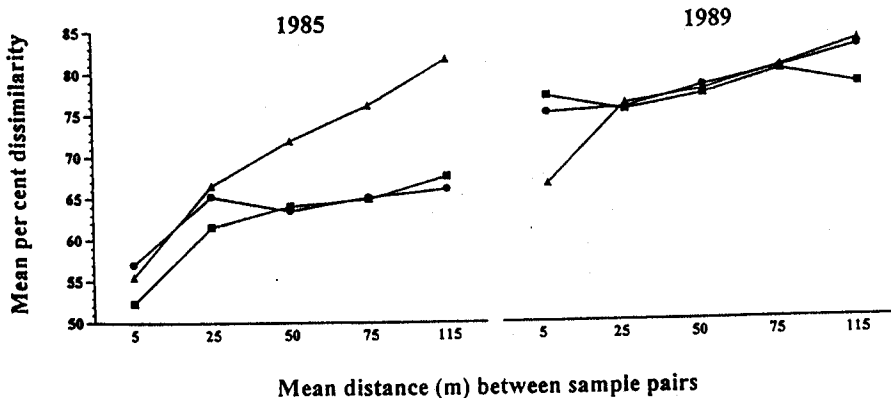

Figure 10.2. The spatial scaling of community dissimilarity (per cent remoteness (PR), see Pielou, 1984) among vascular plants at the outset of secondary succession (a), and 4 years later (b). Data are derived from percent cover estimates from the permanent quadrat grid. PR is a metric measure of community dissimilarity scaled between 0 and 100%. For further details, see Holt et al. (in press) Small patches —■—; medium patches —●—; large patches —▲—.

because edge effects dominate in determining microenvironmental cond
tions, and so widely spaced small patches tend to be more similar, relative t
each other, than are widely spaced samples within large patches.

10.4.2.3 Patch size and plant population persistence

The apparent lack of strong effects of fragmentation on measures such a:
local species richness and rate of succession belies profound effects at the
level of individual species and populations. One striking pattern is tha
clonal herbaceous species persist better locally (i.e. in 1 m^2 quadrats) or.
larger patches, whereas non-clonal species do not show this patch-size effect
(Robinson *et al.*, 1992). This result is consistent with theoretical studies of
the role of internal spatial dynamics within islands in explaining area effects
(Holt, 1992). The authors' intuitive interpretation is that clonal plants
resemble amoebae slowly moving across the landscape. These clones are at
greater risk in highly fragmented habitats, because there is reduced opportu-
nity for re-invasion by vegetative growth from surrounding habitats.

10.4.2.4 Woody plant invasion dynamics

The above plant results largely reflect dynamics in the herbaceous compo-
nents of the plant community. However, woody plant invasion is presently
occurring at an accelerated pace in this system (Chapman *et al.*, 1994).
Judging from historical records in the adjacent Natural History Reservation
(Fitch, 1965 and personal communications), there should be an almost com-
plete turnover in the dominant community members from herbaceous to
woody species during the next decade.

Table 10.1 shows the woody species that have occurred in the fragmenta-
tion project. Figure 10.3 shows temporal trends in number of woody plant
species recorded from the 1 m^2 quadrats during the first 6 years of the
study. Some species have been present from the very beginning, with a rapid
growth in the number of species recorded in the latter 3 years, relative to the
increase in all plants. At present, there are 18 species of woody plants in the
permanent quadrats. Extrapolating from the census samples, it is estimated
that more than 14 000 woody plants over 0.5 m in height are currently
growing within the 106 experimental patches. This surge in woody plant
invasion provides a timely opportunity to document how fragmentation
influences the regeneration of the woody plant community, and how the
influence of fragmentation interacts with heterogeneity in establishment due
to distance effects (Horn, 1981). These topics will be an important focus of
the plant work for some years.

In the next 2 years, a detailed digitized map of the spatial distribution of
woody plants both in the experimental system, and in the surrounding land-
scape (presumed to be the source pool for the system), using a combination

Table 10.1. Woody species listed in descending order of quadrats occupied in 1992. Only stems >1 m in height were included in the number of stems count; asterisks represent species that were present but <1 m in height. All species, regardless of height, were included in quadrats occupied (total number of quadrats = 416)

| Scientific name	Common name	Life form	Dispersal	Number of stems	Quadrats occupied
Cornus drummondii	Rough-leaved dogwood	Shrub	Bird	856	294
Ulmus rubra	Slippery elm	Tree	Wind	63	98
Symphoricarpos orbiculatus	Coralberry	Shrub	Bird	10	64
Rubus sp.	Blackberry	Shrub	Bird	411	48
Toxicodendron radicans	Poison ivy	Vine	Bird	1	42
Juniperus virginiana	Red cedar	Tree	Bird	20	41
Acer negundo	Box elder	Tree	Wind	10	14
Vitis sp.	Grape	Vine	Bird	2	14
Sambucus canadensis	Common elderberry	Shrub	Bird	7	12
Celtis occidentalis	Hackberry	Tree	Bird	2	11
Gleditsia triacanthos	Honey locust	Tree	Gravity	4	7
Morus rubra	Red mulberry	Tree	Bird	4	6
Rhus glabra	Smooth sumac	Shrub	Bird	19	6
Rosa sp.	Wild rose	Shrub	Bird	1	3
Crataegus mollis	Downy hawthorn	Tree	Bird	*	1
Fraxinus americana	White ash	Tree	Wind	*	1
Gymnocladus dioica	Kentucky coffee-tree	Tree	Gravity	1	1
Populus deltoides	Cottonwood	Tree	Wind	*	1
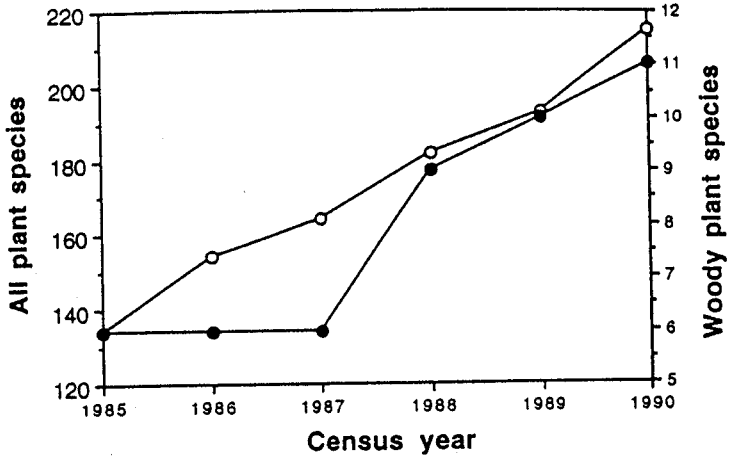
Figure 10.3. Temporal trends in species richness for the entire plant community, and for just the woody species, as inferred from the grid of 1 m² quadrats. —○— all plant species; —●— woody plant species

of ground and remote sensing techniques will·be developed. However, because this work is just beginning, results from only three data sets are presented here: woody species encountered in the general community samples (i.e. the grid of 1 m² permanent quadrats); and censuses in 1990 and 1992 of woody stems in five height categories (<0.25 m, 0.25–0.5 m, 0.5–1 m, 1–2 m, >2 m) in 4 × 4 m quadrats, overlaying the permanent quadrats.

Figures 10.4a and b, respectively, depict how local species richness (number of species per quadrat) and total stem density (for all stems greater than 1 m) varied across the experimental field in 1992. There appears·to be a gradient in invasion, with more rapid invasion toward the south-west than toward the north-east. This can be explained by the present distribution of woodland and the prevailing wind direction (from the south-west). Moreover, there appear to be 'hot spots' of rapid invasion along the southern edge, and scattered elsewhere in the field.

The source pool for the invading woody plant community includes wind-, gravity-, bird-, and mammal-dispersed species. Figure 10.5 shows how the number of wind- and bird-dispersed tree species per sample quadrat varied as a function of distance from presumed source areas (i.e. established woodland), for the 1990 and 1992 samples. There is a clear distance effect in the wind-dispersed species, which is much less obvious in the bird-dispersed species (though rather stronger in 1992 than in 1990). It is reasonable to expect that there will be a roughly exponential decline with distance in the seed rain (and likely recruitment) from any potential maternal plant for a wind-dispersed species. This is less likely for bird-dispersed species, such as the
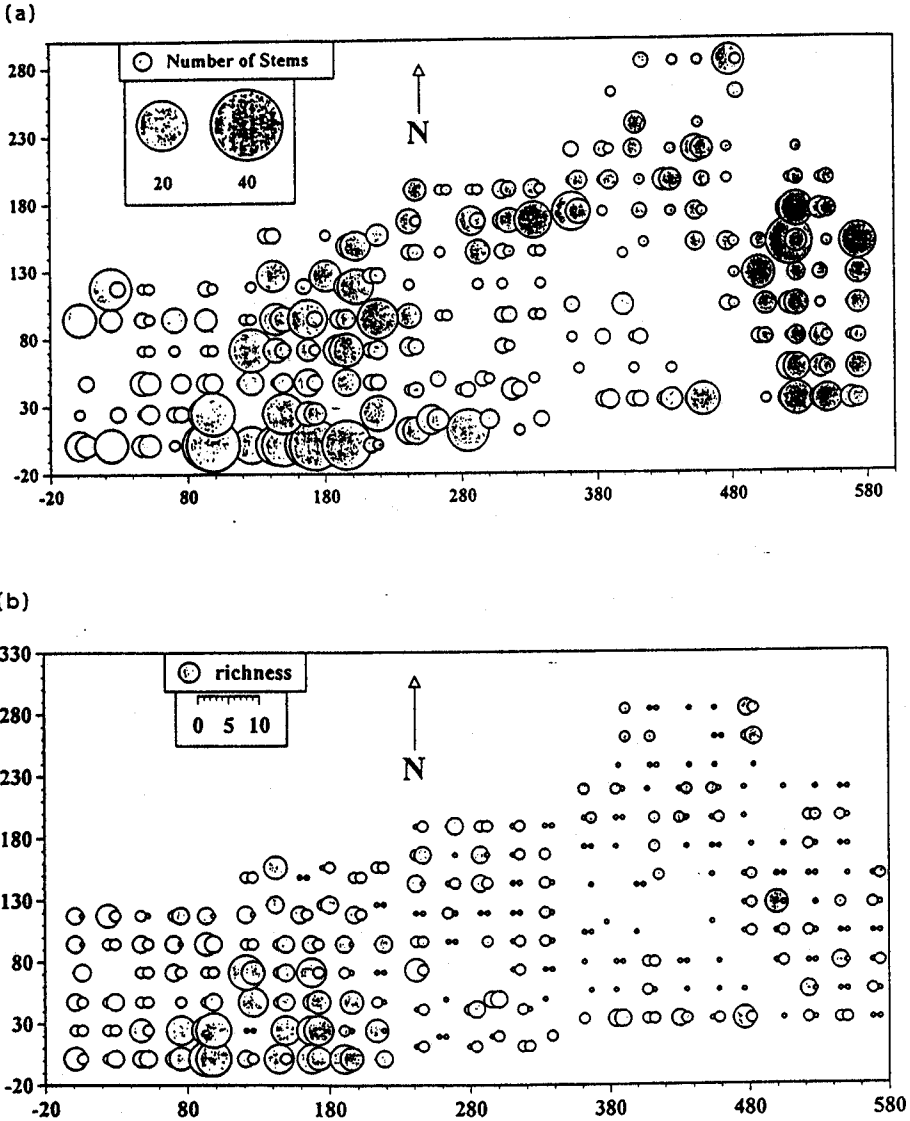
(a)

(b)

Figure 10.4. A bubble plot map of the fragmentation project showing (a) local spe-cies richness of woody plants, and (b) total woody stem abundance. The axes are E–W and N–S directions, in metres. The diameter of each circle is proportional to the number of (a) species, or (b) stems in each 4 × 4 m quadrat in 1992. The stem map does not include vines and rambling shrubs (four species), which have numerous stems per clonal individual, whereas the species richness map is for all woody plants recorded
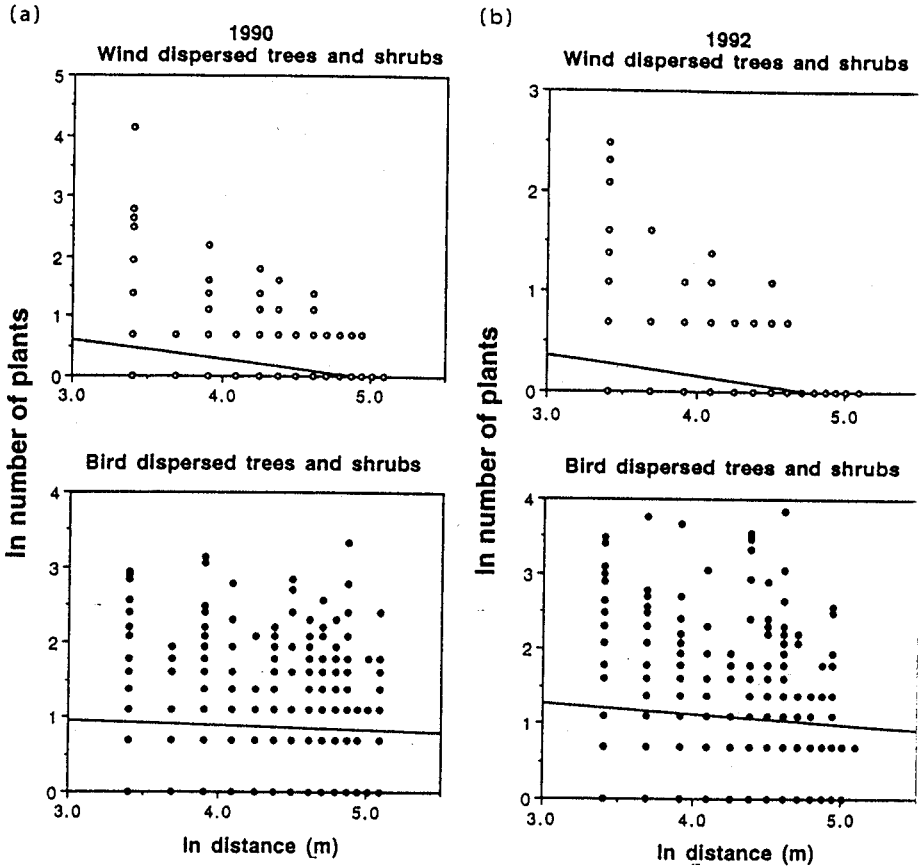
Figure 10.5. Local abundance of woody plants (all species) as a function of distance from putative seed sources in the surrounding woodland, for both wind- and bird-dispersed plants. Data are from two censuses taken using 4×4 m quadrats superimposed on the 4×4 permanent 1 m^2 quadrats among patches of all sizes. (a) 1990 data represent all plants >0.5 m in height; (b) 1992 data represents all plants >1 m in height

rough-leafed dogwood (*Cornus drummondii*). The seed rain from potential source plants is determined largely by whatever factors determine bird movement, and it is unlikely that a simple exponential function would characterize seedling distribution patterns (McDonnell, 1988a,b). In particular, it is likely that some establishment could occur far from the source plant.

There are a number of dominant tree species in the neighbouring woodlands, including several species of oaks, hickories, and the black walnut, which have yet to be recorded in the experimental field. All of these are believed to be dispersed by two species of sciurid (the grey squirrel, *Sciurus*
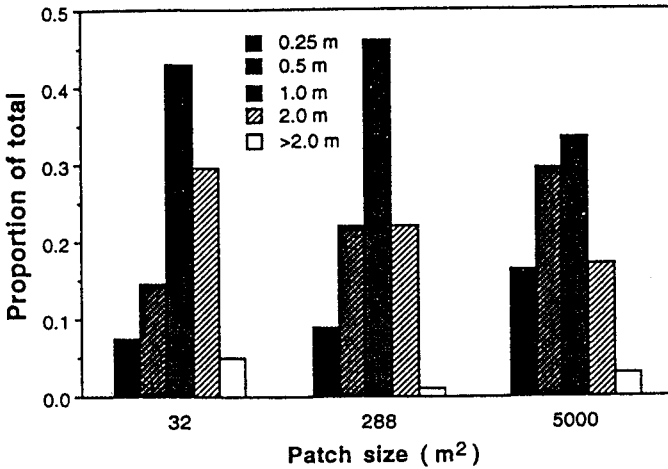
Figure 10.6. Size structure of woody plants recorded in the 1 m² quadrats in 1992. The recruitment of smaller individuals is considerably greater, per unit area, on the large patches

carolinensis, and the fox squirrel *S. niger*) which are prevalent in the region and are common in adjacent tracts of woodland, but which are very rarely seen in the experimental field. It is surmised that the invasion dynamics of these tree species in the fragmented landscape will be governed almost entirely by how these mammal species eventually respond to patch size and to distance from adjacent woodlands.

The importance of distance effects in succession, thus, seems unquestionable. Considerable heterogeneity in the woody plant community within the fragmented landscape will emerge because of the unique, species-specific patterns in the spatial arrangement of potential source populations, and in the differential dispersal capabilities of different species. Are there any evident patch-size effects, also? Figure 10.6 shows how the size classes of woody plants vary as a function of patch size. There is a clear effect of patch size on woody plant size structure.

The spatial patterns are likely to reflect the interplay of gradients in seed dispersal, edaphic factors, and spatial heterogeneity in mortality factors. The bias toward smaller size classes in woody plants shown in Figure 10.6 could result from: (1) greater rates of seedling recruitment in large patches; (2) faster growth rates on smaller patches; and (3) higher mortality rates of small individuals on smaller patches. The authors are intrigued by the potential impact of small mammals on woody plant succession dynamics.

In other systems, small mammals have been shown to be significant mortality agents at the seed, seedling, and sapling stage for trees in secondary succession (e.g. Mittlebach & Gross,1984; Gill & Marks, 1991; Huntly, 1991;

Grover & Holt, in press; Ostfeld & Canham, 1993). Therefore, temporal or spatial variability in mammal dynamics could lead to pulsed recruitment in woody plant species, correlated with troughs in the abundance of mammal herbivores. So, an important long-term, indirect effect of patch size on plant succession may be mediated through the influence of patch size on small mammal abundance and activity patterns. In the authors' system, there is substantial evidence for patch-specific influences on small mammal densities (see below).

10.4.3 SMALL MAMMAL DYNAMICS

The authors' field protocol for small mammals is described in more detail elsewhere (Foster & Gaines, 1991; Gaines *et al.*, 1992a). A grid of trap stations was sampled twice-monthly throughout the year. At each trapping period, Sherman live traps were set and baited over a 3-day period. Each captured animal was individually marked with an eartag, weighed, sexed, assessed for reproductive condition, and then released. The individual mark–recapture histories were used to calculate population abundance and demographic parameters.

Though all small mammal species occur on all patch sizes, a striking distributional pattern exists in the relative densities of the three most common species (Figure 10.7a), a pattern first noted by J. Foster in her dissertation research. Previous analyses of the mammal data (e.g. Foster & Gaines, 1991) have reported relatively short runs of the data set (2–3 years); the data summarized in Figure 10.7a are for autumn 1984 to winter 1991, and comprises a total of 20 000 + individual capture records for the three dominant species (Gaines *et al.*, 1992a).

Sigmodon hispidus, the largest species, was most abundant on the large patches. Contrary to initial expectations, which were that all species would be most abundant on the largest patches, the two smaller species (*Peromyscus maniculatus* and *Microtus ochrogaster*) achieved highest densities on smaller patches. Overall, there was a rank-order relation between a species' body size and the patch size on which it had the highest density. These relationships are all statistically significant in a two-way (species × patch size) ANOVA and have remained qualitatively the same throughout the entire study (Foster & Gaines, 1991; Gaines *et al.*, 1994).

The restriction of *S. hispidus* to the large patches makes excellent biological sense, given what is known about the home range requirements of this species (Foster & Gaines, 1991). However, a more complex explanation is required for the abundance pattern of the two smaller species. The current hypothesis is that this pattern reflects (among other factors) interspecific dominance, so that the smaller-bodied species are more abundant on smaller patches because they have a refuge from competition with the larger, dominant species, *S. hispidus*.
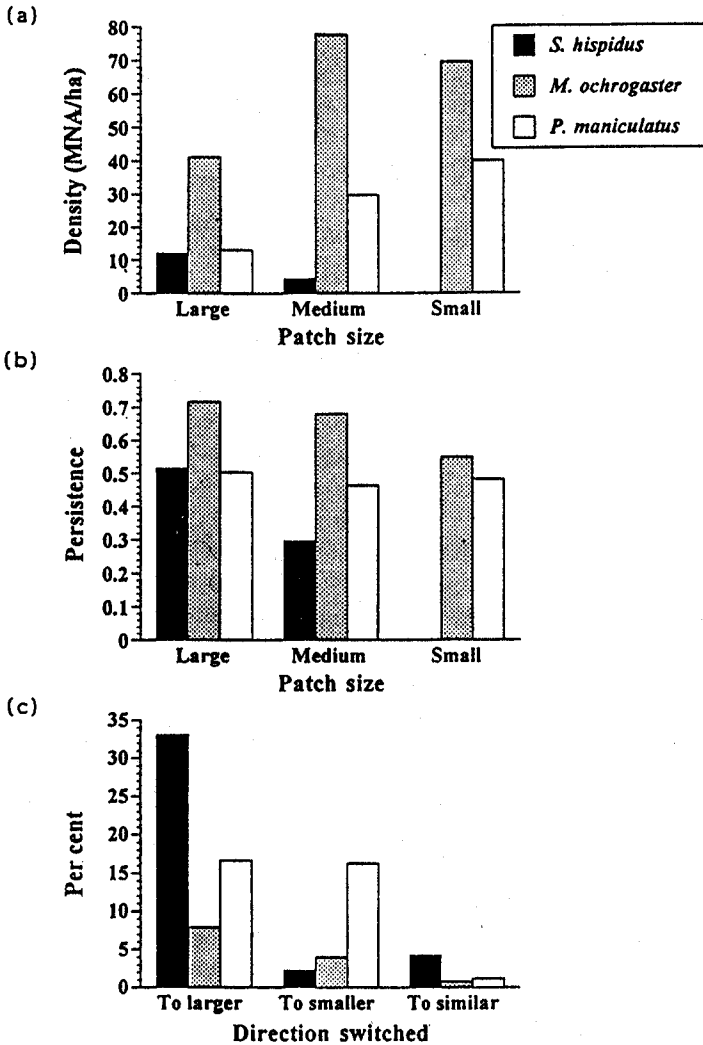
Figure 10.7. Effects of patch size on small mammal populations: (a) mean density by patch size for *Sigmodon hispidus*, *Microtus ochrogaster* and *Peromyscus maniculatus*, (b) mean persistence by patch size for *S. hispidus*, *M. ochrogaster* and *P. maniculatus*, and (c) mean percentage of animals switching by patch size for *S. hispidus*, *M. ochrogaster* and *P. maniculatus*. In each case *S. hispidus* is shown in black, *M. ochrogaster* is shown shaded, and *P. maniculatus* is shown in white

Additional insight into the effects of fragmentation on the small mammal community come from analyses of how individual species' demography and movement vary with patch size. Persistence rates (i.e. the fraction of individuals captured in a given patch class at time t which were recaptured in the same patch class at time $t+1$, where the time unit is one inter-trapping interval) vary among species and patch sizes. Both *S. hispidus* and *M. ochrogaster* persist significantly better (as individuals) on larger patches (Figure 10.7b). In contrast, *P. maniculatus* persists equally well across all patch sizes (for more details of these results see Gaines *et al.*, 1992a, 1994). However, this measure of persistence conflates mortality and dispersal; recent advances in mark–recapture statistics (Zeng & Brown, 1987; Nichols & Pollock, 1990; Pollock *et al.*, 1991) should permit an attempt to be made to disentangle these two components of persistence.

It should be stressed that these patterns in density and persistence as a function of patch size have persisted throughout the study period, despite successional changes in the plant community. This suggests that the effects are fundamentally spatial in character (e.g. reflecting how patchiness modulates direct interference among individuals), rather than an indirect correlate of some other factor associated with patch size.

J. Diffendorfer has recently analysed individual movement behaviour in these three species. Figure 10.7c shows the mean fraction of animals that switched patch clusters between consecutive trapping periods. Because of the spatial arrangement of the habitat fragments, there are few clusters with similar patch sizes juxtaposed, so it is sensible that there are few switches observed among patches of similar size (in different clusters). More surprisingly, there is more movement, on a *per capita* basis, from small patches to larger patches, than in the reverse direction; a physiologist would describe this as a 'countergradient' flow. At first glance, this seems to contradict the usual picture of spatial dynamics in vertebrate populations, in which a relatively small number of individuals occupy optimal sites and force all other individuals to occupy suboptimal sites (although it does match recent theoretical predictions about how local dispersal rates should vary in spatially heterogeneous environments (McPeek & Holt, 1992).

It is a priori possible that the bias in movement towards larger patches reflects the geometric fact that large patches simply provide larger 'targets', compared with smaller patches; hence, an animal moving at random would have a higher probability of encountering larger patches, leading to some bias in movement. However, analysis by Diffendorfer (unpublished data) indicates that the movement biases do not, in fact, result from any such simple geometric bias, but instead represent genuine asymmetries in movement behaviour. An adequate assessment of the implications of these data will require local fitnesses (equal to per capita growth rates) and net fluxes of individuals (rather than just individual movement rates) to be estimated as a function of patch size. These estimates are currently being made and

the intention is to integrate them into a spatially-explicit model, so as to refine the understanding of spatial dynamics in the authors' system.

One striking feature in the mammal data is that three relatively similar species respond in radically different ways to habitat fragmentation. Were one to look only at the number of rodent species present, one would not see any obvious effect of fragmentation—all species are to be found on all patch sizes—but underlying this uniform facade is a great variety of disparate responses to fragmentation.

10.4.4   ARTHROPOD COMMUNITY DYNAMICS

10.4.4.1   Overall survey results

Since 1985, E.A. Martinko and S. Reyes have surveyed the arthropod community using two techniques: sweep samples and pitfall traps. Foliar arthropods were censused with sweep samples in a standardized fashion through 600 m of linear transects within patches of each patch size class. After each sweep, samples were sorted and frozen for later identification. Pitfall traps, spaced along the same transects, were sampled in the years 1987–92.

The authors' experience (which is relatively common in this kind of survey) is that the rate-limiting step is setting up a reference collection in which all specimens are sorted and identified to species. The sampling protocol generates 50 000–60 000 individual specimens to be processed per year. The cumulative number of morphospecies identified to date is about 550. Over the last 2 years, a post-doctoral entomologist has worked full-time on this taxonomic logjam. The results reported here are from only the earlier years of the study, 1985–87 and large and small patches; specimens from later years and the medium patches are still being identified.

Figure 10.8 shows for the sweep samples how species diversity (measured by the Shannon-Wiener statistic, H^1) varied during the year for small and large patches in each of these 3 consecutive years. Large patches were more diverse than small patches throughout almost all of 1986 and, in all 3 years, large patches tended to become more diverse than small patches later in the season. However, looking at the 30 monthly samples taken as a whole (and rounding off the diversity estimates to one significant digit), large patches were more diverse than small ones, rather than the reverse, 18 times out of 30. This is much as would be expected by chance alone. Thus the evidence for a patch size effect is not strong.

These results reinforce the earlier conclusion (Robinson *et al.*, 1992) that at the spatial scale of the experiment, patch size does not have a dramatic effect on species richness, when equivalent samples across patches differing in size (although large patches as a whole harbour more arthropod species) are compared. The results make sense, given what is already known at a
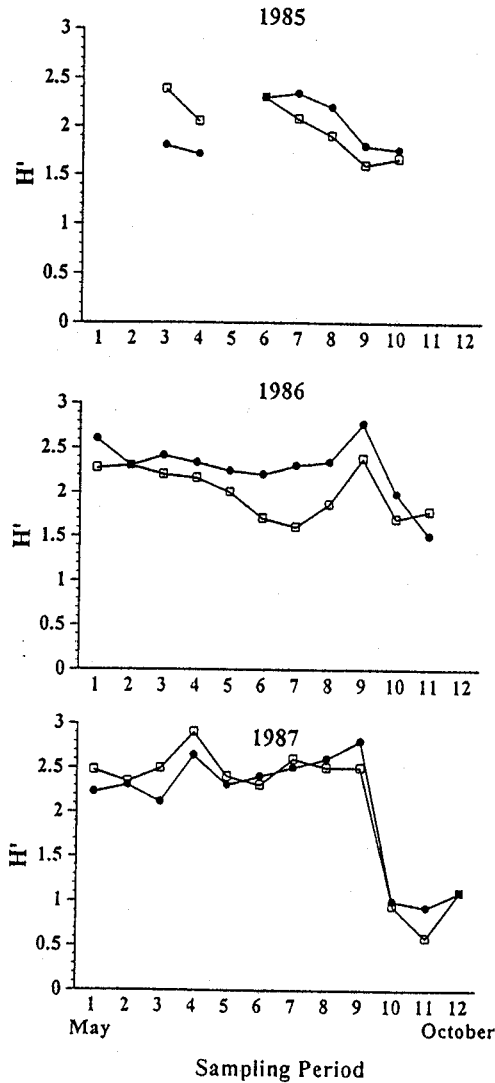
Figure 10.8. Seasonal trends in arthropod diversity (H^1) on small (—□—) and large (—●—) patches. For methods, see text

general level about species–area relationships. The usual species–area rela-
tion considered in the ecological literature is what might be called the 'total
species–total area' relation, which expresses how the length of the total spe-
cies list grows as the size of the patch or the island being completely sam-
pled is increased (Holt, 1992). A rule-of-thumb is that a 10-fold increase in
area is needed to double the species list. But if standardized samples (e.g.

uniform in area or in sampling effort) taken across islands or patches differing in size are considered, the relationship between estimated species richness per sample and area is expected to be considerably weaker than between total species richness and area. Because the data reported in Figure 10.8 are for standardized samples, and a large patch is roughly an order-of-magnitude larger in area than the cumulative area of a cluster of small patches, a quantitatively weak effect might be expected.

However, as emphasized in Robinson et al. (1992), weak to moderate effects of fragmentation as assessed by whole-community measures, such as species richness or diversity, do not imply that there are no significant effects at the level of individual species populations. An indication of such species-level effects comes from recent work on butterflies.

10.4.4.2 Butterfly community

Butterflies were chosen as a focal group for examination of fragmentation effects on the arthropod community as they have many advantages as material for such an investigation. They are known to be strongly influenced by structural features of their habitat (e.g. patchiness and microclimate); are rich in species in eastern Kansas; come in a variety of body sizes; and are easily identified to species on the wing. This work is a new direction in the authors' research programme and is being guided by D. Debinski.

Lepidopteran movement (Warren & Stephens, 1989) and habitat use have been shown, at other sites, to be significantly influenced by habitat patchiness. Fragmentation can conceivably affect butterfly communities in two distinct ways.

First, habitat heterogeneity influences individual movement. For example, Wood & Samways (1991) studied butterfly movements and habitat use in a botanical garden and documented that flight patterns were clearly modified by the structure and orientation of landscape elements. Few individuals landed either in the cut grass area or in the forest; weaker flyers flew over the forest (the authors surmised, to avoid spider predation), whereas stronger flyers flew through the forest. Litsinger et al. (1991) found that both plant density and patch size were significant factors influencing oviposition sites for moths. Fewer ovipositing moths were attracted to low density patches and small patches of maize relative to higher density or larger patches. Given the experimental design, which consists of patches of one habitat type (vegetation undergoing secondary succession) interspersed with another (a low turf plant community), it is sensible to examine how butterfly species are distributed across both habitat types.

Second, in addition to individual-level effects there are population-level effects on local population extinction, colonization, dispersal, and metapopulation persistence. Butterflies often show a distributional pattern in which they are present in small patches separated by large tracts of intervening

habitat (which may or may not be suitable for them). For example, C.D. Thomas & Harrison (1992) found that local populations of the butterfly *Plebejus argus* matched the spatial distribution of suitable habitat patches. Population extinctions were relatively high in small patches, and regional persistence was dependent upon the availability of relatively large areas of occupied, suitable habitat.

10.4.4.2.1 Methods

With these issues in mind, butterflies were surveyed during the summer of 1993 to provide a preliminary evaluation of how patch size affects butterfly community structure. Because of the striking distributional pattern exhibited by small mammals, which was highly correlated with body size, it was of particular interest to assess whether similar relations hold in butterflies (i.e. larger-bodied species preferentially utilize larger patches). Because of the considerable data on plant community composition, it can also be asked whether or not the presence of a required host plant predicts the presence of adults of that species. Here, the former question is concentrated upon. It is emphasized that the results presented here represent just the first sample of what is intended to be a long-term study of the butterfly community; thus the results should be considered as provisional and suggestive, rather than definitive in nature.

During the summer of 1992, a regional survey of butterflies was conducted to construct a species list (with voucher specimens deposited in the University of Kansas' Museum of Natural History). Combined with prior knowledge of the butterfly assemblage (e.g. Fitch, 1965), a reasonably complete picture of the regional source pool has been drawn up. Fortunately, a trained observer can visually identify nearly all the species present in the system without netting individuals, which allows much more data to be gathered than would be possible if collections were required for identification. Each of 15 50 × 100 m areas was surveyed 6 times during the course of the field season (25 May 1993 to 4 August 1993). Butterfly species abundances were estimated using the adaptation by J.A. Thomas (1983) of Pollard's (1977) transect techniques. Transects were established also in the mowed area between rows of small patches to allow comparison of species composition of the interstitial habitat with that found within patches.

Numbers were estimated by tallying the occurrence of butterflies along the transects within a 4 × 4 m square 'window' in front of an observer walking at a steady pace. For each individual butterfly observed, its species, behaviour (flying, resting, nectar feeding, ovipositing, or mating), location, and time were recorded, together with the plant species at which oviposition or nectar consumption occurred. Individuals were netted for positive identification only when necessary.

10.4.4.2.2   *The relationship between patch size, butterfly abundance and*
              species richness

Figure 10.9a shows cumulative abundances of all butterfly species. Because
of the sample protocol, 100% of the small patches, 50% of the medium pat-
ches, and 32% of the large patches were surveyed in each census period.
Assuming the latter provide unbiased samples of butterflies of the medium
and large patches, the estimates shown in the figure for the total number of
individuals present in a given patch size class were arrived at. These num-
bers can be used to calculate different measures of butterfly abundance, each
reflecting a different dimension of population-habitat relationships.

The estimated abundance per patch is strongly correlated with patch size
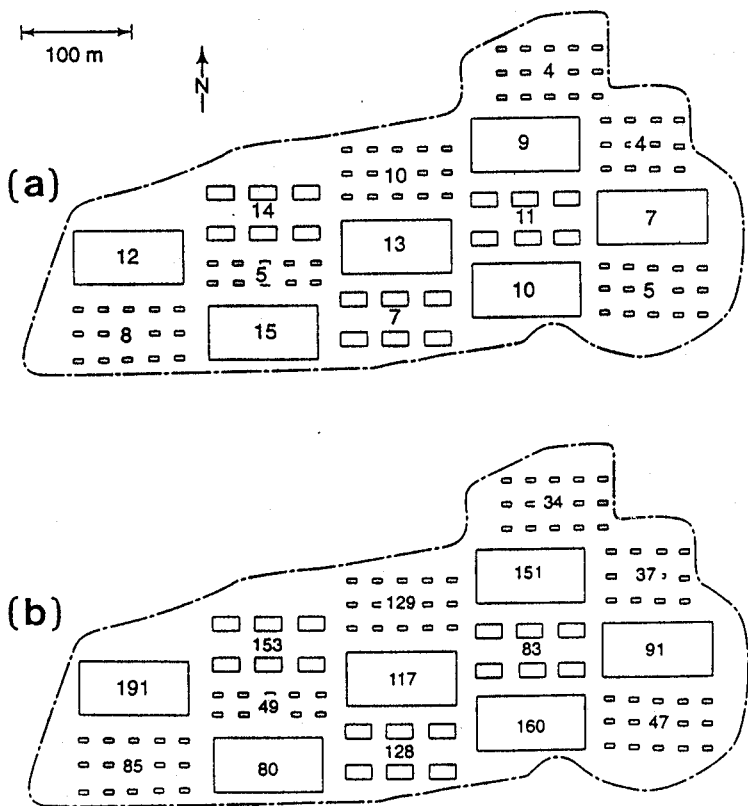(Figure 10.9b); a chi-square test for differences of abundance of individuals

Figure 10.9. Map of the Kansas Biotic Succession Facility, showing (a) the species
richness of butterflies in each large patch or cluster of medium or small patches, and
(b) the total number of butterflies present in each large patch or cluster of medium
or small patches. Mowing boundary (——— -); successional patches (□)

among patches was highly significant (χ^2 = 25.58, d.f. = 2, $P < 0.001$), and this difference also holds in a one-way ANOVA (F = 55.69, d.f. = 2,12, $P < 0.001$). Multiplying the estimated abundance per patch by the number of patches gives the following estimated abundance per 0.5 ha 'block' (i.e. large patch, or clusters of medium or small patches): 411/large; 242/medium cluster; 35/small cluster.

This measure gives the total population size present, were butterflies restricted in their movement to within large patches or clusters of smaller patches, and clearly implies that fragmentation reduces total butterfly abundance. However, these measures may not be biologically reasonable for some species, for instance because they use the interstitial habitat as well as the successional patches (MacIntrye & Barrett, 1992), or span larger patch arrays in their individual movement patterns. One of the research objectives is to analyse in some detail the ways that individual patch use and movement patterns by butterflies are influenced by fragmentation. In particular, it is intended to contrast species restricted in their habitat use to the successional patches (see below), with species that also utilize the interstitial area. Patch size effects should be more pronounced for the former.

A second measure is estimated density (number/area). This measure emphasizes the intensity of use, per unit area, and is particularly pertinent for some ecological issues (e.g. gauging the importance of herbivory in plant population dynamics). If anything, in the butterfly data set, overall density has a weak negative correlation with patch size.

A total of 23 butterfly species from five families were found during the summer of 1993. Ten species were found cumulatively in the small patches, 14 in the medium patches and 21 in the large patches. Species richness increased with patch size (on a log–log plot, slope = 0.237; see Figures 10.9a and 10.10). Mean species richness was 6.00, 10.66, and 10.83 for clusters of small, clusters of medium, and large patches, respectively. Using one statistical test suggests that patch size influences species richness (one-way ANOVA, F = 78.84, d.f. = 2,12, $P < 0.001$), but a chi-square test for differences in species richness among patch sizes was not significant. This inconsistency suggests that larger sample sizes will be needed to discern patch size effects (if any) on species richness. Robinson *et al.* (1992) observed that aggregate community measures may not show pronounced effects of habitat fragmentation, even when individual species' populations do.

The mowed interstitial area contained 10 species. The mowed habitat was comparable with small patches in both species richness and mean abundance.

10.4.4.2.3   *Species-specific patch size preferences*

Species composition of the small, medium, and large patches formed an almost perfectly nested set (Figure 10.10). All species found on medium pat-
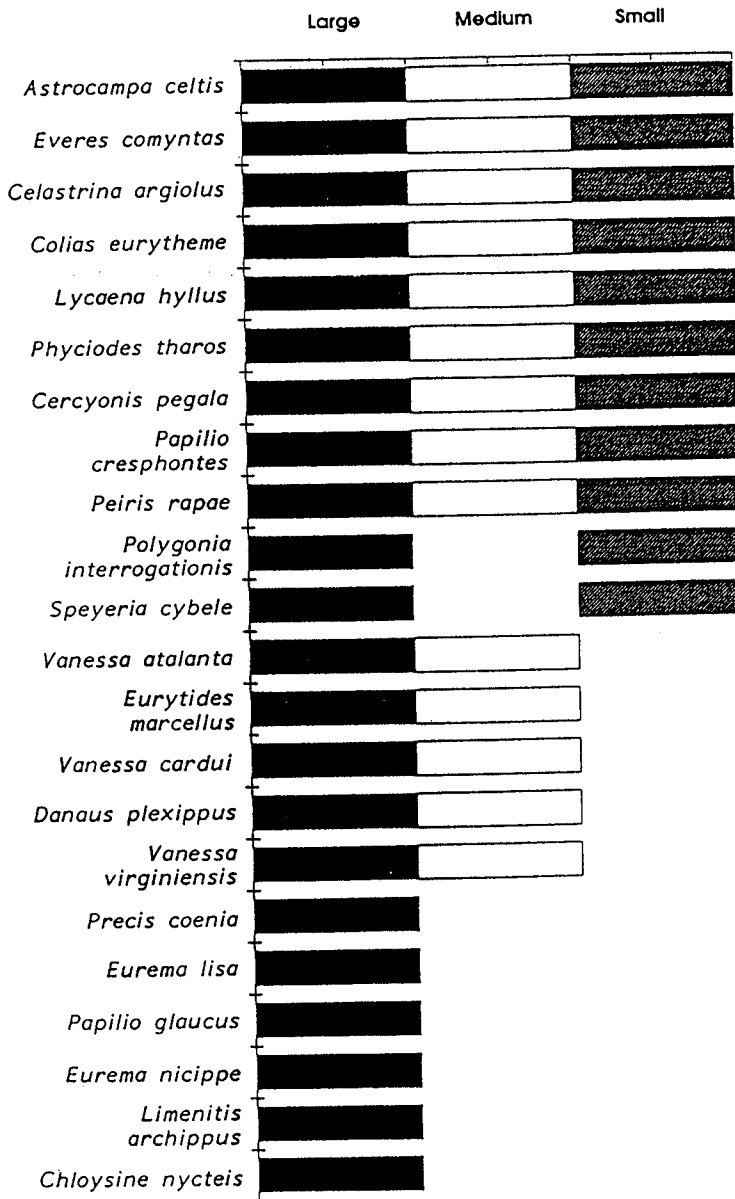
Figure 10.10. Presence of butterfly species in each patch size, arranged to display nested subsets. Black indicates presence in large patches, white indicates presence in medium patches, and hatched indicates presence in small patches

ches were found on large patches; all except two species (*Speyeria cybele* and *Polygonia interrogationis*) found on small patches were found on medium patches; and no species were found solely on small patches. This suggests that certain species may be limited by a minimum home range size. Comparable nesting of faunas on habitat fragments has been observed in survey work at larger spatial scales (Blake, 1991; Cutler, 1991).

A further indication that species' patch size preferences may exist comes from an analysis of overall body size effects. Butterfly size was compared with patch utilization by plotting the proportion of butterflies of three size classes found within the small, medium, and large patches, as well as the mowed areas (Figure 10.11). The total number of individual butterflies recorded were classified as follows: large, 21; medium, 973; small, 567 (see Figure 10.11 for individual species' size classifications). Both small- and medium-sized butterflies showed a significant deviation from a uniform distribution among small, medium, and large patches ($\chi^2 = 60.01$; d.f. $= 2$; $P < 0.001$ for medium-sized butterflies, and $\chi^2 = 96.52$; d.f. $= 2$;
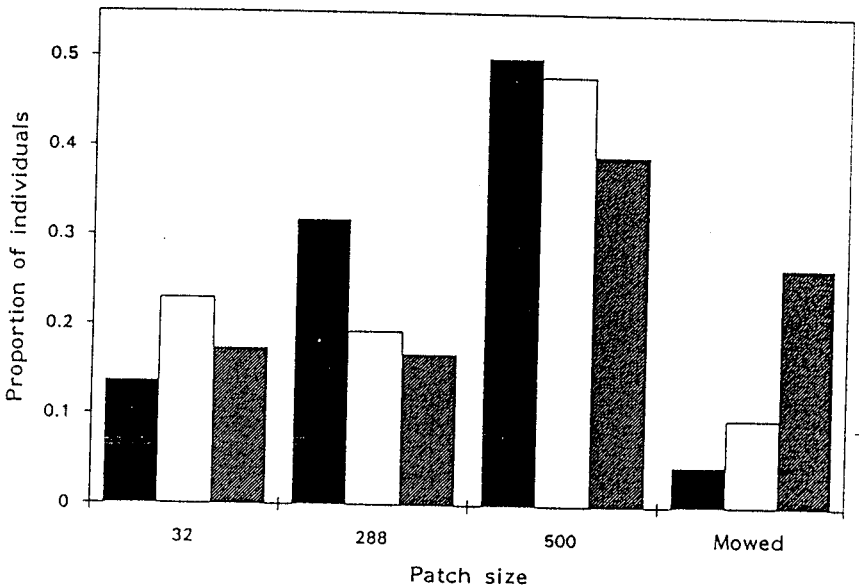

Figure 10.11. For each of three size classes of butterflies, the proportion of individuals captured as a function of patch size. The species *E. comyntas*, *C. argiolus*, *L. hyllus*, *E. lisa*, *E. nicippe*, *P. tharos*, and *C. nycteis* were classified as small (< 38 mm mean wing width); *C. eurytheme*, *C. philodice*, *P. rapae*, *V. atalanta*, *V. cardui*, *V. virginiensis*, *P. coenia*, *P. interrogationis*, and *C. pegala* were classified as medium (38–70 mm mean wing width); and *D. plexippus*, *P. cresphontes*, *P. glaucus*, *E. marcellus*, *L. archippus*, and *S. cybele* were classified as large (> 70 mm wing width). Length is measured as wing width from forewing to forewing. Large butterflies ■; medium-sized butterflies □; small butterflies ▨

$P < 0.001$ for small-sized butterflies). Sample size was probably too small for the large-bodied butterflies to show significant differences in patch utilization.

When patch utilization was compared by grouping butterflies into size classes, butterflies of all sizes were most often found in large patches. Therefore, based on body size, species do not appear to be segregating among patches; almost all individuals preferring large patches. Six butterfly species were found only on large patches. Three of these species were large-bodied and may have been selecting larger patches of contiguous habitat (e.g. to acquire nectar). Four medium-sized species were found only on medium or on large patches. No species were found exclusively on small patches.

As knowledge of butterfly ecology in the system increases, it should become possible to develop and test species-specific explanations for patch size preferences. For instance, *Speyeria cybele* consumes nectar on thistles, which in the reported system tend to be found near edges. Preliminary observations suggest that this species may have a preference for small patches. Small patches have a higher proportion of edges relative to interior habitat. Thus, this patch size effect may be an expression of the functional significance of edges in habitat choice.

10.5 CONCLUSIONS AND SIGNIFICANCE FOR AGROECOLOGY

The concept of scale is central to many problems in ecology (Urban *et al.*, 1987; Levin, 1992). All experimental studies of fragmentation impose an artificial scale on nature, corresponding to the dimensions of artificial habitat islands. Despite the manifest practical concerns over the biological consequences of fragmentation, there are still very few experimental studies to date, perhaps largely because most investigators are, quite naturally, concerned with spatial scales far beyond the reach of feasible experimentation. The reported experimentally fragmented landscape is small relative to most fragmentation systems of concern to conservation biologists or agroecologists, yet large compared with typical experiments in community and population ecology. Though the authors would hesitate to extrapolate to taxa and spatial scales radically different from those encompassed in their system, they believe that studies carried out at this intermediate scale—including especially the long-term study of invasion by woody plant species during succession and the interplay of this process with mammal community dynamics—have much to offer in refining the understanding of potential consequences of scale in ecological systems (e.g. metapopulation dynamics, Hanski, 1991; source-sink population structures, Pulliam, 1988; Pulliam & Danielson, 1991).

The results of a successional island biogeographic study, such as the one

reported here, are broadly pertinent to agroecology, because most agroeco-systems are in a landscape with many patches left fallow and at different stages of secondary succession. The flux of rodent and insect pests into a particular agricultural field may largely reflect dynamics among non-agri-cultural habitat patches. Characterizing the 'ecological neighbourhoods' (*sensu* Addicott *et al.*, 1987) pertaining to particular pest species should be useful in devising environmentally sensitive control strategies. The ultimate drivers of key processes in arable ecosystems may, in the end, not be found within these ecosystems, but rather in the broader landscape of which they are part.

10.6   ACKNOWLEDGEMENTS

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