

# THE INFLUENCE OF REGIONAL PROCESSES ON LOCAL COMMUNITIES: EXAMPLES FROM AN EXPERIMENTALLY FRAGMENTED LANDSCAPE

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## INTRODUCTION

Until recently, most empirical research in terrestrial community ecology—and, in particular, experimental studies (Hairston 1989)—concentrated on phenomena at small spatial scales (Kareiva and Anderson 1988). Yet local communities are embedded in a spatially heterogeneous world and may be influenced by processes operating at a multiplicity of spatial and temporal scales (Ricklefs 1987, Roughgarden et al. 1988, Levin 1988, Wiens 1989, Hastings 1990). There is increasing urgency in understanding the role of spatial processes in community ecology, given that a pervasive effect of humans on the earth is the destruction and fragmentation of natural habitats. Habitat fragmentation potentially influences a multitude of ecological phenomena, ranging from individual behavior to population persistence, to the strength and predictability of interspecific interactions, to ecosystem fluxes (Saunders et al. 1991). Ameliorating the effects of habitat fragmentation will require a deep understanding of the role of spatial processes in population and community dynamics.

A burgeoning body of observational (e.g., Dickman 1987, Quinn and Harrison 1987) and theoretical (e.g., Wilcove et al. 1986; Fahrig and Paloheimo 1988) analyses of habitat fragmentation now exists, but experimental studies of habitat fragmentation are still relatively infrequent (e.g., Robinson and Quinn 1988, Kareiva 1987, Lovejoy et al. 1984). For the past seven years we have been examining community dynamics on an experimentally created archipelago of patches undergoing secondary succession (Figure 1), surrounded by a "sea" of low turf maintained by regular mowing. When we designed this patch array in 1984, we were guided by theoretical notions about how the spatial context of a local community—the size of the area it occupies, and its position relative to source pools for colonization—might influence successional dynamics, either by direct effects on the plant community (Holt et al., *ms.*) or by indirect effects via small mammal herbivores (Louda et al. 1990). We now believe our system provides a more general opportunity for studying the population and community processes involved in habitat fragmentation, and that is the focus of our current research. In this chapter, we present case studies from this system to illustrate a conceptual framework for analyzing the influence of regional processes on local populations and communities (Holt, *in press*, a).

## AN EXPERIMENT IN LANDSCAPE ECOLOGY

The study site is a 12 ha field on the University of Kansas' Nelson Environmental Study Area

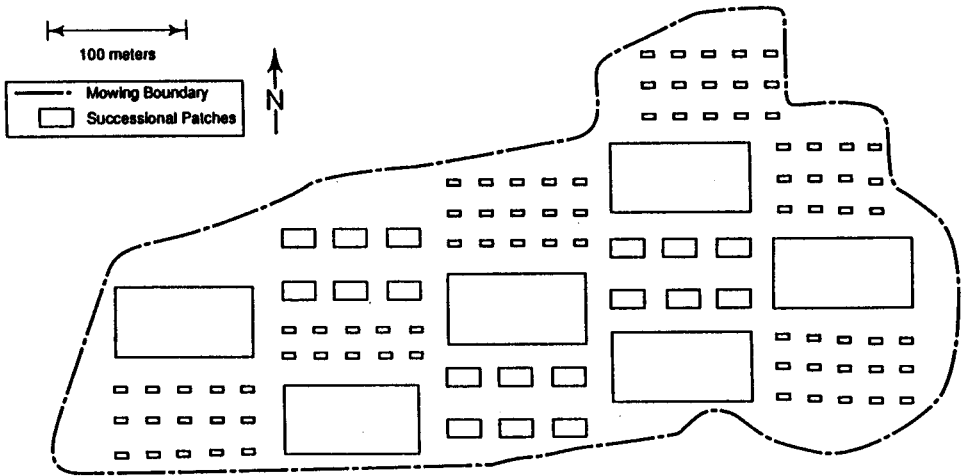


Figure 1. The Biotic Succession Facility at the Nelson Environmental Study Area (NESA), University of Kansas, Leavenworth County, Kansas. The patch sizes are 50 m x 100 m (large), 12 m x 24 (medium), and 4 m x 8 m (small). The medium and small patches are arranged in clusters spanning 50 m x 100 m. Because of the irregular shape of the field, two of the clusters of small patches had to be smaller than this. The low turf plant community on the interstitial habitat (maintained by mowing) substantially differs in species composition from the successional old-field community on the patches (Holt, Robins, and Gaines ms).

(NESA), 16 km north of Lawrence, Kansas. The archipelago of habitat islands shown in Figure 1 was created from an agricultural field in 1984 by intensively mowing interstitial areas between patches at bi-weekly intervals and allowing succession to proceed unhindered within the patches. Old-field succession in our system has followed the familiar script documented throughout the central U.S. in habitats free of fire (e.g., Bazzaz 1968). Substantial changes occurred during the first three years, but the rate of change in the plant community thereafter greatly slowed as perennial forbs and then invading woody plants began to replace annual species (Robinson et al., in press, Holt et al., ms.).

Our choices of patch sizes, their spatial separation, and the spatial arrangement of patches were guided by a knowledge of the dispersal biology of plants and small mammals, by a consideration of local landscape patterns, and by logistical concerns. The largest patches (0.5 ha) are comparable to the sizes of enclosures typically used in experimental studies of small mammal communities (e.g., Johnson and Gaines 1987). The smallest patch size (0.0032 ha), though small, can potentially harbor many hundred individuals of herbaceous plant species. The minimum distance between any two plots was determined from data on plant and

small mammal dispersal (e.g., Gaines et al. 1979); the interstitial habitat created by mowing constitutes a significant dispersal barrier for many organisms (Foster and Gaines, 1991; Gaines et al., in press a). We clustered groups of small and medium patches such that the total area spanned by the perimeter of a cluster equals the total area of a large patch (as best as we could, given constraints imposed on us by the size and irregular shape of the field). This design permits us to compare grids of sampling units (e.g., quadrats, traps) in large patches with comparably spaced sampling grids in clusters of small or medium patches. The patch clusters are arranged in a stratified random design; replicates of each cluster type are near the field edge (to compensate for distance effects in colonization), and no two clusters of the same patch type are adjacent.

In effect, our system incorporates a comparison of large patches with clusters of smaller patches exhibiting two levels of habitat fragmentation. We have monitored in some detail the plant (Holt et al., ms.) and small mammal (Foster and Gaines 1991, Gaines et al., in press, a,b) communities, and have data for some but not all years for soil water and nitrogen, arthropod species richness, snake abundances, and the breeding bird community (Robinson et al., in press; Teravainen, in press; Roth and Holt, in press; and unpublished data).

## LOCAL COMMUNITY RESPONSES

As Levin has remarked (Levin 1988, in press), the spatial boundaries of what we call a "population" or "community" usually cannot be specified unambiguously, and so ecological patterns and processes ideally should be examined across a range of spatial scales. In practice, in experimental community ecology there usually is a maximal spatial scale that is logistically feasible. At or near these logistic limits, one way to conceptualize the spatial processes that have been necessarily excluded from the experimental system is to carry out a thought experiment, schematically illustrated in Figure 2 (after Brown and Gibson 1983; Holt in press 6). Imagine that the area defined to be the "local community" is walled off by an invisible force-field that cuts off dispersal. The magnitude and rate of change in population size and species composition in the patch following isolation measures the importance of dispersal in the dynamics of the initial, non-isolated community. Habitat fragmentation creates an archipelago of patches varying in size and degree of isolation, and so is a complex realization of this thought experiment.

A variety of responses on different time scales may occur in a freshly isolated local community (see Holt, in press (a) for more detail). Four such responses, with case studies from our fragmentation project that seem to fit them, are described below.

### Historical Source-pool Effects

There is always some temporal scale over which dispersal linking a local community to a larger source pool is relevant to understanding the species composition of that community. The real question for terrestrial community ecologists (as opposed to historical biogeographers) is whether or not dispersal episodes subsequent to the initial colonization event that "seeded" the local community with a given species must be considered to explain its persistence or abundance there.

Certain species in a local community might well show no discernible effect of cutting off dispersal with the surrounding landscape, over the time scale with which one is concerned.

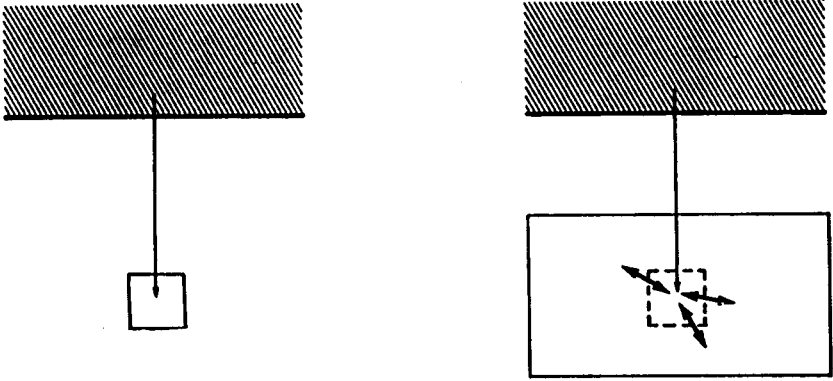


Figure 2. A schematic representation of a thought experiment. To assess regional influences on a local community, indicated by dotted lines (right), one should imagine that dispersal is cut off, in effect creating an isolated small patch (left). In empirical fragmentation studies (e.g., the NESA patch study), where habitat fragments are surrounded by partial or complete barriers to dispersal, one can compare small patches to samples of the same size taken at random from large patches. (Reprinted by permission from Holt, in press, h).

As a case in point, a classical theory of plant succession is the "initial floristic composition" hypothesis. Egler (1954) proposed that chance determines the collection of starting propagules available at the time a site becomes available for succession; subsequent dynamics, he surmised, reflect a sorting out of this initial array of species, in accord with their different life histories and interspecific interactions. Spatial processes may determine the initial condition of the community (e.g., the relative abundance of seeds in a seed bank may reflect the rain of seeds over a broader landscape), but may not matter much once succession starts.

Some patterns in our plant community data are consistent with this idea. Our system displays the expected total species vs. total area relationship (MacArthur and Wilson 1967, see Figure 3a). But if one examines the relationship between species richness per unit area (e.g., sampling quadrat) and the total area of a patch, there is no effect whatsoever of patch area on local species richness (Figure 3b). Local species richness, in fact, was higher during the first year of our study than it has been in any subsequent year, presumably because a diverse preexisting seed bank was present, ready to spring up after the final wheat harvest. Most of the species now present were in that initial community, and succession has mainly consisted of changes in their relative abundances, rather than the addition of species by long-distance colonization. Application of standard ordination techniques used in plant community ecology (e.g., reciprocal averaging, canonical correlation analysis) fails to generate significant

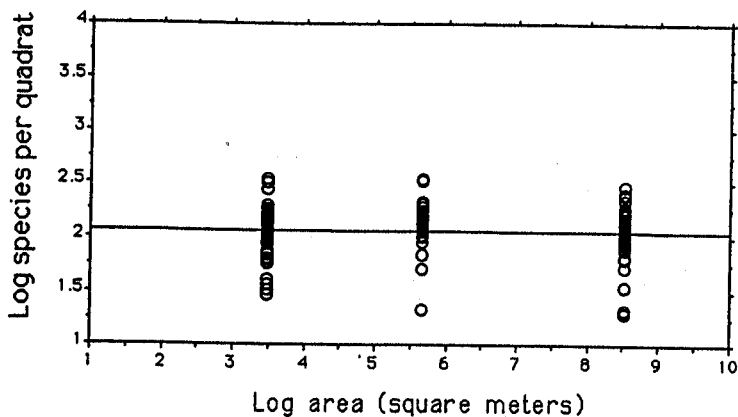
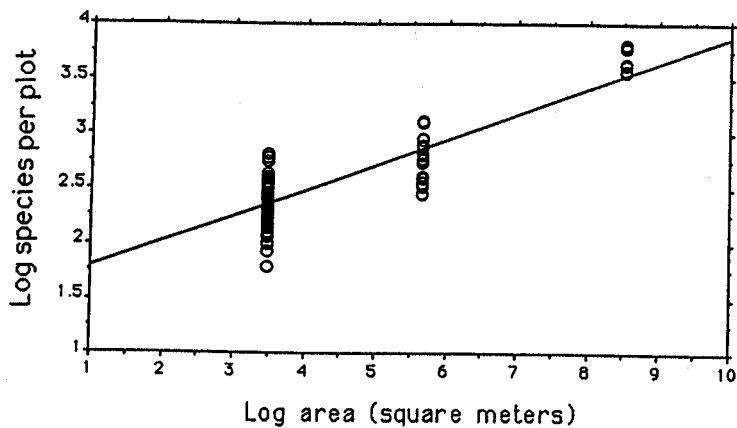


Figure 3. Two kinds of species-area relations for the plant community of the NESA patch study. The top figure shows that total species richness per patch increases with total patch size (as is typical in island biogeographic surveys). The bottom figure shows that local species richness (= the number of species present in permanent, 1 m<sup>2</sup> quadrats) is independent of patch size. (Reprinted by permission from Holt, in press, a).

aggregate axes separating the plant communities occupying different-sized patches. This suggests that there is no systematic impact of patch size on the temporal development of the vegetation. Moreover, there is a temporal autocorrelation for permanent quadrats in species richness, which has decayed with increasing sampling interval but persists even between 1985 and the present (Holt et al., ms.). In other words, the spatial and temporal patterning of species richness during succession on a given patch seems largely to involve an unfolding of a structure latent in the initial conditions of that patch, with little indication of spatial dynamics such as colonization from outside the system. Dispersal from the surrounding landscape was doubtless important as part of the historical explanation of the initial condition of our site, and the significance of dispersal is of course beginning to increase as woody species progressively invade. To a first approximation, however, such dispersal appears relatively unimportant in determining the broad pattern or rate of local succession in our system following site initiation.

### The Spatial Implications of Species' Autecological Requirements

Species differ greatly in the spatial scale required to successfully complete their life cycles (Wiens 1989). Most communities contain a few (and sometimes a great many) species that could not persist as resident members for even one generation, were that community isolated (as in our thought experiment). For instance, large-bodied species with large home range requirements (Peters 1983) should quickly disappear from isolated communities smaller than a single home range. Likewise, many species exploit predictable temporal variation in the environment by migrating among distinct habitats; such species should vanish following isolation. Because these vulnerable species are a biased subset of a local community, fragmentation should lead to a "nesting" in community composition, with fragments containing predictable subsets of the original community. Evidence from biogeographic surveys supports this hypothesis (e.g., Patterson and Atmar 1990).

Taking our system as a whole, certain species (e.g., raptorial birds) would rapidly disappear following isolation from the surrounding landscape matrix. We believe that the spatial expression of autecology requirements also helps to explain the distribution of one member of the small mammal community on our site (Figure 4). The three small mammal species regularly found on the study site, and their respective average body sizes (adult females) are as follows: hispid cotton rats (*Sigmodon hispidus*, 135 g), prairie voles, (*Microtus ochrogaster*, 43 g), and deer mice (*Peromyscus maniculatus*, 20 g). Resident populations of the large-bodied cotton rat are present on the large patches, but on small patches individuals are rarely captured and are virtually never recaptured there (Foster and Gaines 1991) suggesting that small patches are actively selected against by dispersing individuals. The overall distribution of this species in our fragmented landscape almost surely reflects its autecology, and in particular, its home range requirements.

We initially predicted that all three mammal species would be less abundant on smaller patches. This holds for *S. hispidus*, the largest species, but, to our surprise, the other two species achieved their highest densities on smaller patch sizes. In fact, the modal abundances of these three species neatly sort out by body size on different patch sizes (Figure 4)! This intriguing pattern has been present throughout our study, though changing in sharpness with fluctuations in density. Our current hypothesis to explain this distributional pattern involves the interplay of source-sink dynamics and interspecific competition. Before describing this, it is useful to deal with source-sink dynamics at a more general level.

## Source-Sink Population Structures in Heterogeneous Landscapes

For mobile organisms, the effect of fragmentation should reflect individual spatial behavior. Vertebrate community ecologists have explored the consequences of one kind of dispersal behavior—optimal habitat selection—for population dynamics and community structure (Holt 1984, 1985, 1987, in press, a; Sih 1987; Morris 1987; Rosenzweig 1991; Pulliam and Danielson 1991). A principal result of habitat selection theory (Milinski and Parker 1991) is that if individuals choose to reside in habitats where they have the highest fitness, then the distribution of individuals among habitats is adjusted toward the "ideal free distribution" (Fretwell 1972) in which individual fitness is equalized across habitats. The prediction of an ideal free distribution rests on several assumptions (Milinski and Parker 1991): 1) individuals should be able to move freely among habitats; 2) individuals can assess habitat-specific fitness accurately and without cost; and 3) individuals are not excluded from some habitats by intraspecific interference competition.

Relaxing these assumptions leads to source-sink population structures (Holt 1985, Shmida and Wilson 1985, Pulliam 1988, Wiens 1989, Pulliam and Danielson 1991). If in some high-quality habitats ("sources") a species' rate of reproduction exceeds its rate of mortality, whereas in other low-quality habitats ("sinks") its reproduction is less than its mortality, a net flux of dispersers away from sources may sustain populations in sinks. Several distinct mechanisms can produce source-sink population structures in heterogeneous environments, including: 1) density-independent dispersal (Holt 1985), 2) time or energy costs of dispersal (Rosenzweig 1974, 1991), and 3) intraspecific preemptive or interference competition (Pulliam 1988).

Source-sink dynamics is beginning to receive explicit attention from theoretical ecologists (Holt 1985, 1987, in press a; Pulliam 1988; Pulliam and Danielson 1991), and is indeed implicit in many earlier studies (e.g., Levin 1974). Source-sink effects should be most noticeable over moderate spatial scales (e.g., a small multiple of the root-mean-square dispersal distance of individuals), and where there is a slow rate of population decline in the sink. A simple continuous-generation model illustrates the latter point. Assume that density source saturates at  $N_{\text{source}}$ , that these individuals continue to reproduce at a per capita rate  $r_{\text{source}}$ , and that these excess individuals are forced into a sink where the expected per capita growth rate is  $r_{\text{sink}}$  (by assumption,  $r_{\text{sink}}$  is negative in a sink). The rate of change of the sink population is described by

$$\dot{N}_{\text{sink}} = [\text{immigration}] + [\text{local recruitment}] = N_{\text{source}}r_{\text{source}} + N_{\text{sink}}r_{\text{sink}}$$

and the equilibrium abundance of the sink population is

$$N_{\text{sink}}^* = N_{\text{source}}r_{\text{source}}/|r_{\text{sink}}|.$$

A large sink population may be maintained if the rate of decline in the sink is small and the rate of recruitment in the source is large. Analogous predictions emerge from a wide range of models (Holt in press (a)).

Source-sink effects potentially have important implications for community structure and dynamics (Holt 1984, 1985, in press, a; Pulliam 1988; Rosenzweig 1989; Bowers and Sooley 1991). Optimal habitat selection (assuming the conditions for an ideal free distribution) can magnify the effects of spatial heterogeneity in the environment, sharpening

habitat partitioning patterns and promoting the coexistence of competitors (Chesson and Rosenzweig 1991). By contrast, given the kinds of dispersal that lead to source-sink dynamics, 1) habitat partitioning is blurred, for immigration permits species to persist in habitats from which they would otherwise be excluded (Levin 1974); and 2) a species may be individually superior in a particular habitat, yet competitively suppressed there because of a "spillover" of competitors from other habitats—in extreme cases even leading to competitive exclusion (Christiansen and Fenchel 1977, Holt, in press, a). Indeed, whether or not a habitat is a source or a sink for a species may depend upon the presence and abundance of competitors or predators (Holt in press, a).

### A Threefold Example of Source-Sink Dynamics?

Convincing examples of sink populations maintained by density-independent dispersal have been found in several plant species (Keddy 1981, Kadmon and Shmida 1990). However, no direct experimental demonstrations of source-sink population structures exist for vertebrates, though considerable indirect evidence suggests that source-sink structures may be important in vertebrate communities. Many small mammal species display among-habitat variance in fitness and intraspecific aggression (e.g., white-footed mice, Morris 1991; Pulliam and Danielson 1991), a pattern consistent with source-sink population structures. Previous field experiments have shown that preventing dispersal in small mammals can lead to increases in local density (the "fence effect," Krebs et al. 1969), but it is not known whether these local increases are accompanied by population declines elsewhere in the landscape.

We believe that source-sink dynamics are a significant aspect of the small mammal distributions shown in Figure 4. Our reasoning and preliminary supporting evidence, species by species, are as follows.

*Cotton rats.* As noted above, this species is resident on large patches but essentially absent on small patches. It is present in low abundance on medium patches. Individuals there are recaptured at a low rate, but do not persist for long (Gaines et al., in press, a). Moreover, the presence of individuals on the medium patches is correlated with population highs on the large patches. It is reasonable to surmise that cotton rats on the medium patches are a transient sink population maintained by emigration from large patches.

*S. hispidus* is the likely competitive dominant in the system. In the lab, it aggressively dominates *M. ochrogaster* (Terman 1974). Several previous studies have shown that *M. ochrogaster* densities decline when *S. hispidus* is abundant (Glass and Slade 1980, Fleharty and Olson 1969, Frydenhall 1969). We have also observed a significant negative temporal correlation between *S. hispidus* and *P. maniculatus* densities ( $r = -0.26$ ,  $p < 0.05$ ), indicating that *S. hispidus* may also competitively suppress *P. maniculatus*. Because *S. hispidus* is relatively uncommon in small and medium patches (we believe by virtue of its large spatial requirements), both *M. ochrogaster* and *P. maniculatus* may have a refuge from competition in these smaller patches.

*Prairie voles.* *Microtus ochrogaster* is most abundant on medium patches, which we think are sources for it. We believe this species tends to be excluded from the large patches by *S. hispidus*, and that it persists there because of immigration. Our trapping data indicate that a greater proportion of between-patch movements by *M. ochrogaster* occurred from smaller to large patches than in the reverse direction. These results suggest that large patches



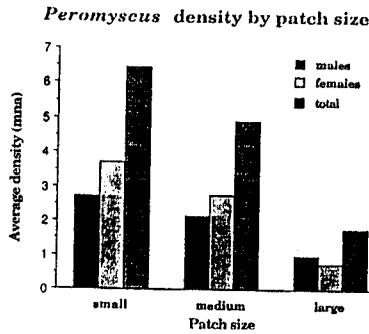
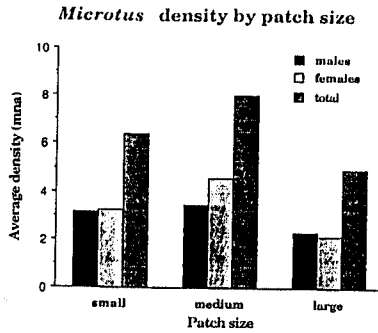
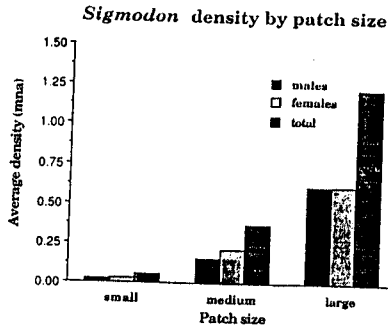


Figure 4. The distribution of three small mammal species on an experimental gradient in patch size. Each species is respectively most abundant on a different patch size. (From data in Foster and Gaines 1991, Gaines et al., in press).

are indeed sinks. *M. ochrogaster* is relatively common in the small patches. But small patches may be sinks for this species, too, because individual persistence rates are much lower on the small patch clusters than on larger patches (Gaines et al., in press, a). This suggestion is consistent with the observed age structure, which is biased toward nonreproductive subadults on small patches (Gaines et al., in press, b).

*M. ochrogaster* could be behaviorally dominant to *P. maniculatus*. We have no direct evidence of interference between these two particular species, but other studies have shown that members of the genus *Microtus* aggressively dominate smaller rodents (Linzey 1984, Blaustein 1980), including *Peromyscus* (Grant 1971).

*Deer mice.* *Peromyscus maniculatus* may have a refuge from interspecific competition in the small patches and in the interstitial area. The high density of *P. maniculatus* on the small patches could be due to this species' ability to exploit, to a moderate degree, the interstitial mowed areas (Foster and Gaines 1991), which in turn allows it to use small patches. Low-density *P. maniculatus* populations on the larger patches could be sink populations maintained by dispersal from small patches and the interstitial area; most movement occurs from small to larger patches, and age structure is biased toward nonreproductive younger individuals in larger patches.

Working hypothesis. The following table summarizes our working hypothesis for the three species' respective source-sink structures in our system:

PATCH SIZE	SPECIES BY BODY SIZE		
	Sigmodon	Microtus	Peromyscus
Large	Source	Sink	Sink
Medium	Sink	Source	Sink
Small	Sink	Sink	Source

In the entries below the diagonal, a patch is a sink because it is too small given that species' autecology; in the entries above the diagonal, a patch is a sink because it contains one or more dominant competing species. We intend to test this hypothesis by using semipermeable enclosures to manipulate dispersal, with and without competitors. For instance, removing the two larger species should convert the two larger patches from sinks into sources for deer mice.

### Metapopulation Dynamics

In its most general sense, a "metapopulation" is defined as a system of local populations coupled by dispersal (Hanski 1991). Usually the term is used more narrowly to describe systems in which local populations go extinct and are then recolonized. In the original metapopulation models of Levins and others (see Hanski 1991), the populations in the metapopulation are on average assumed to be statistically homogeneous, with localized disturbances leading to a probabilistic distribution in extinctions. Dispersal allows a species to exploit this variance in phase among sites, thereby forestalling regional extinction even though every local population eventually goes extinct.

A recent review by Harrison (1991) suggests that this classical metapopulation structure

is rather rare. Instead, one more commonly observes mainland-island and source-sink structures, in which a few local populations resist extinction and permit a species to persist despite frequent extinctions in other local populations. The "size" of a metapopulation is given by the number of constituent local populations making it up. Large metapopulations inevitably occupy a larger total area than do small metapopulations. Given that, in the real world, there is usually a relationship between area and habitat heterogeneity, large metapopulations almost inevitably will subsume substantial variation in local demographic parameters, colonization, and extinction rates. This spatial heterogeneity permits a number of important processes to operate, including source-sink dynamics within single species, the sorting out of species in communities along spatial gradients, and the regional balancing of colonizations and extinctions.

Many plant species in our experimentally fragmented landscape have short-distance dispersal (e.g., vegetative growth or large seeds) and can have large populations even within our smallest patches. For such species, our system may usefully be viewed as a hierarchically structured metapopulation. Each successional patch is a metapopulation of contiguous local populations, potentially coupled more strongly by dispersal among themselves than to populations on other patches; patch size scales the "size" of a metapopulation. The classic "area effects" of island biogeography may in part result from the internal spatial dynamics of such contiguously coupled metapopulations (Holt, in press, b).

There are intriguing hints in our data to suggest the operation of within-patch metapopulation dynamics (Holt et al., ms.). Because our plant samples are taken within grids of permanent quadrats, we can examine temporal trends in the spatial structure of the community. Figure 5 shows the spatial scaling of community dissimilarity at two points in succession (1985, the summer following the fall 1984 site initiation; and 1989, four years into succession). The data leading to this figure consist of all quadrat pairs within a given patch or patch cluster spanning .5 ha. For each quadrat pair, we computed a measure of dissimilarity in community composition (percentage remoteness, see figure legend), which ranges from 0 when two community samples have identical species lists and relative abundances of those species, to 1 when the species lists of the two samples are nonoverlapping (Pielou 1984).

Early in succession, the further apart two points are, the more dissimilar are the plant communities on those points. Interestingly, paired quadrats in the large patches separated by  $> 50$  m in the large patches are more heterogeneous than paired quadrats the same distance apart in the medium-sized or smaller patches. It is likely, we suspect, that this reflects a more homogeneous physical environment in the smaller patches in the very first year of succession, but unfortunately we do not have the data to support or refute this suggestion.

As succession proceeded, community dissimilarity grew at all spatial scales, but particularly at small scales. The initial spatial scaling of between-community heterogeneity dissipates; so that the three patch size classes are essentially indistinguishable at scales  $\geq 10$  m. The exception to this trend is at the smallest spatial scale, where the rate of divergence between nearby quadrats on the large patches has been much less than on the smaller patches. This is consistent with the idea that there is some kind of short-range spatial coupling on large patches that tends to break down on smaller patches.

An additional line of evidence pointing to such coupling comes from analyses of local population persistence, defined here as the presence of a given species in a permanent quadrat in successive years. When we compute persistence for each vascular plant species in our system, and then combine the species into two broad functional groups—clonal species, which

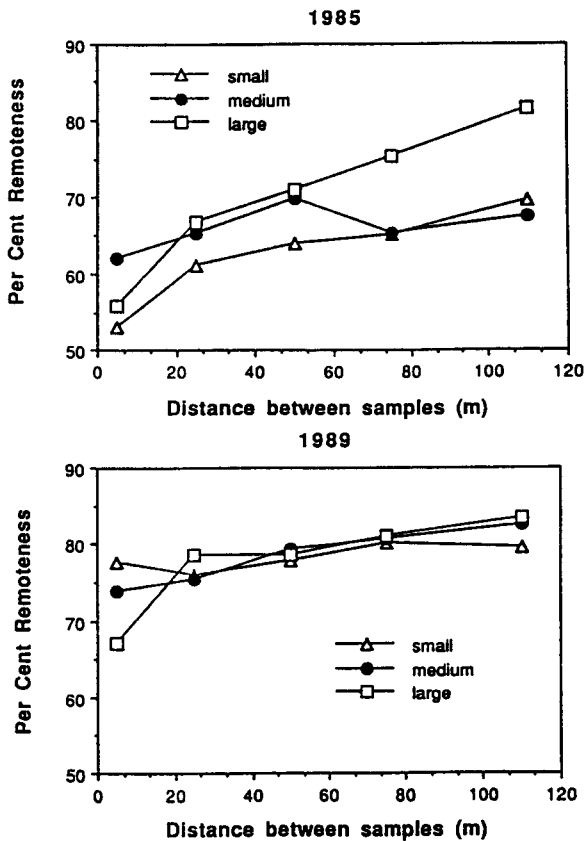


Figure 5. The spatial scaling of community dissimilarity with distance at two points in succession. The plant data includes point cover estimates in a grid of permanent quadrats, sampled from 1984 until the present. Let  $N_{i1(t)}$  and  $N_{i2(t)}$  be the amounts of plant species  $i$  in quadrats 1 and 2 at sampling period  $t$ , and  $s(t)$  the total number of species in both quadrats combined. A metric measure of dissimilarity between pairs of community samples (Pielou 1984) is percentage remoteness, PR, defined as

$$PR = 100 \times \left( 1 - \frac{\sum_{i=1}^s \min(N_{i1}(t), N_{i2}(t))}{\sum_{i=1}^s \max(N_{i1}(t), N_{i2}(t))} \right)$$

We computed PR for each quadrat pair within the .5 ha large patches, and within the .5 ha clusters of small and medium patches. The figure plots PR (for a given patch size class) as a function of the distance separating the quadrat pair. By 1989, the initial strong spatial scaling of community dissimilarity had largely disappeared, except at small spatial scales within the large patches. (Holt et al., ms.)

reproduce in large measure by vegetative growth over short spatial scales; and non-clonal species reproducing by seed, which can be dispersed over longer distances—we find that over the three years of the study, the local persistence of non-clonal species was independent of patch size, but clonal species persisted significantly better on larger patches (Figure 6). Individuals or ramet populations of clonal species are akin to amoebae moving over the landscape. The probability that a species will persist on a given sample area (as in the embedded quadrat of Figure 2) may be enhanced because there may be a greater opportunity for rapid re-colonization following a local extinction, and possibly a lower probability of extinction in the first place (Holt, in press, b). These are essentially metapopulation effects reflecting the internal spatial structure of the patch.

#### CODA

The four spatial processes described above differ in the relationship assumed between the probability of extinction and the amount of time following isolation, relative to a comparable, non-isolated community. If dispersal is only of historical importance, there should be no increase in local extinction rates because of isolation. If, by contrast, individuals in a species require more space than contained within the local community to complete their life cycle, extinction should be very rapid following isolation. Sink populations deterministically go extinct following isolation, at a rate dependent upon initial densities and the rate of population decline. In a classical metapopulation, some isolated populations may last a long period of time. As in our experimental study of habitat fragmentation, any given community is likely to include species that fit each of these spatial syndromes.

The above ruminations have a decidedly terrestrial cast. The relative importance of the various spatial processes outlined above are likely to be quite different in marine vs. terrestrial ecosystems. It is not obvious that our thought experiment--isolating a patch of land and watching the subsequent decay of the trapped community therein--has much relevance, even as a metaphor, for marine systems. Many terrestrial communities, we tentatively suggest, have a substantial number of species for which dispersal is relatively unimportant in determining their persistence and abundance (except at very small spatial scales, or if one is considering

large biogeographic time scales). Over evolutionary time, this cadre of low-dispersal species finds expression in endemic species with highly restricted geographic ranges, and in spatially reticulated patterns of genetic differentiation within widespread species. Such species are essentially absent in marine communities. Source-sink dynamics, by contrast, are likely to be at least as important in marine systems as in terrestrial systems, if not more so.

A largely unexplored dimension of community ecology is to ascertain how local community structure reflects the interplay of the different spatial processes different species in the ensemble. For instance, the vast literature on the structure and associated with dynamics of food webs (Cohen et al. 1990) has until very recently ignored the potential importance of spatial dynamics in governing food webs (Holt, in press, b). Yet there is often a strong positive correlation between the trophic rank of a species and the spatial scale relevant to its dynamics. Grasping the full implications of spatial dynamics in determining the structure of local communities is, we believe, one of the most important challenges facing community ecologists today.

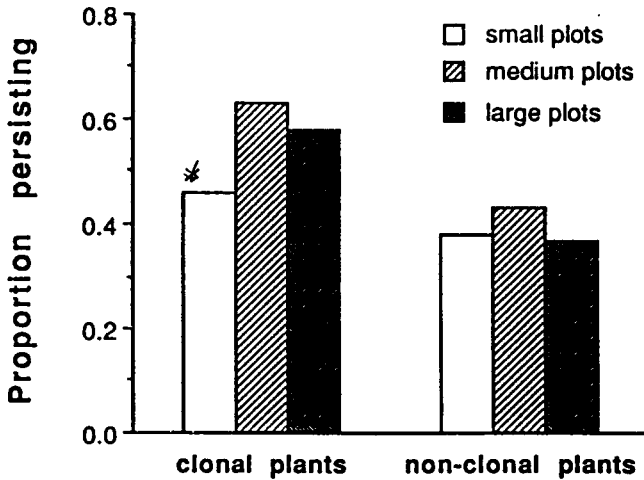


Figure 6. Local population persistence as a function of patch size and life history. If  $N_{ij}(t)$  is the abundance of plant species  $i$  on quadrat  $j$  in sampling year  $t$ , our operational measure  $P_{ij}$  of local population persistence (for samples one year apart) is that a population persists ( $P_{ij} = 1$ ) if  $N_{ij}(t + 1) > 0$ , given that  $N_{ij}(t) > 0$ , and that a population does not persist ( $P_{ij} = 0$ ) if  $N_{ij}(t + 1) = 0$ , given that  $N_{ij}(t) > 0$ . For each species on each patch size, we computed its mean persistence during the years 1987-1990. We then categorized species by basic life history into those with clonal growth (runners, rhizomes, etc.), and those reproducing solely by seed. Clonal species collectively show a significantly higher rate of local persistence on medium and large patches, compared to small patches. Non-clonal species show no effect of patch size, and overall persist less well than do clonal species (Robinson et al., in press).

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## REFERENCES

- Bazzaz, F.A. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology* 49:924-936.
- Blaustein, A. R. 1980. Behavioral aspects of competition in a three-species rodent guild of coastal California. *Behav. Ecol. Sociobiol* 6:247-255.
- Bowers, M.A., and J.L. Dooley, Jr. 1991. Landscape composition and the intensity and outcome of two-species competition. *Oikos* 60:180-186.
- Brown, J.H., and A.C. Gibson. 1983. *Biogeography*. Mosby, St. Louis.
- Chesson, P., and M. Rosenzweig. 1991. Behavior, heterogeneity, and the dynamics of interacting species. *Ecology* 72:1187-1195.
- Christiansen, F.B., and T.M. Fenchel. 1977. *Theories of Populations in Biological Communities*. Springer-Verlag: New York.
- Cohen, J.E., F. Briand, and C.M. Newman. 1990. *Community Food Webs*. Springer-Verlag, New York.
- Dickman, C.R. 1987. Habitat fragmentation and vertebrate species richness in an urban environment. *J. Appl. Ecology* 24:337-351.
- Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio* 4:412-417.
- Fahrig, L., and J. Paloheimo. 1988. Determinants of local population size in patchy habitats. *Theor. Pop. Biol.* 34:194-213.
- Fleaharty, E.D., and L.E. Olson. 1969. Summer food habitats of *Microtus ochrogaster* and *Sigmodon hispidus*. *J. Mamm.* 50: 475-486.
- Foster, J., and M.S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72:1358-1373.
- Fretwell, S.D. 1972. *Populations in Seasonal Environments*. Princeton University Press, Princeton.
- Frydenhall, M.J. 1969. Rodent populations on four habitats in central Kansas. *Trans. Kansas Acad. Sci.* 72:213-222.
- Gaines, M.S., G.R. Robinson, J.E. Diffendorfer, R.D. Holt, and M.L. Johnson. In press (a). The effects of habitat fragmentation on small mammal populations. In: *Wildlife 2001: Populations*, D.R. McCullough and R.H. Barret (eds.).
- Gaines, M.S., J. Foster, W. Sera, J.E. Diffendorfer, and R.D. Holt. In press (b). Population processes and biodiversity. *Trans. N. Amer. Wildlife and Natural Resources Conference* 57
- Gaines, M.S., A.M. Vivas, and C.L. Baker. 1979. An experimental analysis of dispersal in fluctuating vole populations: Demographic parameters. *Ecology* 60:814-828.
- Glass, G.E., and N.A. Slade. 1980. Population structure as a predictor of spatial association between *Sigmodon hispidus* and *Microtus ochrogaster*. *J. Mammal.* 61:473-485.
- Grant, P.R. 1971. Experimental studies of competitive interaction in two-species systems III. *Microtus* and *Peromyscus* species in enclosures. *J. Anim. Ecol.* 40:323-350.
- Hairston, N.G., Sr. 1989. *Ecological Experiments: Purpose, Design, and Execution*. Cambridge University Press, Cambridge.
- Hanski, I. 1991. Single-species metapopulation dynamics: Concepts, models, and observations. *Biol. J. Linn. Soc.* 42:17-38.
- Harrison, S. 1991. Local extinction in a metapopulation context: An empirical evaluation. *Biol. J. Linn. Soc.* 42:73-88.
- Hastings, A. 1990. Spatial heterogeneity and ecological models. *Ecology* 71:426-428.
- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* 124:377-406.
- \_\_\_\_\_. 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.* 28:181-208.
- \_\_\_\_\_. 1987. Prey communities in patchy environments. *Oikos* 50:276-290.
- \_\_\_\_\_. In press (a). Ecology at the mesoscale: The influence of regional processes on local communities. In: R. Ricklefs and D. Schluter (eds.). *Community Diversity: Historical and Geographical Perspectives*, University of Chicago Press, Chicago.
- \_\_\_\_\_. In press (b). Internal spatial dynamics: A neglected facet of island biogeography. *Theor. Pop.*

## Biol.

- Holt, R.D., G.R. Robinson, and M.S. Gaines. Manuscript. Vascular plant diversity and succession in experimental habitat fragments.
- Johnson, M.L., and M.S. Gaines. 1987. The selective basis for dispersal of the prairie vole, *Microtus ochrogaster*. *Ecology* 68:684-694.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* 326:388-390.
- Kareiva, P., and M. Anderson. 1988. Spatial aspects of species interactions: The wedding of models and experiments. In: A. Hastings (ed.). *Community Ecology*. Springer-Verlag, New York.
- Kadmon, R., and A. Shmida. 1990. Spatiotemporal demographic process in plant populations: An approach and a case study. *Am. Nat.* 135: 382-397.
- Keddy, P.A. 1981. Experimental demography of the sand-dune annual, *Cakile eduntula*, growing along an environmental gradient in Nova Scotia. *J. Ecol.* 69: 615-630.
- Krebs, C.J., B. Keller, and R. Tamarin. 1969. *Microtus* population biology. *Ecology* 50:587-607.
- Levin, S.A. 1974. Dispersion and population interactions. *Am. Nat.* 108:207-228.
- \_\_\_\_\_. 1988. Pattern, scale, and variability: An ecological perspective. In: A. Hastings (ed.). *Community Ecology*. Springer-Verlag, New York, pp. 1-24.
- \_\_\_\_\_. In press. Concepts of scale at the local level.
- Linzey, A.V. 1984. Patterns of coexistence in *Synaptomys cooperi* and *Microtus pennsylvanicus*. *Ecology* 56:382-393.
- Louda, S.M., K.H. Keeler, and R.D. Holt. 1990. Herbivore influences on plant performance and competition interactions. In: J.B. Grace and D. Tilman (eds.). *Perspectives on Plant Competition*. Academic Press, New York, pp. 414-444.
- Lovejoy, T.E., J.M. Rankin, R.O. Bierregard Jr., K.S. Brown Jr., L.A. Emmons, and M.E. Van der Voort. 1984. Ecosystem decay of Amazon forest remnants. In: M.H. Nitecki (ed.). *Extinctions*. University of Chicago Press, Chicago, pp 295-326.
- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton.
- Milinski, M., and G.A. Parker. 1991. Competition for resources. In: J.R. Krebs and N.B. Davies (eds.). *Behavioural Ecology*: Sunderland, MA, pp. 137-169.
- Morris, D.W. 1987. Habitat-dependent population regulation and community structure. *Evol. Ecol.* 2:232-252.
- \_\_\_\_\_. 1991. Fitness and patch selection in white-footed mice. *Am. Nat.* 138:702-716.
- Patterson, B.D., and W. Atmar. 1990. Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* 28:65-82.
- Peters, R.H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Pielou, E.C. 1984. *The Interpretation of Ecological Data*. Wiley, New York.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* 110:107-119.
- Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *Am. Nat.* 137:50-60 (supplement).
- Quinn, J.F., and S.P. Harrison. 1987. Effects of habitat fragmentation on species richness: Evidence from biogeographic patterns. *Oecologia* 75:132-140.
- Ricklefs, R.E. 1987. Community diversity: Relative roles of local and regional processes. *Science* 235:167-171.
- Robinson, G.R., and J.F. Quinn. 1988. Extinction, turnover and species diversity in an experimentally fragmented California annual grassland community. *Oecologia* 76:71-82.
- Robinson, G.R., R.D. Holt, M.S. Gaines, S.P. Hamburg, M.L. Johnson, H.S. Fitch, and E.A. Martinko. In press. Consequences of habitat fragmentation vary within and among ecosystem components. *Science*.
- Rosenzweig, M.L. 1974. On the evolution of habitat selection. Proceedings of the First International Congress of Ecology. Wageningen, Centre for Agricultural Publishing and Documentation, The Hague, Netherlands, pp. 401-404.
- \_\_\_\_\_. 1989. Habitat selection, community organization and small mammal studies. In: D.W. Morris, Z. Abramsky, B.J. Fox, and M.R. Willig (eds.). *Patterns in the Structure of Mammalian Communities*. Texas Tech University Press, Lubbock, pp. 5-23.



- Abramsky, B.J. Fox, and M.R. Willig (eds.). *Patterns in the Structure of Mammalian Communities*. Texas Tech University Press, Lubbock, pp. 5-23.
- \_\_\_\_\_. 1991. Habitat selection and population interactions: The search for mechanism. *Am. Nat.* 137:5-28 (supplement).
- Rosenzweig, M.L., Z. Abramsky, B. Kotler, and W. Mitchell. 1985. Can interaction coefficients be determined from census data? *Oecologia* 66: 194-198.
- Roth, J.D., and R.D. Holt. Manuscript. Habitat selection of birds in a fragmented landscape: Effects of habitat structure, patch size, and edge on a bird community in northeastern Kansas.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460-1466.
- Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18-32.
- Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. *J. Biogeography* 12:1-20.
- Sih, A. 1987. Prey refuges and predator-prey stability. *Theor. Pop. Biol.* 31:1-12.
- Teravainen, E. In press. Distribution of the soldier beetle *Chauliognathus pennsylvanicus* in a spatially fragmented environment. *Oecologia*.
- Terman, M.R., 1974. Behavioral interactions between *Microtus ochrogaster* and *Sigmodon*: A model for competitive exclusion. *J. Mamm.* 55: 705-719.
- Wiens, J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385-397.
- Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. In: M.E. Soule (ed.). *Conservation Biology*. Sinauer, Sunderland, MA, pp 237-256.