

Patch size effects on plant species decline in an experimentally fragmented landscape

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Abstract. Understanding local and global extinction is a fundamental objective of both basic and applied ecology. Island biogeography theory (IBT) and succession theory provide frameworks for understanding extinction in changing landscapes. We explore the relative contribution of fragment size vs. succession on species' declines by examining distributions of abundances for 18 plant species declining over time in an experimentally fragmented landscape in northeast Kansas, USA. If patch size effects dominate, early-successional species should persist longer on large patches, but if successional processes dominate, the reverse should hold, because in our system woody plant colonization is accelerated on large patches. To compare the patterns in abundance among patch sizes, we characterize joint shifts in local abundance and occupancy with a new metric: rank occupancy–abundance profiles (ROAPs). As succession progressed, statistically significant patch size effects emerged for 11 of 18 species. More early-successional species persisted longer on large patches, despite the fact that woody encroachment (succession) progressed faster in these patches. Clonal perennial species persisted longer on large patches compared to small patches. All species that persisted longer on small patches were annuals that recruit from the seed bank each year. The degree to which species declined in occupancy vs. abundance varied dramatically among species: some species declined first in occupancy, others remained widespread or even expanded their distribution, even as they declined in local abundance. Consequently, species exhibited various types of rarity as succession progressed. Understanding the effect of fragmentation on extinction trajectories requires a species-by-species approach encompassing both occupancy and local abundance. We propose that ROAPs provide a useful tool for comparing the distribution of local abundances among landscape types, years, and species.

Key words: abundance; extinction; grassland; habitat fragmentation; island biogeography theory (IBT); occupancy; ROAP; species abundance distribution; succession.

INTRODUCTION

The structure of all local communities reflects both colonization from external sources and local extinctions (MacArthur and Wilson 1967, Holt 1993). Two major areas of ecology explore how extinction influences community organization: island biogeography theory (IBT), together with its intellectual descendants metapopulation and metacommunity ecology (MacArthur and Wilson 1967, Ovaskainen and Hanski 2004, Holyoak et al. 2005), and the study of succession (Horn 1981, Pickett et al. 1987). IBT asserts that species richness reflects the influences of island area on extinction, and island isolation on colonization. Since 1967, additional theory has clarified that both island size and distance can influence both immigration and extinction processes (Brown and Lomolino 2000; Schoener, *in press*). Spatially realistic metapopulation theory likewise emphasizes the joint role of patch area and isolation as

determinants of spatial occupancy (Ovaskainen and Hanski 2004).

Because landscape fragmentation reduces habitable area and isolates remaining habitat patches, ecologists have often invoked IBT as the theoretical context for examining habitat fragmentation. All else being equal, small islands and patches have small populations, which, in turn, have elevated extinction risks (Gilpin and Soule 1986, Holsinger 2000). Although terrestrial habitat fragments are not “true” islands because some species can utilize both the fragments and the matrix (Cook et al. 2002, Fischer and Lindenmayer 2006), empirical studies have shown that, as predicted by IBT, populations on small fragments often do experience faster extinction (e.g., Pimm and Askins 1995 [birds], Schoeder et al. 2004 [ants], Joshi et al. 2006 [plants]).

Colonization and extinction are also fundamental components of ecological succession, the directional change in community composition over time (Fig. 1 inset). Many mechanisms can contribute to temporal turnover in community composition, including plant–soil feedbacks (Kardol et al. 2006), facilitation, inhibition, herbivory, life history traits, and competition–

Manuscript received 28 July 2008; revised 16 December 2008; accepted 22 December 2008. Corresponding Editor: J. Franklin.

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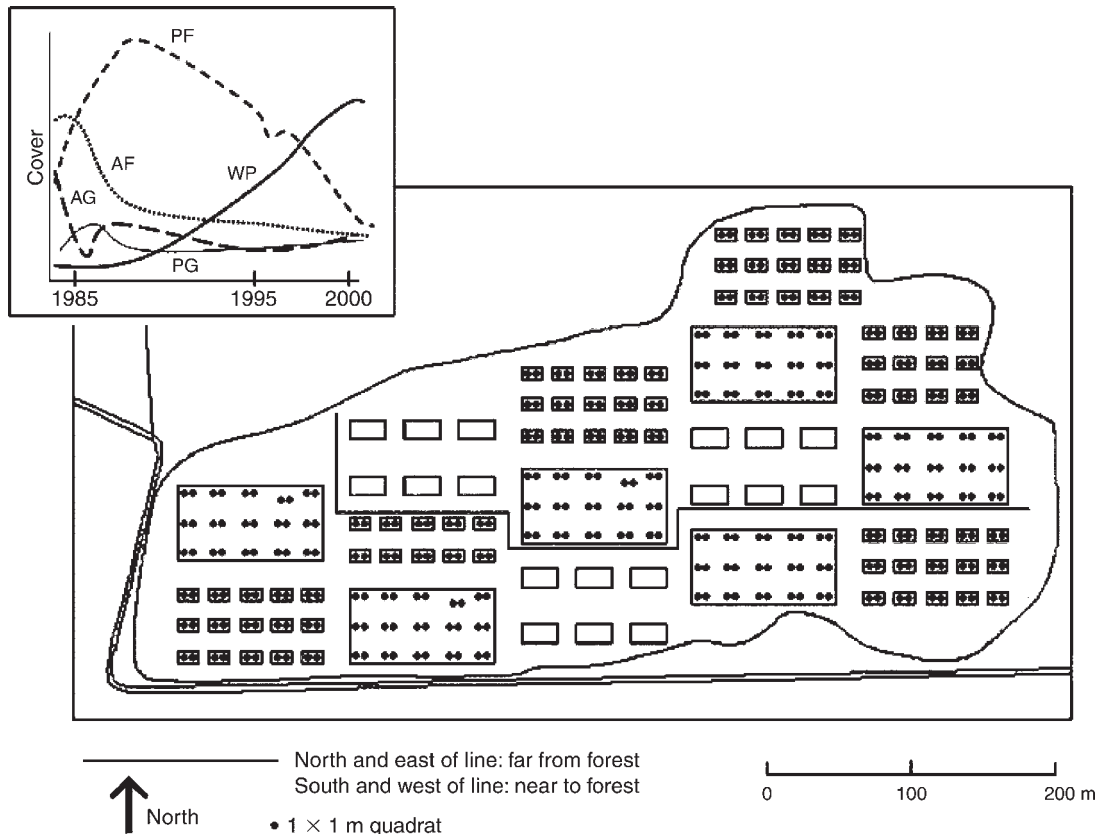


FIG. 1. The experimentally fragmented landscape in northeast Kansas, USA. Black dots represent sampling quadrats. Patches considered near vs. far from the forest source on the south side are separated by a solid line. Inset: Temporal shifts in relative abundance (cover) of life history groups in the fragmentation landscape. Key to abbreviations: AG, annual grasses; PG, perennial grasses; AF, annual forbs; PF, perennial forbs; WP, woody plants (adapted from Cook et al. [2005]). Patch size and distance effects both emerged by 1998; between 1998 and 2003, quadrats in large patches contained 20% more woody stems >2 m in height, compared to small patches (Cook et al. 2005).

colonization trade-offs (Pickett et al. 1987). Additionally, landscape features such as proximity to the seed source and size of the patch undergoing succession influence the rate at which succession proceeds (Cook et al. 2005). Specifically, sites close to a source of late-successional species undergo succession faster than distant sites (e.g., Grashof-Bokdam and Geertsema 1998, Yao et al. 1999), and large patches (which may trap more colonists, as well as allow for efficient local dispersal once a late-seral species has colonized), undergo succession more rapidly than small patches (Yao et al. 1999, Cook et al. 2005). Most studies of succession dynamics emphasize colonization (e.g., Boeken and Shachak 1998, Cutler et al. 2008), even though succession clearly involves patterns of declining abundance. Although we expect early-successional species to become rare as they approach local extinction (Christensen and Peet 1984), they can linger for surprisingly long periods at low density as succession proceeds (Pickett and Cadenasso 2005).

In their purest forms, these two bodies of theory, i.e., IBT as a spatial explanation for extinction, and

succession as a temporal one, provide contrasting predictions for the pattern of declining abundance of early-successional species in a fragmented landscape. IBT predicts that in a fragmented landscape, species will decline more rapidly on small patches. In a successional system, one expects extinction of early-successional species to happen where colonization by late-seral species occurs more rapidly (assuming colonization-competition trade-offs). We know from earlier work at our site (a landscape-scale experiment focused on the successional transition from an abandoned agricultural field to woodland in a fragmented landscape; Fig. 1) that succession, measured by the rate of encroachment by woody species, occurs significantly faster on large patches, and on patches near an established forest which is the source of late-seral propagules (Yao et al. 1999; Fig. 3, Cook et al. 2005:1272).

Our experimental design thus allows us to assess the relative influence of patch size vs. successional processes on patterns of species decline toward extinction. If early-successional species wane faster on small patches despite slower rates of colonization there by late-seral species,

then the demographic (or other) effects of small patch size emphasized in IBT and metapopulation theory would seem to have a relatively greater influence on local extinction. If early-successional species instead decline faster on large patches or patches closer to the forest source, factors associated with the more rapid rate of woody plant establishment likely have a strong influence on early-seral species' declines. Prior studies have shown that colonization in fragmented old fields is influenced by life history strategies of individual species, as well as by fragment size and distance from the colonizing source (Yao et al. 1999), and so we consider how the patterns of species' declines reflect these factors, as well.

In this paper, we examine species-specific patterns of plant extinction in an experimental system that involves the interplay of succession, patch area, and patch distance effects. Specifically, we address the following questions: (1) As secondary succession proceeds, does patch size influence the rate and pattern of decline in early-successional plant species? (2) If so, can we infer the relative importance of succession (establishment of woody plant species) vs. patch size in driving this decline? To address these questions, we explore patterns of abundance in both time and space of 18 early-successional plant species within an experimentally fragmented Kansas grassland undergoing succession. While we do not study regional extinction per se (these species are still present somewhere in our landscape), we do observe many local extinctions and assume that in this landscape, "extinction is merely the end of the path of decline" (Gaston et al. 2000).

A new approach: rank occupancy-abundance profiles (ROAPs)

Ecologists typically measure abundance in one of two ways: occupancy (proportion of sites occupied by a species) or mean local abundance (average number of individuals per site, sometimes conditional on occupancy) (Hanski 1982, Gaston 2003). During succession, we expect species abundances, by both measures, to change; what is needed is a metric capturing both aspects of change. To this end, we developed a technique to characterize species' patterns across time and space that includes both occupancy and local abundance. Though developed for our specific study, the approach is generally useful to any ecological study involving changes in occupancy and abundance.

The technique is based on a graphical representation of abundances across a landscape, which we call a "rank occupancy-abundance profile" (ROAP). ROAPs plot abundance data from all sampled locations on a single graph, thereby providing a useful visual representation of the pattern of variation in abundances within a species among sampling locations across a landscape. Essentially, ROAPs can be viewed as a single-species analog of rank-abundance plots for species abundances in community ecology (Preston 1948).

A ROAP shows three things about a species at a glance (see Fig. 2a): (1) its maximum local abundance, (2) its pattern of variation of abundances among sampling stations, and (3) its occupancy (a measure of distribution). Furthermore, ROAPs provide a useful comparative device for examining differences in patterns of abundance among landscape types, years, or species. For example, in the Kansas experimental fragmentation system, available data come from an array of permanent quadrats sampled repeatedly over time. For any single year, we can compare the ROAPs for a species on large vs. small patches (e.g., Fig. 2b). Alternatively, for a single species and patch size, comparing ROAPs among years allows us to visually assess the relative degree to which local abundance, vs. occupancy, changes during succession (e.g., Fig. 2c, d).

This metric makes few assumptions about underlying processes or the functional form of spatial patterns in abundance. Using randomization, we can apply a nonparametric statistical approach to assess differences in the distribution of abundances between experimental treatments. We first use ROAPs to examine how patch size influences species' declines during succession. Then, we use them to propose heuristic conceptual models for distinct patterns species show as they decline toward extinction.

METHODS

Study site.—The system is a large-scale landscape experiment established to explore how habitat fragmentation influences succession. Initiated in 1984 in the prairie-forest ecotone of eastern Kansas, USA (described in Holt et al. [1995] and Cook et al. [2005]), this study continues to this day (Fig. 1). The study site is located at the University of Kansas Field Station and Ecological Reserves (39°3' N, 95°12' W), 12 km north of Lawrence, Kansas. In 1984, an array of patches of three sizes (4 × 8 m, 12 × 24 m, 50 × 100 m; Fig. 1) was demarcated in a fallow agricultural field. The patch sizes and separations were determined by considering seed shadows and population sizes of early-successional plants (see Holt et al. 1995). Patches are maintained by frequent mowing of the interstitial (matrix) area; the patches themselves have been left alone to undergo natural secondary succession, as documented in earlier publications (Robinson et al. 1992, Holt et al. 1995, Yao et al. 1999, Cook et al. 2005). The perimeter of a full cluster of medium or small patches collectively spans 50 × 100 m, the same area as a large patch (where permitted by the irregular shape of the field). Thus, most clusters of small patches contain the same number of permanent sampling quadrats as a single large patch. In this analysis, we focused only on the small and large patches because there were too few medium-sized patches to warrant direct comparison among all patch sizes. Within a patch, quadrats are arranged in pairs with 4 m separating quadrats in a single pair. Quadrat pairs are separated by 12–15 m; see Fig. 1). A single small patch contains 1 quadrat pair (a cluster of

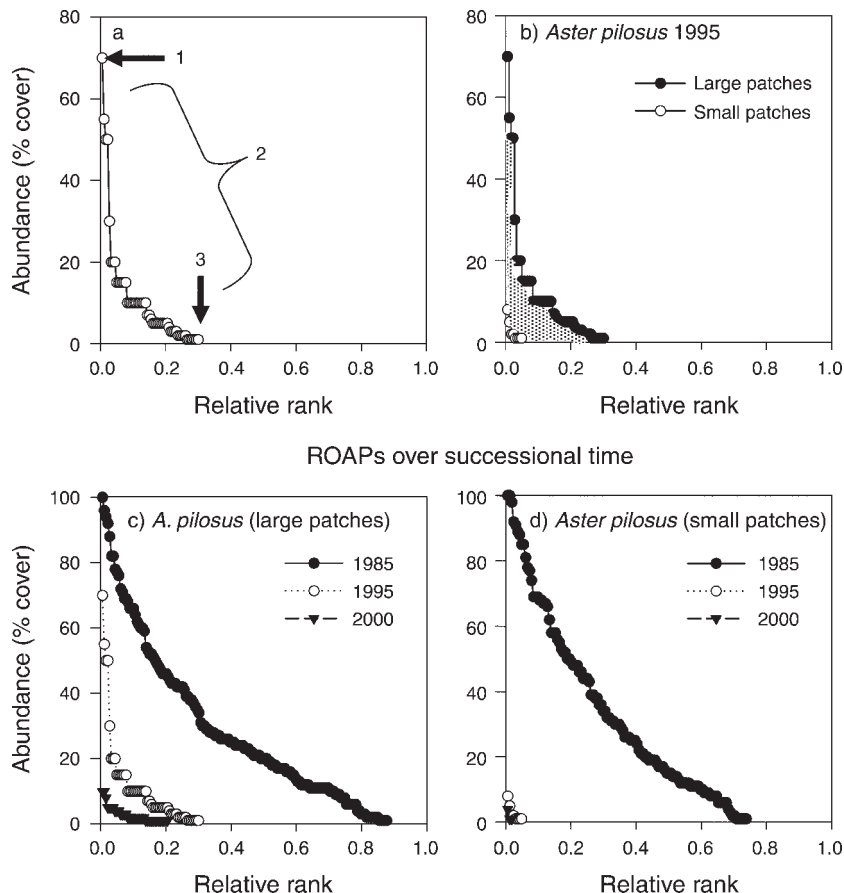


FIG. 2. (a) Sample rank occupancy-abundance profile (ROAP) for a single species. Local abundance was measured as percent cover in a 1-m² quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the number of quadrats sampled. Each quadrat in which the species was found is represented by a single point on the ROAP. ROAPs describe abundance in three ways: (1) maximum local abundance in the landscape, (2) distribution of abundance among quadrats across the landscape, and (3) proportion of occupied quadrats. (b) ROAPs used to compare two patch sizes in a single year: the area D^* was calculated by summing the absolute value of differences between the two ROAPs (shaded area). (c, d) Example of how ROAPs can be compared across successional time for (c) large patches and (d) small patches. For clarity, quadrats with zero abundance are not shown.

small patches therefore contains 30 quadrats), and large patches contain 15 quadrat pairs. Our analyses are for abundance and occupancy at the quadrat scale.

We analyzed ROAPs to assess effects of both patch size and distance to the forest on early-successional species' declines. Specifically, we compared species' abundances in quadrats which are embedded in large patches, vs. those embedded in small patches that are clustered together but separated by a minimum of 12 m of interstitial habitat (Fig. 1). We also compare abundance values from quadrats embedded in patches considered "near" vs. "far" from the forest source (designated by the solid line in Fig. 1).

Data collection.—Data were collected most years between 1985 and 2002. Sampling intensity varied between 1985 and 1995 due to funding gaps; in 1990 and 1992 no data were taken at all. Plant richness and cover by individual species were measured in permanent 1-m² quadrats, usually in the month of July. After 1994,

all woody stems >2.0 m in height were identified, counted, and measured in 4 × 4 m quadrats centered on the 1-m² quadrats. Additionally, in 2001, 110 quadrats were established and sampled in the interstitial matrix. We focused our study on three years representing different stages of succession (Fig. 1 inset), each with a complete sample of quadrats in each year ($n_S = 164$ samples in small patches, $n_L = 180$ in large patches). In 1985, a mix of grasses, annuals, and perennial forbs dominated the site. In 1995, perennial forbs characterized the landscape, but woody encroachment had begun. By 2000, woody species were ubiquitous.

Nearly 300 plant species were identified during the 18 years of the study. For the analyses presented here, we included a plant species if it (1) was present in >2 quadrats in at least one large and one small patch in 1985, 1995, and 2000; (2) was relatively common in the landscape during early phases of succession (specifically, plant species were excluded if their mean abundance in

1985 fell in the bottom 25% of all species in the patch type, following the definition of rarity in Gaston [1994]); (3) declined in mean density and/or occupancy across the site over time (i.e., many fewer plants or quadrats in 2000 than in 1985 or 1995); and (4) showed taxonomic consistency among years. For *Juncus* and *Melilotus*, the two genera we included for which discriminating among species at the time of sampling was challenging, we analyzed distributions using lumped data for the genus as a whole. Our intent in this protocol for species selection was to focus on early-successional species that might be expected to disappear as the site shifts from an old field to woodland. We identified 18 species that met these standards (see Appendix A). These species were not detected in surveys of the nearby woodland, the source pool for woody plant colonization (R. D. Holt, *personal observation*). Moreover, all focal species were highly detectable, so we have confidence in the accuracy of the data. Nomenclature for plant identification and categorization of major functional groups follows Barkley et al. (1986).

Data analysis.—To generate a ROAP for a single species, we first ranked all individual quadrats embedded in the patch size of interest (e.g., all quadrats located in large patches in the landscape) by the abundance of the species in that quadrat, from most abundant (quadrat of rank 1) to least, including all zero values. We then plotted on the ordinate the abundance in each quadrat, against the rank of that quadrat on the abscissa (Fig. 2). To standardize the abscissas for comparison among ROAPs constructed for two different treatments (e.g., large vs. small patch sizes, or year 1995 vs. 2000) that contain different numbers of sampling stations, we divided the rank by the total number of quadrats sampled in the landscape treatment (in our case, 180 quadrats embedded in large or 164 quadrats embedded in small patches). We called the measure of a given quadrat along this standardized abscissa its “relative rank.” The point at which the curve intersects the abscissa is the occupancy of the species in the landscape. Here, we refer to “quadrats” because quadrats were the source of our data; however, the technique we present could be useful whenever one has a large number of spatially discrete samples (e.g., sweep net draws or point censuses for birds at points spaced along transects).

We generated ROAPs for each of the 18 species for each patch size in 1985, 1995, and 2000. We then converted ROAPs to cumulative distribution functions (CDFs); the CDF is essentially a ROAP rotated. To test for differences between the distribution of abundances for a single species on large vs. small patches within a single year, we calculated the total area between the CDFs for small and large patches: the integral of absolute value of the difference between the CDFs over all abundances. We call this area D^* . This approach resembles a Kolmogorov-Smirnov test, only instead of measuring the maximum difference between two distributions (D_{\max}), we measured the entire area between the

CDFs to account for differences in both maximum abundance (ordinate) and occupancy (abscissa), as well as intermediate abundances (Fig. 2b). We used randomization to test for significance of D^* . For each pair of CDFs, we resampled the data 1000 times, randomly assigning each abundance to large or small patches (without replacement such that $n_S = 164$, $n_L = 180$), then calculated the corresponding CDFs and D^* for each run. This yielded a distribution for D^* assuming no patch size effect. Finally, we compared the empirical D^* to the distribution generated by our randomizations, and considered results significant at $\alpha = 0.05$ (i.e., results were significant if less than 5% of the distribution exceeded the empirical D^*).

The area under a ROAP (and above the horizontal axis) or to the left of a CDF (and to the right of the vertical axis) is the total abundance across all quadrats. So the difference in the areas under two ROAPs or CDFs is the difference in the total abundances, and would be equal to the integral of the difference between the distributions. However, we were interested in detecting any difference at all in the form of the two distributions. Therefore, we used the integral of the absolute value of the difference between the CDFs; this quantity is 0 only if the CDFs are identical, and so reflects not only total abundance but also the shape of the distributions.

We also used D^* to test for differences between distributions of abundance for species in patches near vs. far from the forest source in 1995 and 2000 (Fig. 1); by this time, woody plant colonization was well underway, particularly in patches near the forest source area.

To facilitate comparison of patch size effects over time, we contrasted the number of species for which D^* was significant with the number of species which showed no patch size differences (i.e., D^* was not significant) for 1985 vs. 1995–2000. We combined results for 1995 and 2000 because the year when the greatest patch size differences in abundance occurred depended on whether the species had declined initially, or whether it had peaked in 1995 (among our three focal years) but declined later (“wax-wane” species). We used binomial tests to test whether the probability of a species showing patch size effects or distance effects differed from 0.5, and Fisher’s exact test to compare the probability of patch size effects in 1985 and 1995–2000. For statistical analyses, we used Minitab, version 14.1 (Minitab, Inc., State College, Pennsylvania, USA) and Microsoft Excel/Visual Basic 2003 (Microsoft, Redmond, Washington, USA).

RESULTS

For most species, the highest local abundance (of the three years considered here) was 1985, shortly after initiation of the study; however, consistent with general patterns of old-field succession (Bazzaz 1996; Fig. 1 inset), five mid-successional forbs (*Apocynum cannabin-*

num, *Solidago canadensis*, *Melilotus* spp., *Helianthus annuus*, *Aster praealtus*) increased between the initial survey (1985) and 1995, but then showed substantial declines in 2000. For three of those five species (*A. cannabinum*, *H. annuus*, and *Melilotus* spp.), the 2000 mean local abundance, occupancy, or both, fell below their 1985 levels.

In 1985, the majority of species showed no patch size effects (16 of 18, binomial probability $P < 0.01$). *H. annuus* and *Ambrosia artemisiifolia* were both significantly more abundant on large patches (D^* randomization, $P < 0.01$). By chance alone, one might expect to see a few species with what appears to be a patch size effect, and we suspect that is the case here. By contrast, in 1995 and 2000, patch size differentially affected abundance for nine and seven species, respectively (Appendix B). Combining 1995 and 2000 to account for differential timing of peak abundance by pioneer and wax-wane species, and counting each species only once, 11 out of 18 species total showed substantial patch size effects, significantly more than in 1985 (Fisher's exact test, $P < 0.01$). Visual inspection of ROAPs in conjunction with D^* indicate that among these 11 species, the direction of the effect varied: four species persisted in greater abundance on the small patches, whereas seven persisted on large patches (select cases shown in Fig. 3; summaries in Appendices A and B). *H. annuus*, a species that was significantly more prevalent on large patches in 1985, persisted in greater abundance on small patches by 1995. For *A. artemisiifolia*, the other species with a significant D^* in 1985, there was no patch size effect in 1995; however, *A. artemisiifolia* was significantly more abundant in large patches than small by 2000. All four species that persisted longer on small patches are short-lived species that rely on seeds for reproduction and dispersal (Appendix A). By contrast, perennial species showing patch size effects (all of which also have the capacity to propagate clonally) persisted longer on large patches.

Distance from the forest did not greatly influence the pattern of extinction of these species. For 1995 and 2000, 16 and 14 (respectively) of the 18 species showed no significant abundance differences on patches located near and far from the forest (16 of 18; binomial probability $P < 0.01$, 14 of 18; binomial probability $P = 0.01$, Appendix B). *Cirsium altissimum* was more abundant on patches far from the forest (and also on small patches overall) in both 1995 and 2000. By contrast, *Hypericum punctatum* was more abundant on near (and large) patches in 1995. In 2000, the significant patch size effect for *H. punctatum* emerged because ROAPs crossed: there was greater occupancy on near patches, but higher maximum abundance on far patches. *Apocynum cannabinum* and *Melilotus* spp. also showed distance effects in 2000, persisting in significantly greater abundance on near and far patches, respectively. For all three species with both patch size and distance effects, the ones that persisted better on far patches also persisted better on small patches (Appendix B).

DISCUSSION

The dynamics of local extinction play a key role during the build-up of island communities, during the decay of communities experiencing habitat fragmentation, and during ecological succession. In this paper, we examined patterns of species decline for early-successional plant species in an experimentally fragmented landscape. To do so, we developed a method of characterizing changes in distribution and abundance we refer to as "ROAPs," for rank occupancy-abundance profiles. Our approach here differs from traditional approaches to intraspecific abundance distributions which explore the well-documented observation that species tend to be abundant in relatively few sites, and rare in the majority of sites in which they occur (Gaston 2003). Much of the literature has focused on the issue of which parametric model best describes this distribution (e.g., the negative binomial), on expansions of Taylor's suggestion that the mean and the variance of local densities among sites are related (Taylor 1961), and on the problem of elucidating mechanisms that may generate this relationship (Holt et al. 1997). We used a nonparametric D^* statistic applied to ROAPs to explore spatial and temporal shifts in abundance during succession. Using ROAPs, we show that the spatial pattern and timing of declining abundance varies among species and, in many cases, clearly depends on patch size. Moreover, the trajectory toward extinction, as depicted by comparing ROAPs over time, qualitatively varies among species.

Patch size effects

The number of species showing patch size effects increased over the course of succession. That we did not detect many patch size effects in 1985 was no great surprise, given that early-successional plant communities reflect primarily seed bank and wind-dispersed species, both of which should initially be present independent of patch area in our randomized-block, experimental landscape (Glenn-Lewin and van der Maarel 1992, Holt et al. 1995). We did not expect extinction to begin until later in succession, when the number of species increased (Cook et al. 2005) and woody, competitively dominant species had become established, albeit at different rates and densities on small and large patches. A shift toward dominance by woody species is expected to alter the competitive milieu and abiotic environments in ways that disfavor species that are highly abundant in early succession (Pickett and Cadenasso 2005). Thus, as early-successional species declined concurrent with woody encroachment, patch size effects on abundance of early-successional species emerged. Fig. 4 shows an example: white aster (*A. pilosus*) declined greatly from 1985 to 1995, but lingered longer on each of the large patches, sometimes at high local abundance.

Interestingly, the particular direction of the patch size effects we observed varied among species. On the one hand, consistent with predictions made by IBT and metapopulation theory, we identified seven species that

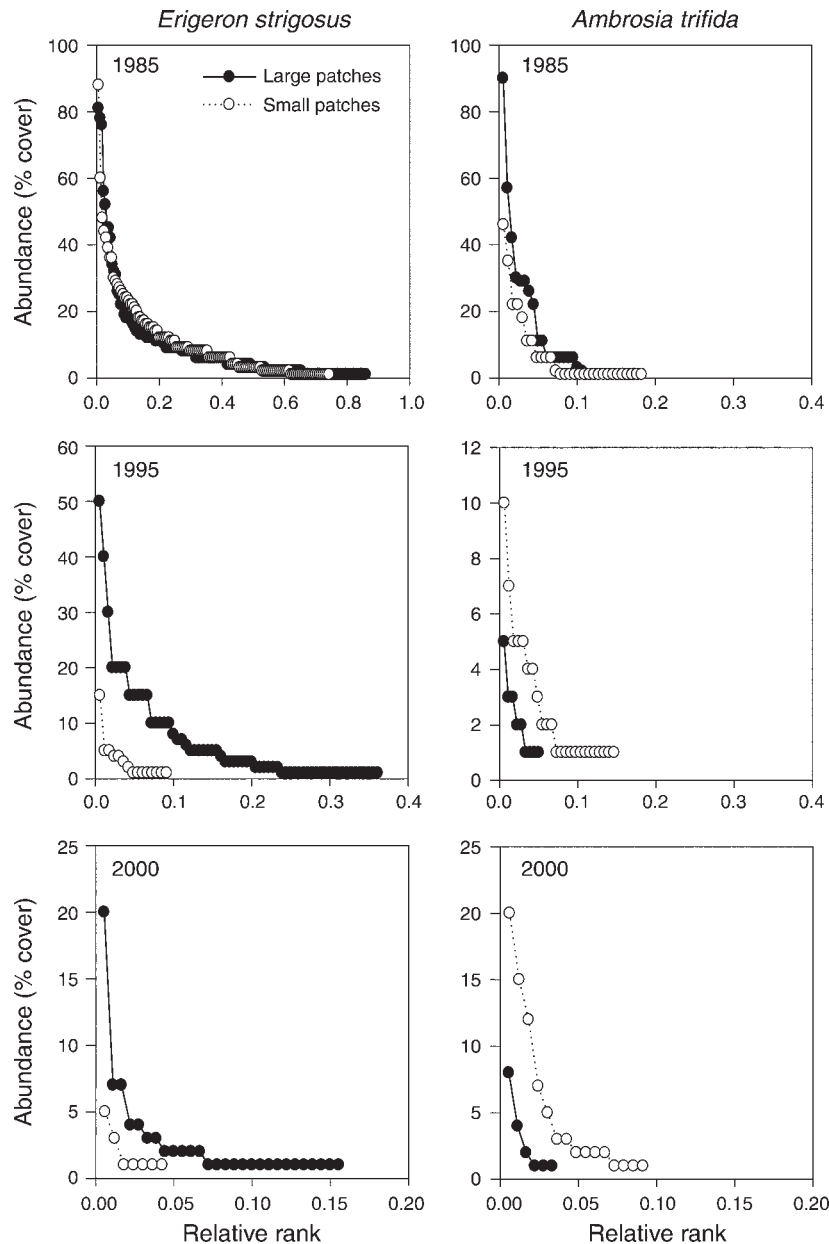


FIG. 3. Examples of ROAP comparisons between large and small patches for two species at three different time periods (1985, 1995, and 2000) during succession. Abundance was measured as percent cover in a 1-m² quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the total number of quadrats sampled. For both species, ROAPs on large vs. small patches differed significantly ($P < 0.05$) in 1995 and 2000. *Erigeron strigosus* declined in abundance more rapidly on small patches; *Ambrosia trifida*, by contrast, declined in abundance more rapidly on large patches. Zeros were removed to emphasize differences in occupancy on the abscissa. Please note that the scale of the axes differs among plots.

declined in abundance more rapidly on small patches vs. large patches. On the other hand, consistent with succession theory, we found four species that declined faster on large patches, where woody encroachment had progressed most rapidly. Similar observations of widely ranging species-specific responses to fragmentation have been documented in other studies (Margules 1996, Debinski and Holt 2000). Bissonette and Storch (2002)

suggest that the idiosyncratic effects often reported in fragmentation studies reflect the complex, multi-causal nature of ecological systems. Indeed, fragmentation is a “whole-system” experiment, where processes at multiple levels (from ecosystem processes, to plant dynamics, to herbivory) are affected in a complex way by treatments such as patch area, and these processes play out over different temporal scales (Debinski and Holt 2000).

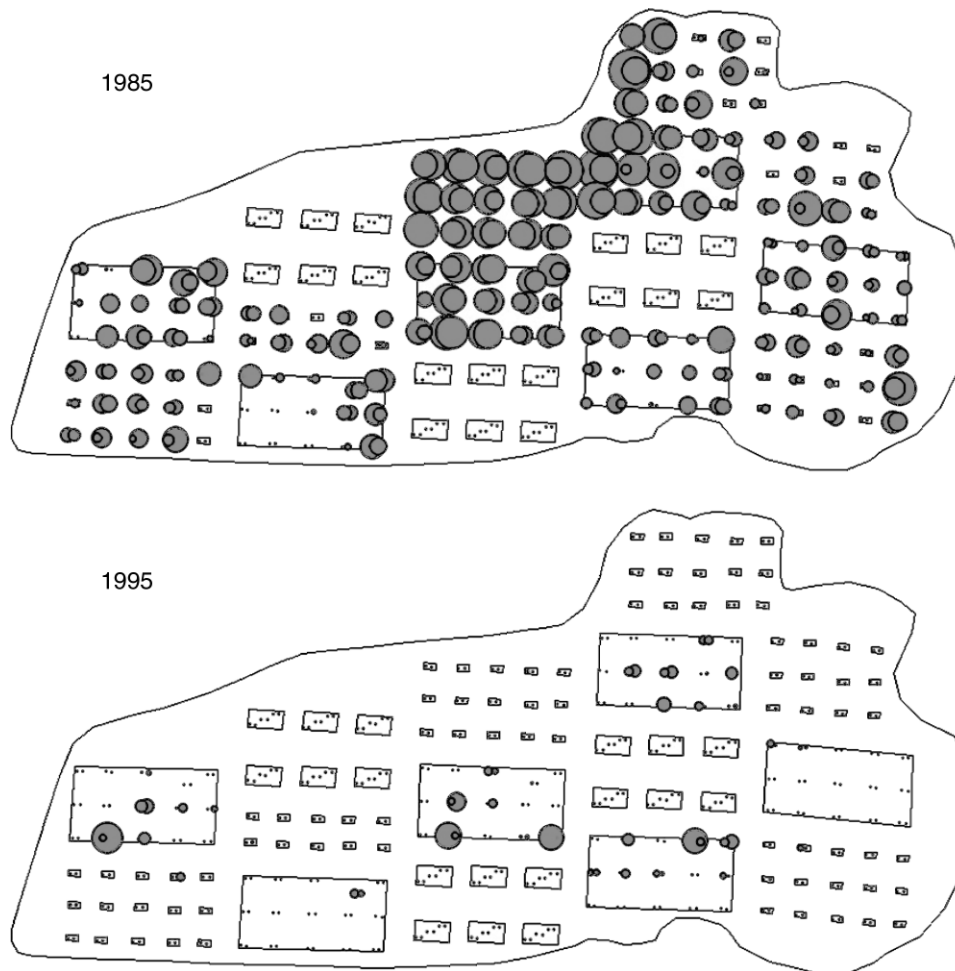


FIG. 4. Visually compelling evidence for patch size effects on abundance during extinction of an early-successional species. This example shows *Aster pilosus*, a species that persisted preferentially on large patches. Bubbles (gray) are scaled to reflect the percent cover within quadrats of *Aster pilosus* in 1985 (top) and 1995 (bottom). The largest bubbles indicate 100% cover, the smallest bubbles represent 1% cover, and intermediate bubble sizes reflect cover estimates in 10% increments. The tiny dots are quadrats empty of the species.

Consequently, the responses of any given species are influenced by how its traits respond to this shifting template of causal processes.

All perennial species that showed significant patch size effects are clonal, and persisted longer on large patches. None of the species that persisted on small patches are clonal, and neither of the two non-clonal perennial species showed patch size effects. This pattern tentatively suggests that clonality (vegetative reproduction) can influence persistence. One mechanism potentially driving persistence of clonal plants on large patches is intra-patch dispersal, which links a quadrat to the surrounding area. In large patches, if a clonal species goes locally extinct, the quadrat may be recolonized rapidly from the surrounding area, thereby boosting occupancy at small, within-patch (i.e., quadrat) scales (Holt 1992). In small patches surrounded by a relatively uninhabitable matrix, this "rescue effect" (Brown and Kodric-Brown 1977) is much less likely. Further, perenniality may augment this

spatial effect, permitting long-lived plants to remain in a landscape long after ecological changes (in this case, woody encroachment) alter habitat quality (Eriksson 1996), as a kind of "extinction debt" (Tilman et al. 1994).

Environmental heterogeneity within large patches may provide another mechanism explaining the persistence of early-successional species, including non-clonal species, on large patches. For example, spatial heterogeneity in woody cover within large patches of continuous habitat may create local "hotspots," i.e., well-lit gaps among clusters of trees, where early-successional species thrive. As woody species expand, early-successional species may contract toward these optimal habitats within large patches and sustain local populations, as has been suggested for declining species at the spatial scale of the geographic range (e.g., Rodriguez and Delibes 2002). Alternatively, the persistence of early-successional species on large patches in the face of

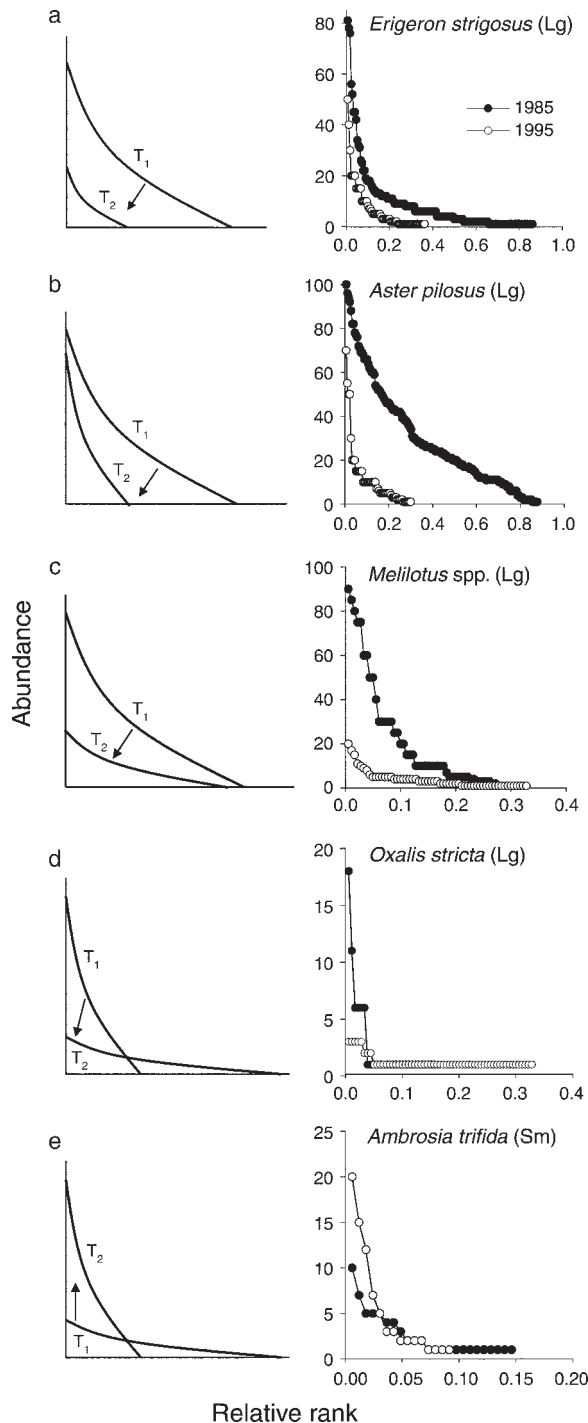


FIG. 5. Models of ROAPs depicting possible trajectories of abundance decline between two periods. T_1 and T_2 are respectively early and later snapshots in time along the trajectory. Empirical examples were selected based on visual congruence to the conceptual models; thus, examples were drawn from both large (Lg) and small (Sm) patch sizes (solid circles, 1985; open circles, 1995). Collectively, these data illustrate the diverse patterns of decline exhibited by early-successional species in our system. For empirical ROAPs, abundance was measured as percent cover in a 1-m² quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the total number of quadrats sampled.

woody encroachment may reflect preexisting abiotic heterogeneity in the landscape that acts to filter colonizing species from the species pool (Keddy 1992). Although our analyses cannot discriminate between these hypotheses, we can be relatively certain that unmeasured environmental heterogeneity plays a role in the localized persistence of early-successional species.

Short-lived species were not restricted to small patches, but the four species that preferentially persisted on small patches were short-lived, and three of the four were not found in the matrix habitat. Relative to perennial plants which often reproduce vegetatively, annual and biennial species rely less on short-distance dispersal over space and more on dispersal through time via seed banks (a “storage effect,” Warner and Chesson 1985). The combination of seed banks and frequent disturbances that trigger germination may have allowed plant species to avoid extinction in small patches, even in the absence of immigration (Stocklin and Fischer 1999). For example, early-successional species in a nearby field are more abundant in areas disturbed by prairie voles (Questad and Foster 2007). As succession progressed in our system, vole densities increased to higher levels in small patches than in large (Schweiger et al. 2000), and may have inflicted higher levels of localized disturbances in these patches.

Models of decline

Species’ trajectories toward extinction vary in many ways, and for many different reasons (Gaston and Kunin 1997). Furthermore, rarity, arguably the last stage of persistence, can be expressed in many forms (Rabinowitz 1981). Using ROAPs to depict changes in abundance, we propose five conceptual models for species declines; they vary in the relative degree to which maximum abundance vs. occupancy declines during a given time step (Fig. 5). Followed through to their logical conclusions, these models lead to different types of rarity, i.e. species that are both regionally and locally rare (Fig. 5a), regionally rare but locally abundant (Fig. 5b, e), or regionally common but locally rare (e.g., Fig. 5c, d). As depicted in the figure, a species may attain the same type of rarity via different trajectories. Indeed, the different “types” of rarity may represent different phases (and to some extent, degrees) of rarity on the trajectory toward extinction for a given species. For instance, on large patches *Aster pilosus* experienced a more dramatic drop in occupancy relative to maximum abundance from 1985 to 1995, leading us to classify it—in this phase—as “locally abundant, regionally rare” (Fig. 5b). By 2000, however, the species was both locally and regionally rare (Fig. 2c). The shape of the ROAPs that comprise the trajectories could be influenced by variation in intrinsic growth rates (in this case, often negative) across a landscape. Differences between two ROAPs may, in turn, emerge from density-independent factors. Which trajectory a species exhibits may reflect phylogenetic history, life history traits, competitive ability, dispersal ability, or a wide range of

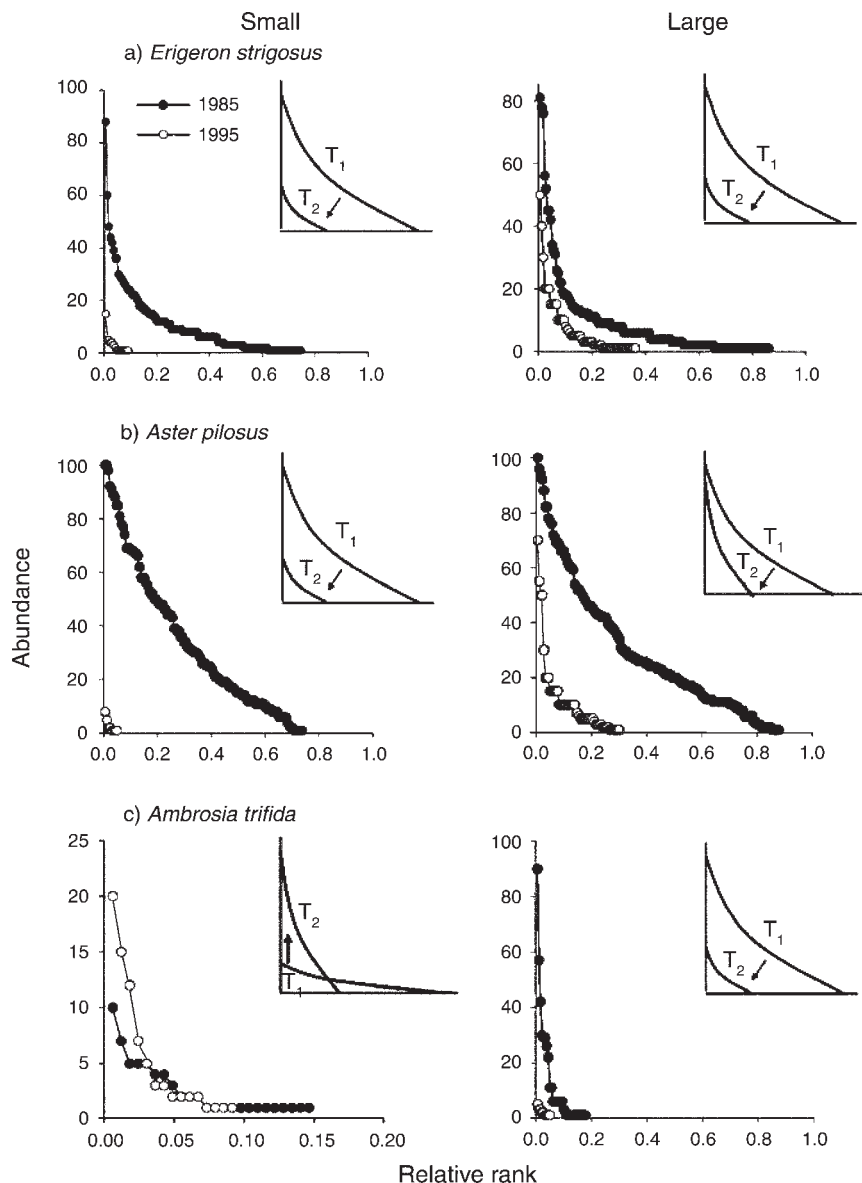


FIG. 6. Patch size effects on species declining in abundance may emerge due to (a) different rates of decline on each patch size (i.e., occupancy and local abundance decline proportionally on a given patch size, but the magnitude of overall change is greater on one patch size than the other); (b) different patterns of decline (i.e., relatively greater changes in occupancy than abundance on one patch size); or (c) differences in both rate and pattern of decline. For empirical examples, abundance was measured as percent cover in a 1-m² quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the total number of quadrats sampled. Scales on axes vary to enable detailed examination of ROAPs.

environmental drivers; we plan in future work to explore the link between underlying population mechanisms and the shape of these curves.

Patch size effects on patterns of decline manifested differently among species. For some species, the trajectory toward extinction appears similar on both patch sizes, but the rate of decline differs. For instance, *E. strigosus* declines proportionally in occupancy and abundance on both large and small patches, but overall, the decline occurs faster on small patches (Fig. 6a). By contrast, there are species for which patch size appears to

influence local abundance and occupancy disproportionately. *A. pilosus*, for example, declines in occupancy and local abundance equally and dramatically on small patches; however, on large patches, occupancy shows a stronger decrease relative to maximal abundance (Fig. 6b). *A. trifida* increases occupancy on small patches, even as numbers decline overall, compared to relatively uniform declines in both abundance measures on large patches (Fig. 6c). These examples suggest that understanding patch size effects extends beyond simply noting the acceleration or slowing of decline.

That there appear to be species consistent with each model in Figs. 5 and 6 highlights the idiosyncratic nature of the pattern and timing of declining abundance among species. As alluded to above, it is not immediately clear whether any particular trajectory of decline is more likely to occur on small vs. large patches, irrespective of species identity. Given the variation we found among only 18 species declining in our system, it is most likely that a suite of species traits interact synergistically with fragment size to determine the independent extinction trajectories for each species (Freville et al. 2007).

Conclusions

Consistent with Preston's (1960) observation that space and time are tightly linked in ecology, we have shown that in at least one empirical system, habitat fragmentation interacts with succession to influence species extinction dynamics. Using a novel approach (ROAPs), we show that patch size influences patterns of abundance as early-successional species decline toward extinction. If successional processes were governing extinction dynamics, we would expect to see declines in occupancy and/or abundance first in larger patches and patches near the source, where woody plant colonization occurred earlier. Instead, 7 of 11 species showing patch size effects persisted on large patches longer, and distance affected relatively few species as succession progressed. Moreover, plants that persisted on small patches were short-lived plants that may have emerged from long-lived seed banks and therefore were potentially less vulnerable to the negative effects of area on populations. These lines of evidence argue for patch size being a primary driver of plant species declines. Importantly, our results emphasize the fact that the relative influence of area on small populations (IBT) and of time (species replacement during succession) varies among species. Thus, summarizing community responses to habitat fragmentation by a single diversity measure obscures important species-specific extinction trajectories. Effective management in the face of landscape change will require that we consider life history attributes of individual species to better predict their responses to fragmentation. ROAPs serve as a useful tool in this effort by providing a detailed and visual representation of data that incorporates the variation in the distribution of abundance across space into commonly-used occupancy-abundance plots. Moreover, using ROAPs we can statistically compare distributions of abundances among landscapes, species, or time periods. We suggest that comparable analyses jointly assessing occupancy and abundance could be illuminating in a wide range of ecological studies.

ACKNOWLEDGMENTS

This paper was improved by suggestions made by two anonymous reviewers. We also thank M. Barfield and B. McGill for comments on earlier drafts of this manuscript. We are grateful to the National Science Foundation (DEB01-08302) for funding this work. The study was conducted at and

supported by the University of Kansas Field Station and Ecological Reserves, a research unit of the Kansas Biological Survey and the University of Kansas. R. D. Holt thanks the University of Florida Foundation for support.

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APPENDIX A

Table of focal species and life history characteristics, arranged according to the direction of the patch size effect they show in either 1995 or 2000 (*Ecological Archives* E090-180-A1).

APPENDIX B

Patch size and distance effects on rank occupancy–abundance profiles for the 18 focal species broken down by year (*Ecological Archives* E090-180-A2).