POPULATION AND COMMUNITY RESPONSES TO ANTHROPOGENIC ENVIRONMENTAL CHANGES

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ABSTRACT

Ecologists are currently faced with the challenge of understanding ecological patterns in the context of a rapidly changing planet. Meeting this challenge may ultimately enable ecologists to predict the consequences of global change, as well as find ways to mitigate human impacts on species and communities. In this dissertation I use classic ecological theory, original conceptual models, and a novel analytical tool to explore the effects of anthropogenic environmental changes on grassland plants and North American birds.

Humans continue to increase the amount of nutrients in the environment. Nutrient enrichment directly alters plant communities by increasing productivity, often at the expense of diversity. In tallgrass prairies, arbuscular mycorrhizal fungi (AMF) also mediate diversity because plant species differ in the degree to which they rely on AMF for nutrient acquisition. In Chapter 1, I investigate whether soil nutrient levels alter the effects that AMF have on plant communities. By manipulating phosphorus and AMF in experimental mesocosms containing native prairie grass communities, I show that the influence of AMF on plant community diversity and productivity depends on soil nutrient levels. Thus, nutrient enrichment imposes environmental constraints on plant soil-mutualisms that may have ecosystem- and community-level consequences.

Habitat fragmentation is thought to be the leading cause of contemporary species extinctions. In Chapter 2, I use long-term data from a landscape-scale experiment to explore the effects of habitat patch size on rates and patterns of early-successional plant species declines. I quantify declines with a new metric, the Rank Occupancy-Abundance Profile (ROAP), which depicts shifts in both local abundance and occupancy. Patch size influenced the rate and spatial pattern of local extinction in fragmented grasslands; however, the patch size on which declines were most rapid varied among species. I suggest that persistence on a particular patch size may be linked with a species' life history traits.

In Chapter 3, I use ROAPs to assess the magnitude and patterns of decline in North American breeding birds. I show that 20% of 209 sampled birds have declined significantly since 1970, including both rare and common species. Patterns of declines varied according to the initial regional abundance of the bird species: rare species experienced proportionally higher losses in regional abundance due to local extinctions than did abundant species. I also propose a conceptual model for a general pattern of decline species experience as they approach extinction.

Overall, results from this dissertation confirm that humans are dramatically altering the relative abundance of species—at local, landscape, and continental scales. Early detection of declines—and the factors driving them—may help preserve biodiversity in the face of enduring anthropogenic environmental changes.

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GENERAL INTRODUCTION

For more than a century, ecologists have sought to understand the distribution, abundance, and diversity of organisms. Pioneering studies such as those on species ranges by Elton and Grinnell, on succession by Clements and Gleason, and on competition and niches by Gause, Hutchinson, and MacArthur set the conceptual and theoretical stage for future community ecologists. We are still refining our understanding of the fundamental ecological questions these seminal ecologists first addressed; however, our intellectual curiosity has been fueled with a new sense of urgency inspired by our rapidly changing planet. Earth's biodiversity is currently threatened by the sixth mass extinction event—the first mass extinction induced by humans. In addition to the ethical issues that human-caused extinctions raise, maintaining biodiversity is of wide public interest because it provides people with vital goods (such as timber) and services (such as prevention of soil erosion). Thus, our challenge is no longer to simply understand the nature of organisms, populations, and communities; rather, we must expand our goals to identifying (and potentially mitigating) the complex interactions and contingencies that global changes impose on natural systems. As a result, a framework is emerging in ecology in which humans are viewed as an influential and integral component of the ecosystem. The agenda entails addressing basic ecological questions in the context of anthropogenic global changes.

The main drivers of human-induced environmental changes fall into five broad categories (Sala et al. 2001): changes in atmospheric CO_2, climate warming, landscape conversion which results in loss and fragmentation of natural habitats, nutrient enrichment, and biotic invasions. These changes threaten biodiversity and ecosystem function directly and indirectly (Tylianaki et al. 2008), independently and synergistically (Brook et al. 2008). In this dissertation I examine these consequences of global changes at different spatial scales (local, landscape, and continental), at different levels of ecological organization (communities, species, local populations), and using different investigative approaches (mesocosm experiment, field experiment, and analyzing observational data). In Chapter 1, I use experimental mesocosms to investigate whether soil nutrients alter the ability of arbuscular mycorrhizal fungi (AMF) to mediate prairie plant diversity and productivity. In Chapter 2, I explore the influence of habitat fragmentation on populations of early-successional plant species in a Kansas grassland and introduce a novel tool (ROAPs) for measuring population changes over time. In chapter three, I use ROAPs to document the patterns of decline in North American breeding birds. In all of the research contained within my dissertation, I use classic ecological theories as a foundation from which to make (and test) predictions regarding species interactions and species declines in environments shaped by contemporary human impacts. Below I briefly describe the global change impetus for my research in each chapter, the theoretic framework that guided my inquiry, and a concise summary of the main results.

Chapter 1: Community-level consequences of mycorrhizae depend on phosphorus availability

Nutrient deposition continues to increase globally. Currently, there are places in the world where nitrogen (N) deposition rates exceed 10 kg N $ha^{-1}yr^{-1}$, more than an order of magnitude greater than estimated natural deposition rates (Galloway et al. 2008). Less attention is paid toward phosphorus (P) deposition, despite the fact that net P storage in terrestrial and freshwater ecosystems is estimated to be over 75% greater then before the industrial age (Bennett et al. 2001). In terrestrial systems, P-enrichment is due primarily to P-fertilizer that accumulates in agricultural soils (Carpenter 2008). We know that adding nutrients increases plant productivity, often at the expense of diversity; both N and P have been implicated as drivers of local extinctions (Tilman 1987; Wassen 2005).

Historically, research on plant diversity has focused on local competitive interactions, the outcome of which is determined by efficient acquisition of limited resources, such as nutrients (Tilman, 1982). Recently, microbes that have mutualistic relationships with plants have gained attention as playing a key role in driving plant diversity patterns (Reynolds et al. 2003). Arbuscular mycorrhizal fungi (AMF), for example, help plants acquire nutrients in exchange for photosynthetic carbon. The presence or absence of AMF alters plant diversity because plant species respond differentially to their presence (Hartnett & Wilson 1999). Enhancing the nutrient environment in which this plant-fungal symbiosis operates may alter the influence that AMF have on plant diversity by changing the degree to which various plant species benefit from hosting AMF.

In Chapter 1, I build on recent studies of AMF-mediated plant diversity (e.g. Hartnett & Wilson 1999; Van der Hiejden 2002) and basic coexistence theories (e.g. Tilman 1985) to generate a conceptual model that predicts community-level outcomes of AMF-mediated competition along a P-gradient. Using experimental mesocosms and native prairie grass communities, I test the general prediction that AMF mediate plant community responses to soil nutrients. I found that the influence of AMF on plant diversity, composition, and productivity depended on P-levels. My results suggest that anthropogenic changes in soil nutrients could impose environmental constraints on AMF-plant mutualisms, and thereby ultimately affect communities and ecosystems.

Chapter 2: Patch size effects on plant species decline in an experimentally fragmented landscape

Land-use change—which typically leads to habitat loss and fragmentation—is considered the most acute driver of biodiversity loss (Sala et al. 2001). Approximately 40% of the land on earth as has been converted for agricultural use (Foley et al. 2005), and estimates for loss of natural habitats in the U.S. exceed 90% (World Resources Institute 1998). Such land-use changes have negatively affected the breeding, foraging, and dispersal behaviors of individual species across a wide range of taxonomic groups, as well as ecological processes such as species interactions and trophic length of food chains (Fahrig et al. 2003). Researchers studying fragmentation have traditionally focused on quantifying rates of species extinctions, and identifying what traits make certain species vulnerable to extinctions in fragmented habitats (e.g. Davies 2000; Fréville et al. 2007; reviewed in Fischer & Lindenmayer 2007). In Chapter two of this dissertation, I use data from a long-term, large-scale habitat fragmentation experiment in a Kansas grassland to explore the influence of patch size on patterns of decline in early-successional plant species.

I based my predictions for this chapter on two bodies of theory: Island Biogeography Theory (IBT; MacArthur and Wilson 1967), and general succession theory (Pickett et al. 1987). The two theories make contrasting predictions for the habitat patch size (fragment size) on which species will go extinct most quickly: if patch size effects dominate (as predicted by IBT), early-successional species should persist longer on large patches which allow for larger populations. If successional processes dominate, I expect early-successional species to persist longer on small patches, where woody species established more slowly. Thus, the interaction between habitat fragmentation and old field succession allow me to test the relative importance of area effects and successional processes on rates and patterns of decline in early-seral plant species.

To address my questions, I introduce a new metric which can be used to visually and statistically assess the distribution of abundance of an organism across a landscape. The metric, called Rank Occupancy-Abundance Profiles (ROAPs), fill a gap that existed in our ability to analyze species-level data because it incorporates both site occupancy and local abundance. I used ROAPs to compare patterns of decline in large versus small patches for 18 plant species.

I found that patch size influenced patterns of decline in most species; however, some species declined faster on small patches, and some declined faster on large. These results emphasize the fact that the relative influence of area on small populations (i.e. IBT) and of successional proccesses (i.e. competitive replacement) varies among species. Moreover, summarizing community responses to habitat fragmentation by a single diversity measure obscures important species-specific extinction trajectories. To illustrate this point, I generated a suite of conceptual models using ROAPs that propose various trajectories a species might follow as it nears extinction. These models provided the foundation for my research in Chapter 3.

Chapter 3: Phases of Decline in North American Breeding Birds

Populations of many taxa are declining worldwide (Balmford et al. 2003). There is little doubt that human activities play a key role; anthropogenic threats such as climate change and habitat loss reinforce each other, acting simultaneously and additively to drive populations toward extinction (Brooke et al. 2008). The World Conservation Union (IUCN) considers population decline a key component of assigning species to the Red List; however, little is known about the rate and patterns of decline as species approach rarity. What we do know is that reducing local population sizes and extirpating local populations increase the probability of entire species going globally extinct (Ehrlich & Daily 1993).

The observation that local abundance and regional occupancy are positively correlated is one of the oldest and most general macroecological patterns (Darwin

1859; Brown 1984; Gaston et al. 2000). Typically, this pattern is recorded across species (i.e. locally common species occupy many sites and locally rare species occupy few sites), although shifts in abundance and occupancy for a single species over time also show a positive correlation (though exceptions exist; Gaston et al. 2000). Abundance-occupancy patterns are of considerable interest because they suggest that local and regional processes are linked (Freckleton, 2006). If occupancy and local abundance are positively correlated for declining species, we can use one measure to estimate the other, predict the consequences of specific threats (e.g. habitat loss), and accurately assess the status of imperiled species.

In Chapter 3, I explore the patterns of decline in North American breeding birds. I chose birds as my focal taxonomic group for several reasons. First, birds are good indicators of global changes. Many species migrate long distances, and collectively, bird species occupy most habitats on the globe, as well as various trophic levels. Consequently, changes we see in bird populations tend to integrate many ecological factors. Second, we know much about the natural history of birds. They have been at the center of ecological studies since ecology emerged as a discipline, are highly visible, and frequently observed by amateur naturalists around the world. Last, the existence of a unique, long-term, large-scale dataset—the North American Breeding Bird Survey (NABBS)—makes it plausible to address questions about ecological processes that happen on time scales longer than the tenure of a PhD student. Using data from 209 North American birds, and guided by the ROAPs models of extinction that emerged from Chapter 2, I found that patterns of declines varied across bird species according to their initial regional abundance. Regionally abundant bird species lost more individuals due to declines in their local populations, versus local extinctions. Regionally rare birds lost proportionally more individuals due to local extinctions. A primary result from this chapter is a general model of decline that I propose depicts time-lags between losses in occupancy and local density that a single species may experience as its regional abundance declines.

The effects of anthropogenic environmental changes are evident at many spatial scales and levels of ecological organization. Moreover, both pattern and mechanism play unique and key roles in our ability to assess human impacts on ecological processes. My hope is that this dissertation demonstrates that 1) we can apply classic ecological theories toward predicting the effects of anthropogenic environmental changes and 2) we can combine local, experimental and landscape-scale, observational approaches to better document and predict the distribution and abundance of species in a rapidly changing world.

CHAPTER 1: **Community-level consequences of mycorrhizae depend on phosphorus availability**

Abstract.

In grasslands, arbuscular mycorrhizal fungi (AMF) mediate plant diversity; whether AMF increase or decrease diversity depends on the relative mycotrophy in dominant versus subordinate plants. In this study we investigate whether soil nutrient levels also influence the ability of AMF to mediate plant species coexistence. First, we present a conceptual model that predicts the influence of AMF on diversity along a soil nutrient gradient for plant communities dominated by mycotrophic versus non-mycotrophic species. To test these predictions, we manipulate phosphorus to create a soil nutrient gradient for mesocosm communities comprised of native prairie grasses, and compare community properties for mesocosms with and without AMF. We found that where P was limiting, AMF increased plant diversity and productivity, and also altered community structure; however, at high P, AMF had little influence on above-ground communities. Compositional differences among treatments were due largely to a trade-off in the relative abundance of C_3 versus C_4 species. Our study emphasizes how environmental constraints on mutualisms may govern community- and ecosystem-level properties.

INTRODUCTION

Identifying factors that generate and maintain plant diversity and productivity remains one of the central goals of ecology. Until recently, microbes have been largely ignored as drivers of plant community dynamics (Reynolds et al. 2003; Wardle et al. 2004). Given their pivotal role in nutrient cycling and nutrient transfer, microbes are gaining attention as key players in ecosystem processes (van der Heijden et al. 2008) and the crucial role they may play in mediating plant response to global changes (Johnson et al. 2003a; Tylianakis et al. 2008). Human-induced global changes such as nutrient deposition alter the environmental context for species interactions. In order to predict the above-ground consequences of altering soil environments, we must account for biotic interactions below-ground, such as the symbiosis between plants and mycorrhizae. We know little about how the changing abiotic environment shapes microbial influences on plant communities (Bever 2003; van der Heijden et al. 2008). In this paper, we examine how soil nutrient levels impact plant-fungal symbioses and, ultimately, plant community diversity and productivity.

Arbuscular mycorrhizal fungi (AMF) are soil organisms that colonize most terrestrial plants species (Smith and Read 1997). This symbiosis is typically considered mutualistic because the fungus provides soil resources—particularly phosphorus—to the plant, and receives photosynthate in return (Smith and Read 1997). However, environmental conditions can alter the costs and benefits of the AMF-plant symbiosis along the spectrum of mutualism to parasitism (Johnson et al.

1997). For instance, high phosphorus environments may eliminate resource limitation such that AMF impose a carbon drain on plants, depressing plant growth (Koide 1991; Johnson et al. 1997). Independent of soil nutrient status, not all plants benefit equally from AMF symbioses. Reliance on AMF for optimal growth varies among plant species (Klironomos 2003), plant functional groups (Wilson and Hartnett 1998), and plants characteristic of different successional stages (Janos 1980). Given the significant role AMF play in plant resource acquisition, together with observed variation among plant species in the benefits derived from AMF colonization, it is no surprise that AMF-mediated competition contributes to grassland plant community diversity (van der Heijden 2002).

AMF affect plant diversity positively or negatively, depending on the degree to which the dominant plant species depend on AMF (Hartnett and Wilson 2002; Urcelay and Diaz 2003). When the competitively subordinate plants derive substantial growth benefits from hosting AMF, the presence of AMF increases diversity (e.g. Grime et al. 1987; van der Heijden et al. 1998). By contrast, AMF decrease diversity when AMF disproportionately enhance growth in dominant plants (e.g. Hartnett and Wilson 1999; O'Connor et al. 2002). In Kansas tallgrass prairie, for instance, co-occurring warm-season (C_4) and cool-season (C_3) grasses and forbs vary in their dependence on AMF; the dominant grasses are C_4 and rely on AMF for optimal growth (Wilson and Hartnett 1998). Suppressing AMF results in competitive release of many subordinate C_3 grass and forb species which rely less (or not at all) on AMF (Hartnett and Wilson 1999). Additionally, AMF can influence ecosystem function both directly and indirectly. In nutrient-deficient substrates, the presence of AMF increase primary productivity directly through nutrient acquisition and enhanced photosynthesis (Smith and Read 1997). When AMF increase plant diversity, this, in turn, may increase plant productivity indirectly by enhancing plant complimentarity and community-wide resource use efficiency (Klironomos et al. 2000; van der Heijden 2002).

Competition for nutrients plays a major role in governing grassland plant community dynamics (Tilman 1982). Adding a single nutrient alters the absolute abundance of that nutrient, as well as its abundance relative to other nutrients (e.g. N:P), often shifting the identity of the limiting nutrients and ultimately plant community composition (Tilman 1985). For instance, enriching soils with N favors N-limited species, and increases plant productivity at the expense of diversity (Tilman 1987; Foster and Gross 1998). To the extent that AMF mediate competition via nutrient acquisition, anthropogenic inputs of N and P will influence the role AMF play in mediating plant species coexistence. Indeed, pairwise studies have shown that AMF and soil nutrient levels interact to determine the competitive “winner” among plant species (Hartnett et al. 1993; Daleo et al. 2008, Johnson et al. 2008).

If we link our knowledge of a plant community’s structure—and the degree of mycotrophy of plants comprising the community—with knowledge of soil resource availability, we can predict the influence of AMF on plant communities in different soil environments or under various nutrient deposition scenarios. For example, where dominant plant species are highly mycotrophic (e.g. tallgrass prairies), the presence of

AMF will depress diversity by reinforcing competitive superiority of a few species; however, this effect will be most pronounced where P is limiting (Fig. 1a). Where P is abundant, AMF will play a minimal role in governing plant diversity. In communities where the subordinate species benefit from AMF more than the dominants (e.g. cool-season grasslands), AMF will increase diversity; again, this effect will be most dramatic where P is limiting (Fig. 1b). Thus, we propose that AMF mediate plant diversity, but the influence of AMF at the community level will depend on both soil nutrient levels and plant community composition. Specifically, the influence of AMF on diversity will be strongest at low nutrient (specifically P) levels; the direction of the influence will depend on the relative degree of mycotrophy among plants in the community.

In this study, we explore the plant community consequences of altering the resource environment in which plants and AMF interact. We hypothesize that 1) the influence of AMF on plant diversity will depend on soil nutrient levels, 2) the influence of AMF on plant communities will be greatest in P-limited environments, and 3) shifts in community composition will result from differential responses of C_4 (highly mycotrophic) and C_3 (less mycotrophic) species to AMF along the soil nutrient gradient. To test these hypotheses, we devised an experiment using mesocosm communities comprised of native tallgrass prairie species. By manipulating the presence and absence of AMF and soil P, we quantified the effects of AMF on plant community diversity, composition and productivity along a soil nutrient gradient.

METHODS

This study was conducted at the University of Kansas Ecological Reserves, 20 km north of Lawrence, Kansas. We chose a mesocosm approach because we could have strict control over nutrients and the presence/absence of AMF. Two AMF treatments (+ AMF and –AMF) were combined with five nutrient treatments in a factorial design, with five replicates for each treatment combination. Initially, each mesocosm contained identical plant communities comprised of nine perennial, native grass species that coexist in Kansas tallgrass prairies: *Agropyron smithii* Rydb. (C_3), *Andropogon gerardii* Vitman (C_4), *Bouteloua curtipendula* (Michx.) Torr. (C_4), *Elymus canadensis* L. (C_3), *Hordeum jubatum* L. (C_3), *Koleria pyramidata* (Lam.) Beauv. (C_3), *Schizachrium scoparium* (Michx.) Nash (C_4), *Sorgastrum nutans* (L.) Nash (C_4), and *Sporobolus heterolepis* (A. Gray) A. Gray (C_4). We used perennial grasses because they dominate native prairies and are targeted for restoration efforts in our region. Species were selected based on frequency of occurrence in our region, functional group (five C_4 grasses and four C_3 grasses to maximize variability in response to AMF), and availability (Stock Seed Farms, Murdock, NE, USA; Critical Site Products, Inc., Prairie & Wetland Center, Belton, MO, USA). Seeds were planted in trays of vermiculite during the first week of March, 2007, and allowed to germinate and grow in a greenhouse (LD: 14:10h; 25º:17º C) for 8 weeks. Seedlings were watered daily, but no nutrient or AMF treatments were applied until mesocosm communities were assembled.

Soil inoculum for +AMF mesocosms was collected from a native prairie in northeast Kansas. We sieved freshly-collected soil through 1-cm^2 hardware cloth to remove large root clumps and rocks. For the –AMF treatment, we autoclaved sieved field soil at 121º C for 60 minutes on two consecutive days.

Mesocosm (38 cm (diameter) x 29.5 cm (ht)) held 38 L of a 50:50 mixture of sand and coarse perlite (Therm-o-Rock Perlite, Hummert International^{TM}, Topeka, KS, USA). In each mesocosm we added a 1 cm-deep layer of field (+AMF) or autoclaved (-AMF) soil 10 cm below the substrate surface. To equalize the microbial community, we added 500 ml of microbial slurry to each mesocosm (Koide and Li 1989). We prepared the slurry by passing filtrate from the extra field soil inoculum twice through a 20 micron sieve. To ensure that each mesocosm received the same amount of liquid, we added 500 ml of water to mesocosms containing field soil inoculum.

Most seedlings were in the second-leaf stage (~5-7 cm tall) when we transplanted them from the greenhouse to mesocosms in the second week of May. Mesocosms received four individuals of each species, randomly arranged in a 6 x 6 grid. We replaced any seedlings that died during the first three weeks. We randomized the location of the mesocosms in an outdoor lath house—an open-sided structure with wire mesh designed to exclude large herbivores. Throughout the summer, we applied nutrient solution every three days; on the two interim days we watered each mesocosm to field capacity. Mesocosm buckets were elevated to allow for drainage and to prevent nutrient contamination among treatments.

We applied nutrients as pH-adjusted aqueous solutions. The standard recipe was an adjusted Hoagland's solution (Johnson 1993) and contained: 65 mg/L $K_2SO_{4;}$ $_{72}$ $MgSO_4$; 0.03 mg/L NaCl; H_3BO_3; 0.54 mg/L $MnCl_2{\cdot}4H_20$; 0.07 mg/L $ZnSO_4{\cdot}7H_20$; 0.02 mg/L $CuSO_4{\cdot}5H_20$; 0.011 mg/L FeEDTA; 433 mg/L KNO_3; 8.4 mg/L $Ca(NO_3)_2{\cdot}4H_20$. The pH was adjusted to 6.5 with 0.1M NaOH. To create a gradient in P-availability, we calculated four levels of P relative to a "standard P" of 44 mg/L KH_2PO. We added 0.1, 0.5, 10, or 20 times the standard P (hereafter denoted as 0.1 x P, 0.5 x P, 10 x P, 20 x P). Altering P necessarily changes the N:P of the nutrient solutions because N was held constant for each treatment. Solutions were added to field capacity; the amount of nutrient solution (and water on interim days) was adjusted across the summer accordingly.

After 15 weeks, we clipped all aboveground biomass from each mesocosm, and sorted by species. Biomass was dried at 74° C for 72 hours. We recorded the mass of each species separately, summing across species in a single mesocosm to estimate aboveground net community productivity (g). We sampled soils from each mesocosm immediately following harvest to verify the efficacy of our +/- AMF treatments. Tangled roots prevented us from estimating root colonization for each species. In an effort to minimize the effect of plant species on our estimates of root colonization, we analyzed roots sampled directly beneath *Andropogon gerardii* from each mesocosm. We cleared and stained roots following Koske and Gemma (1989) and quantified percent colonization following (Giovannetti and Mosse 1980).

Shannon diversity (H′) for plant communities was calculated in PC-Ord, v. 4. Because our mesocosms contain the same number of species (and therefore have the same value for species richness), H′ reflects only the evenness (relative abundances) of species. Shannon diversity was the most appropriate measure because H′ captures both richness and evenness components of diversity, both of which may be influenced by AMF and nutrients. Thus, expressing diversity as H′ unifies the model, our results, and other experiments that manipulate AMF. We used biomass of each species as our measure of abundance in all diversity calculations. We tested for treatment effects on evenness, biomass, proportion of total community comprised of C_4 plants, and single species abundances using a balanced 2-way ANOVA with AMF and nutrient levels as fixed effects. Residuals were tested for normality using the Ryan-Joiner test ($P>0.1$) and for homogeneity of variance with Bartlett's test ($P>0.1$). We used a one-way ANOVA to test for effects of P-level on root colonization of root samples collected from +AMF mesocosms. To characterize plant community composition, we conducted a principal components analysis (PCA) using the nine species in each community as variables. Our data do not contain zeros, nor are their nonlinear relationships associated with the environmental gradient, thus, we felt PCA was an appropriate tool for visually comparing communities in multivariate space. We statistically compared the locations of the communities in each treatment in multivariate space using PERMANOVA (Anderson 2001; McArdle and Anderson 2001), which relies on permutation methods to compute *P*-values for distances between group centroids. We then compared the degree of dispersion among treatment communities using PERMDISP (Anderson 2004). For both permutation tests we calculated Bray-Curtis distances and used 999 permutations. Parametric statistics were performed in Minitab 14.1.

RESULTS

Roots from mesocosms containing autoclaved soil contained either no AMF, or extremely low levels (Fig. 2). Among the field-soil-inoculated mesocosms, root colonization increased as added P decreased; communities receiving the least P (highest N:P) had the highest percent colonization ($F_{4,20} = 5.78$; $P = 0.003$). Communities with 10xP and 20xP did not differ from one another, but had significantly (20% on average) less colonization than both treatments receiving reduced amounts of P (Tukey Simultaneous Test, $P<0.05$).

Community structure for plant communities with and without AMF diverged as phosphorus became more limiting (Fig. 3a). Diversity at any given nutrient level depended on the presence of AMF (Fig. 3b; AMF*nutrient: $F_{4,40} = 4.15$; $P = 0.007$). AMF increased diversity where P was less available. By contrast, where P was abundant, we detected no difference in diversity between communities with and without AMF (Tukey Simultaneous Test, $P>0.1$).

Communities segregated in multivariate space (Fig. 4) illustrating that nutrients and AMF interact to determine community composition. The first axis of the PCA ordination (Fig. 4) represents the effect of nutrients on the biomass of species in each community (P is more limiting on the right-hand side of the graph); the second

PC axis reflects species' growth response to AMF. AMF strongly affected community composition, but moreso where P was most limiting (Fig. 4; AMF*nutrient: $F_{4, 40\ \mathrm{PERMANOVA}} = 4.02$, $P = 0.001$). This is illustrated by the greater separation of +AMF and –AMF plots on the right-hand side of the PCA ordination (Fig. 4). By contrast, only nutrient levels significantly influenced community dispersion ($F_{4,40,\mathrm{PERMDISP}} = 4.40$ $P = 0.007$); although AMF and the interaction between AMF and nutrients both influenced dispersion at the $\alpha = 0.1$ significance level.

In all but one nutrient treatment, both mycorrhizal and nonmycorrhizal communities were dominated by *Elymus canadensis* which contributed between 31-42% of the total community biomass (Fig. 5). Neither of the two species dominant in most treatments, *E. canadensis* and *Bouteloua curtipendula,* responded significantly to AMF. Both species achieved greater biomass in soils with high P levels, regardless of AMF treatment (Fig. 6; *E. canadensis*: $F_{\mathrm{nutrient}\ 4,40} = 18.06$, $P < 0.001$; $F_{\mathrm{AMF}\ 1,40} = 1.02$, $P > 0.2$; $F_{\mathrm{AMF*nutrient}\ 4,40} = 1.38$, $P > 0.2$; *B. curtipendula*: $F_{\mathrm{nutrient}\ 4,40} = 15.78$, $P < 0.001$; $F_{\mathrm{AMF}\ 1,40} = 0.19$, $P > 0.2$; $F_{\mathrm{AMF*nutrient}\ 4,40} = 2.02$, $P > 0.1$). Differences in overall community composition we observed among nutrient and AMF treatments were manifested primarily through responses by the subordinate species, many of which responded dramatically to the presence of AMF (Fig. 5 & 6).

Although there were some species-specific differences in the degree to which AMF influenced biomass across the nutrient gradient (Fig. 6), responses were generally consistent among species within a functional group (defined by photosynthetic pathway): at low P, maximum growth for most C_4 species occurred in the presences of AMF while C_3 species performed better in the absence of AMF. Consequently, in mesocosms lacking AMF, the proportion of the community comprised of C_4 grasses declined significantly at low P-levels (AMF * nutrient interaction: $F_{4,40} = 5.90$, $P = 0.001$).

Total community biomass increased as P-availability increased; however, at low P, communities with AMF were significantly more productive than those without AMF (Fig. 7; AMF* nutrient: $F_{4,40} = 4.67$, $P = 0.003$).

DISCUSSION

Our study demonstrates that soil nutrient levels and AMF interact to determine prairie plant community diversity, composition and productivity. While previous work has shown that the presence, abundance, and diversity of AMF (van der Heijden 2002 and references therein), as well as AMF species identity (Klironomos 2003; Vogelsang et al. 2006) can influence plant communities, our results emphasize that contingences of resource supply may govern community-level outcomes of AMF-plant interactions.

At low P-levels, we found that AMF increased diversity in our mesocosm communities. Although we used native tallgrass prairie species, our results contrast with Hartnett and Wilson's (1999) work in tallgrass prairies. They found that AMF decreases diversity and proposed that because the dominant C_4 grasses are highly mycotrophic, removing AMF allowed for competitive release of the subordinate (often C_3) species. Our results better match those obtained in the European grassland experiments in which the dominant plants were cool-season, relatively non-mycotrophic species (Grime et al. 1987; van der Heijden et al. 1998). Accordingly, in our study, *Elymus canadensis* (C_3 grass) dominated nearly all treatment communities, and showed no significant positive growth response to AMF. The fast growth rate of *E. canadensis*, paired with atypically cool spring and summer temperatures in 2007, may explain its competitive success over mycotrophic, warm-season plant species (e.g. *Andropogon gerardii*) that typically dominate native prairies. Regardless, our results are consistent with the general prediction that the relative mycorrhizal dependency of the dominant versus the subordinate plants determines the direction of the community diversity response to AMF.

Importantly, our results also demonstrate that the effect of AMF on plant communities is not uniform across soil nutrient levels (Fig. 3). Where P-availability was lowest, AMF were most influential, increasing diversity and biomass relative to communities lacking AMF. When P was not limiting, AMF did not influence diversity or productivity. These results are consistent with the model presented in Fig. 1b and suggest that by combining our knowledge of the relative mycotrophy of coexisting species with our knowledge of soil resource availability, we may be able to predict the influence of AMF on plant communities.

Previous models that predict the effects of AMF on plant communities have also considered soil nutrients. For example, van der Heijden (2002) presented a model based on Tilman's (1982) resource-ratio theory. He suggested that by increasing the access of host-plants to P (presumably at the expense of N-acquisition), AMF may increase species richness of a community. Our results are consistent with van der Heijden's model because we found that in a community in which subordinate species are mycotrophic, AMF increase diversity at low P (albeit through evenness and not richness). However, the resource-ratio modeling approach applies only to low P soils in which AMF are necessary to access P, and in communities in which mycotrophic species do not dominate. By contrast, we provide a model that takes into account a soil nutrient gradient, as well as plant community composition, emphasizing that the role of AMF in mediating plant community diversity depends both on nutrient status and the degree of mycotrophy of the dominant species.

Because our model focuses specifically on the impact of AMF on diversity as mediated by P supply, we rely on several implicit assumptions. For instance, we assume that P-availability does not directly influence plant diversity (i.e. through mechanisms other than via AMF). In most terrestrial systems, direct effects of P on diversity appear to be the exception (e.g. Wilson et al. 1996, Goldberg and Miller 1990), rather than the rule (Gough et al. 2000). Indeed, we have seen no effect of long-term P-addition on diversity in field experiments at our site (B.L. Foster, *unpublished manuscript*). Still, it is worth noting that our model may not fully apply to wetland and moist systems where diversity is often sensitive to P-additions (e.g. Wassen et al. 2005).

We also assume that parasitic effects of AMF are not strong (or consistent) enough to have community-level consequences. Our results were consistent with this assumption: even at the highest amounts of P added, we observed few indications of nutrient-induced parasitism, and no consistent response across functional groups was apparent. For instance, only two species, *Bouteloua curtipendula (C_4)*, and *Koleria pyrimidata (C_3),* showed significant biomass declines in the presence of AMF when P was plentiful (Fig. 6). *Agropyron smithii* (C_3) was negatively affected by AMF at all nutrient levels. Notably, violating this assumption would yield data that deviate from our model in a predictable way. If, for example, mycotrophic plants were parasitized under high-P conditions (in a community with AMF in which mycotrophic plants are subordinate), we would have expected their relative abundance to decline, and consequently diversity to decline as well. Testing our model in systems where parasitism is suspected to occur would likely be very instructive.

The last assumption implicit in our model was that the primary benefit to plants hosting AMF is P-acquisition. While other benefits of AMF have been documented (e.g. pathogen resistance, Newsham et al. 1995), ample evidence suggests that AMF play a prominent role in acquiring P in prairies (Hartnett and Wilson 2002)—and indeed, in many ecosystems (Smith and Read 1997). Moreover, we observed significant growth response in plants hosting AMF at low P-levels. Still, it is possible that AMF provided additional benefits to plants in our experiment. For instance, AMF are capable of helping plants acquire N (Govindarajulu et al. 2005). If AMF increased N-acquisition under high P (and potentially N-limited) conditions, this could help explain the relative lack of parasitism we observed. Such functional switches by AMF along a nutrient gradient are not well-documented (Reynolds et al. 2005), although Sylvia and Neal (1990) recorded increases in root colonization when plants were deficient in N relative to P. In their study, P additions only suppressed colonization when N was sufficient. We also found that roots of plants in high P treatments were colonized, but to a significantly lesser degree than at low P.

There are other possible explanations for why we didn't see more evidence of parasitism. For example, we might not have added enough phosphorus to discount benefits provided by AMF. The fact that adding 20 x P did not increase biomass relative to 10 x P suggests that communities were saturated in P at the high P end of the gradient. Still, we might not have reached the threshold of P (concurrent with carbon limitation) to induce parasitism. Alternatively, although root colonization is not consistently linked with growth benefits (McGonigle 1988), it is possible that the limited benefit plants derived from AMF in high P treatments is due, at least in part, to lower colonization rates. A decline in AMF colonization may be expected if, in the presence of additional P, plants allocate photosynthate to growth and AMF become C-limited.

Because the dominant species in our experiments generally showed no response to AMF regardless of nutrient level, the differences in community structure we observed were due primarily to shifts in the relative abundance of subordinate species. Among the subordinates, a tradeoff existed between the relative and absolute abundance of C_4 versus C_3 species. For example, at low P, maximum growth for most C_4 species occurred in the presence of AMF, while C_3 species performed better in the absence of AMF (Fig. 6). Community composition shifted accordingly: in the absence of AMF at the lowest P-levels, *Hordeum jubatum* (C_3) became the most dominant species, and *Koleria pyrimidata* (C_3) increased from being the most rare (9th) in high P treatments to 5th most common. The ranks of *Bouteloua curtipendula, Andropogon virginicus*, *Schizachyrium scoparium*, and *Sorgastrum nutans* (all C_4) declined (Fig. 5). We may have seen distinct functional group differences in part because we attempted to minimize phenological differences in our experiment by germinating seeds in a greenhouse at the same time and providing ample water throughout the season. Timing of peak biomass production and flowering vary according to functional group, which may decrease competition in the field. Still, despite phenological differences, there remains significant overlap in the periods of growth activity of C_3 and C_4 plants in natural prairies (Ode et al. 1980). Field experiments in tallgrass prairie provide additional support for the role of AMF in mediating competition among functional groups in native prairies, despite phenological differences (Hartnett and Wilson 1999).

Van der Heijden et al. 2008 proposed that the significance of microbes to plant productivity will be greatest in nutrient-poor soils. Our results support this hypothesis: although in all communities biomass declined as available P declined, plant communities with AMF were significantly more productive relative to those without AMF at all but the highest levels of P. As we described for diversity, this result is likely reliant on whether the dominant plants are mycotrophic. It is worth noting that P-limitation can be exacerbated by decreasing P, as in our experiment, or by increasing N (e.g. Johnson et al. 2003b; Johnson et al. 2008). The fact that in either case AMF enhances plant growth reinforces the idea that from the plant perspective, nutrient availability is not just a matter of absolute abundance. Rather, the availability of one vital nutrient can only be understood relative to the available amounts of other key nutrients (Tilman 1982). This has important consequences for anthropogenic nutrient deposition: regardless of whether we enhance N or P, we likely alter community productivity and AMF-mediated competitive outcomes. Regardless, the importance of absolute versus relative abundance of nutrients for plant-fungal interactions is a research area that deserves more attention.

We detected significant effects of AMF and nutrients on biomass and diversity in only one growing season. The community dymanics we observed do not necessarily reflect equilibrium outcomes for competition among the species, nor do they reflect the influences of AMF on species richness via effects on plant recruitment (van der Heijden 2004). Rather, we may be seeing transient dynamics that are strongly influenced by differential growth rates among species (Tilman 1988). It is therefore possible that several seasons of growth may alter the competitive hierarchies we observed. However, we believe that because nutrient limitation drives competition in grasslands, and because AMF-mediated competition operates primarily via nutrient acquisition, the mechanisms driving community outcomes in our experiment are relevant regardless of the equilibrium state of the communities. Moreover, transient states may have long-lasting effects on the community via priority-effects (Fukami 2004) and plant-soil feedbacks (Reynolds et al. 2003).

Our results confirm the need to identify conditional outcomes of mutualisms (Bronstein 1994) if we are to predict the influence of anthropogenic nutrient deposition on plant communities. Furthermore, given the primary role of nutrient competition in prairies, restoring prairies or managing for diversity requires that we understand the influence of abiotic environments on plant-fungal symbioses and how these, in turn, influence plant diversity and productivity. Johnson et al. (2006) proposed a need for "...a synthesis that couples our understanding of the plant-fungal symbioses with community-and ecosystem level process in a way that allows us to predict the results of mycorrhizal interactions." We believe that identifying the resource contingencies for community level outcomes of AMF-plant interactions brings us one important step closer to achieving that goal.

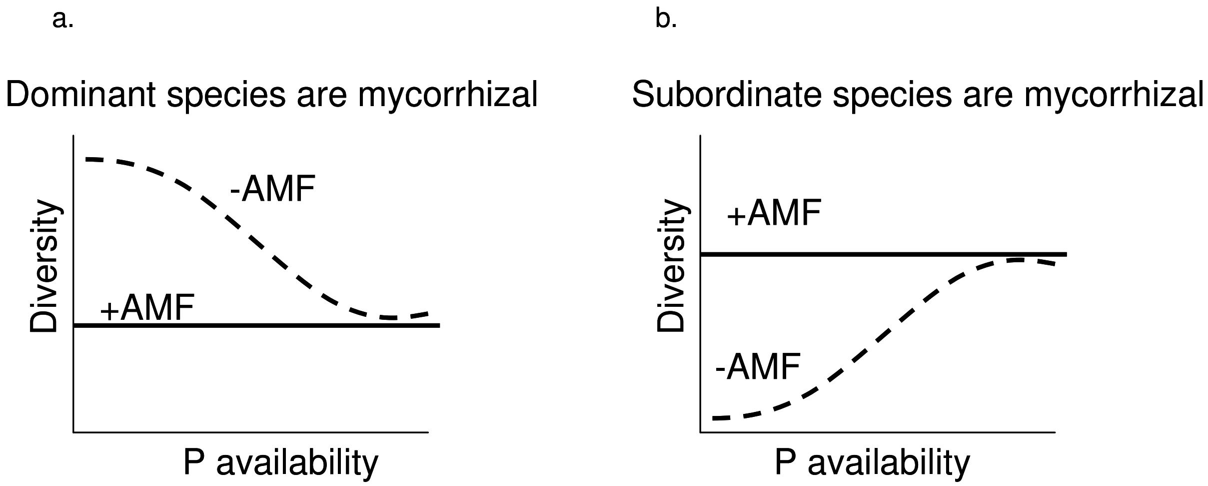


Figure 1. Conceptual model illustrating the interactive effects of AMF and soil nutrient levels on plant communities dominated by (a) highly mycotrophic or (b) less-mycotrophic species. As P becomes less available, AMF play a stronger role in mediating plant community diversity. If the plant community is dominated by highly mycotrophic species, AMF suppress diversity by enhancing growth of dominants. If the subordinate species in the community are relatively more mycotrophic, AMF enhance their growth, thereby increasing diversity. For systems in which nutrients are the primary host-benefit to AMF, this model predicts that the influence of AMF on diversity will be strongest at low nutrient (specifically P) levels. Whether AMF increase or decrease diversity at low P depends on the relative degree of mycotrophy among plants in the community. Note: diversity values are not meant to be compared among community types (i.e. Fig. 1a vs Fig 1b). The influence of AMF across a nutrient gradient applies only within community types.

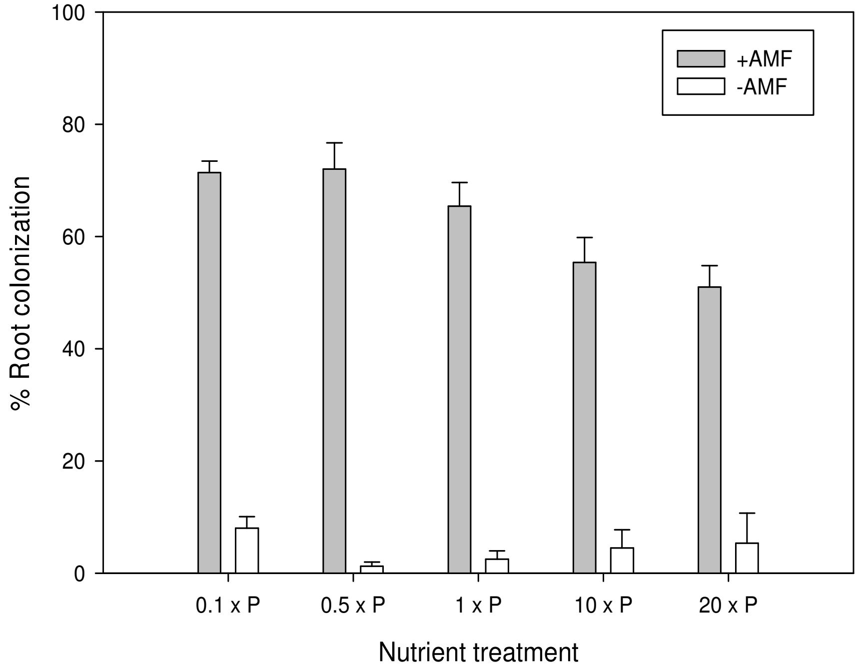


Figure 2. Percent root colonization (± 1SE) of roots collected from beneath *Andropogon gerardii* in each mesocosm.

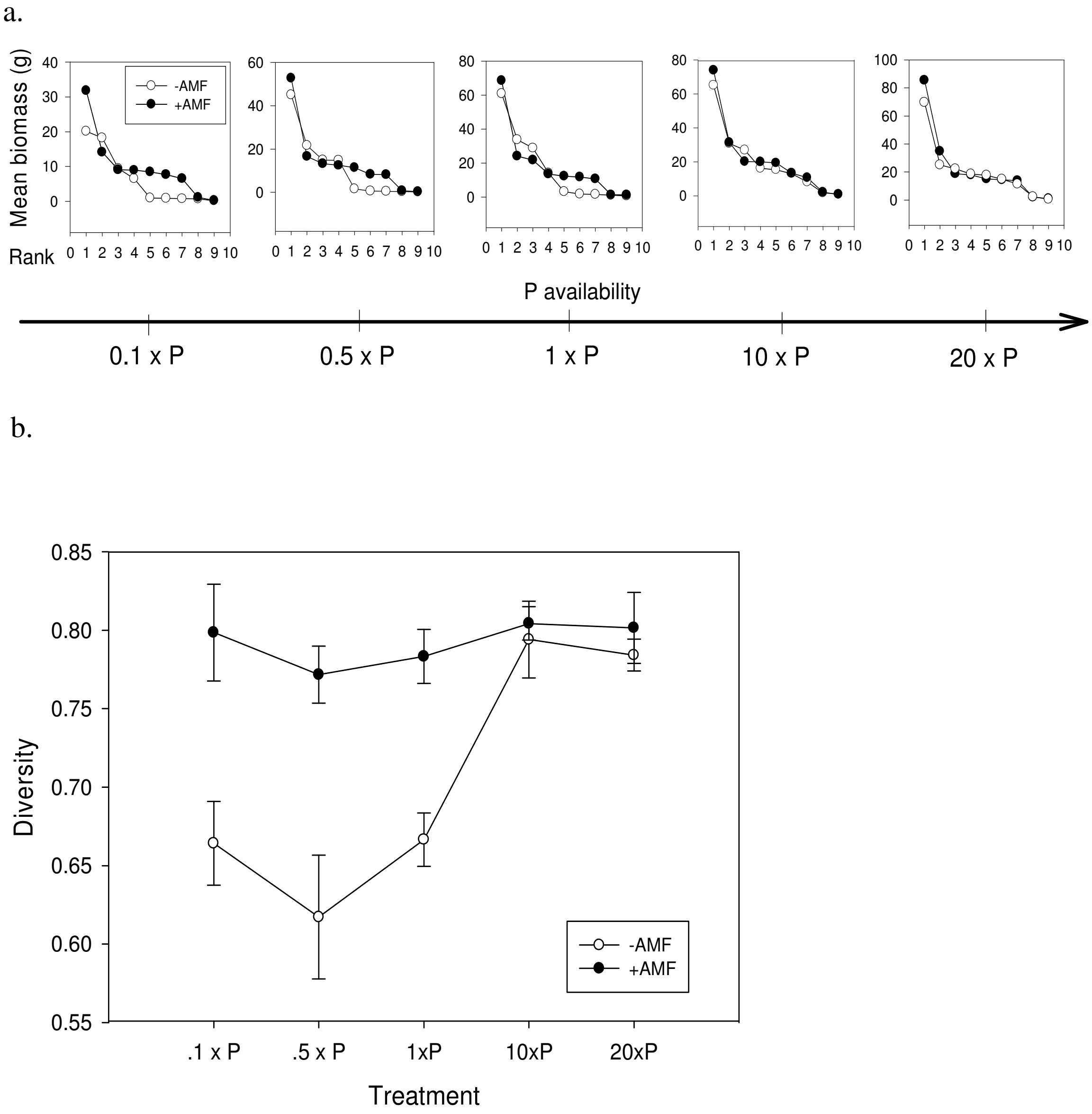


Figure 3. (a) Community rank abundance curves for + AMF (●) and – AMF (○) mesocosms along a gradient from low to high P availability. Each point represents the mean abundance (n=5, measured as biomass) of a species, ranked in order of abundance relative to other species in the community. (b) Interactive effect of soil P and AMF (+ AMF (●) and – AMF (○)) on mean plant diversity (+ 1 SE).

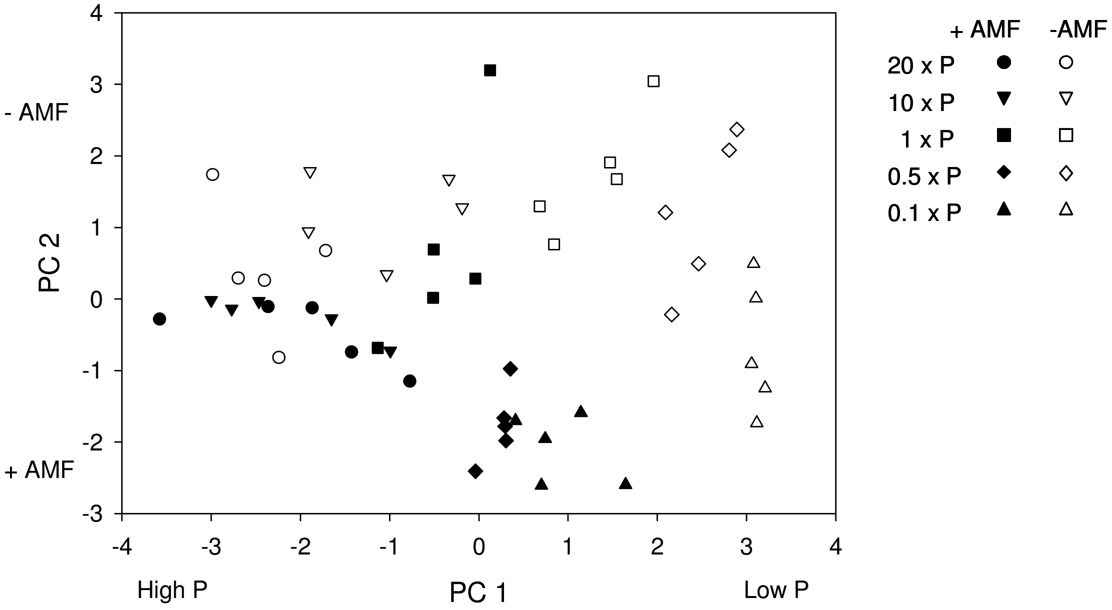


Figure 4. Principal Components Analysis for mesocosm communities comprised of nine species. Communities are coded for + AMF (shaded) and –AMF (open) treatments, as well as nutrient treatments: 20 x P (●), 10 x P (▼), 1 x P (■), 0.5 x P (♦) and 0.1 x P (▲). AMF determined community composition most strongly where P was limiting (*P*<0.001).

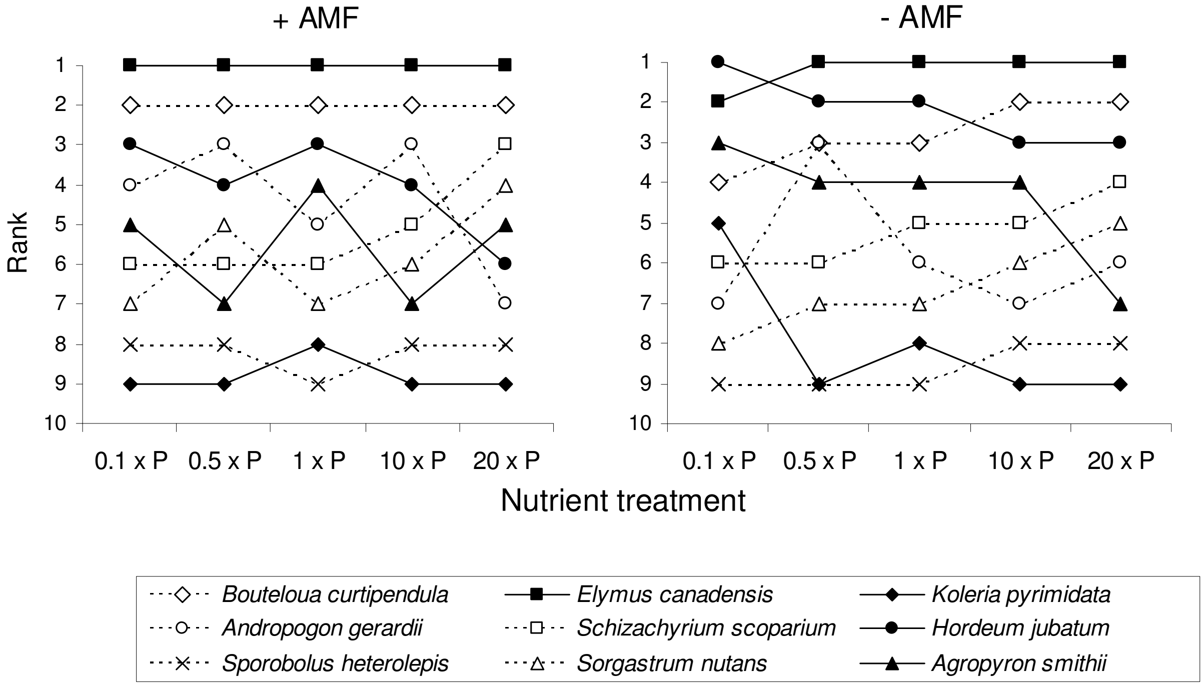


Figure 5. Shifting ranks of each species within its community across the P gradient for both +AMF (a) and –AMF (b) treatments. C_3 species are represented by shaded symbols and solid lines; C_4 species are represented by open symbols and dotted lines. Species are ranked in order of their abundance, but to ease interpretation, data are not scaled by biomass.

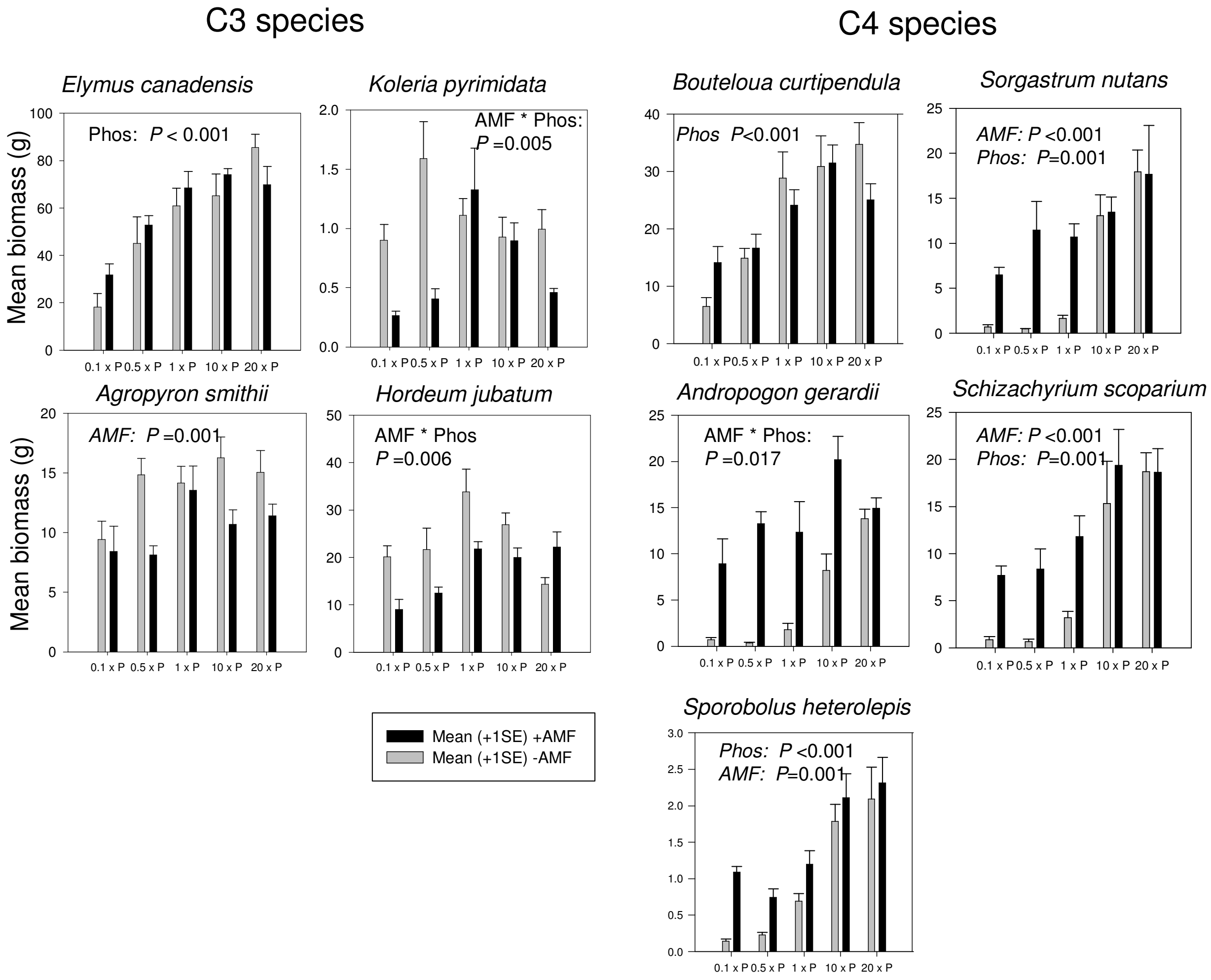


Figure 6. Mean aboveground biomass (+ 1 SE) for each species +/-AMF at each phosphorus (Phos) level. The left-hand, dark shaded bars show +AMF; the right-hand, lighter bars show –AMF treatments. Values on the ordinate axes differ among graphs. *P*-values from 2-way ANOVAs are presented for statistically significant results. In cases where the interaction is significant, results for main effects are not shown.

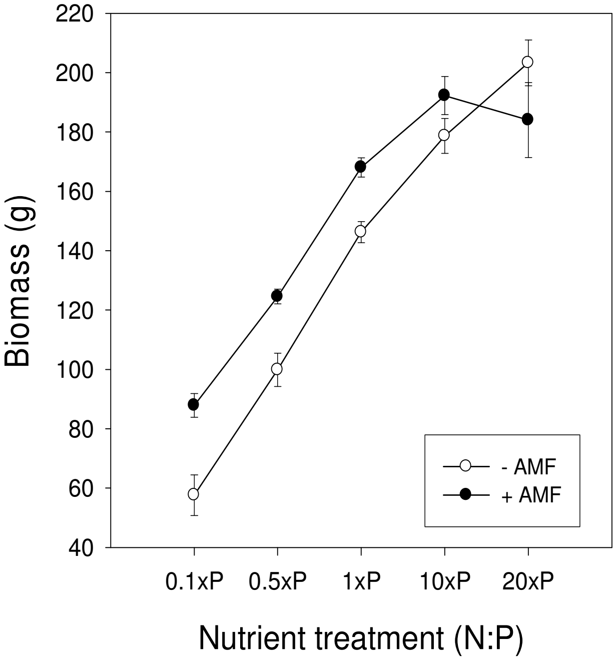


Figure 7. Mean total community biomass (+ 1 SE) for +AMF (●) and –AMF (○) mesocosms. The degree to which AMF influenced biomass depended on nutrient levels: AMF increased total biomass, but only where P was limiting (*P*<0.01).

CHAPTER 2: Patch size effects on plant species decline in an experimentally fragmented landscape

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 versus succession on species' decline by examining distributions of abundances for 18 plant species declining over time in an experimentally fragmented landscape in Northeast Kansas. 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 versus abundance varied dramatically among species: some species declined first in occupancy, others remain 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.

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 & Askins 1995 (birds); Schoereder 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-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, page 1272 in Cook et al. 2005).

Our experimental design thus allows us to assess the relative influence of patch size versus 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) versus 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 graphic, 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 versus 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, versus 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 non-parametric 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 on how habitat fragmentation influences succession. Initiated in 1984 in the prairie-forest ecotone of eastern Kansas (described in Holt et al. 1995; 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˚03' N, 95˚12'W), 12 km north of Lawrence, Kansas. In 1984, an array of patches of three sizes (4 x 8 m, 12 x 24 m, 50 x 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 x 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 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, versus 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" versus "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-m^2 quadrats, usually in the month of July. After 1994, all woody stems > 2.0 m in height were identified, counted, and measured in 4 x 4 m quadrats centered on the 1-m^2 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 in small patches, n_L=180 in large patches). In 1985, a mix of grasses, annual 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 analyze 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 (Holt, pers. obs.). 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 179 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 versus 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 re-sampled the data 1,000 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 average abundance across all quadrats. So the difference in the areas under two ROAPs or CDFs is the difference in the average 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 average 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 versus 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 versus 1995-2000. We combined results for 1995 and 2000 because the year when the greatest patch sizes 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 and Microsoft Excel/Visual Basic 2003.

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 cannabinum, 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 *Meiliotus* 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 & 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 do 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. Figure 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 declined in abundance more rapidly on small patches versus large patches. On the other, 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). 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 Kodrick-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 woody encroachment may reflect pre-existing 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.

Although short-lived species were not restricted to small patches, all species which 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 versus 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 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 differently and 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 Figures 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 versus 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.

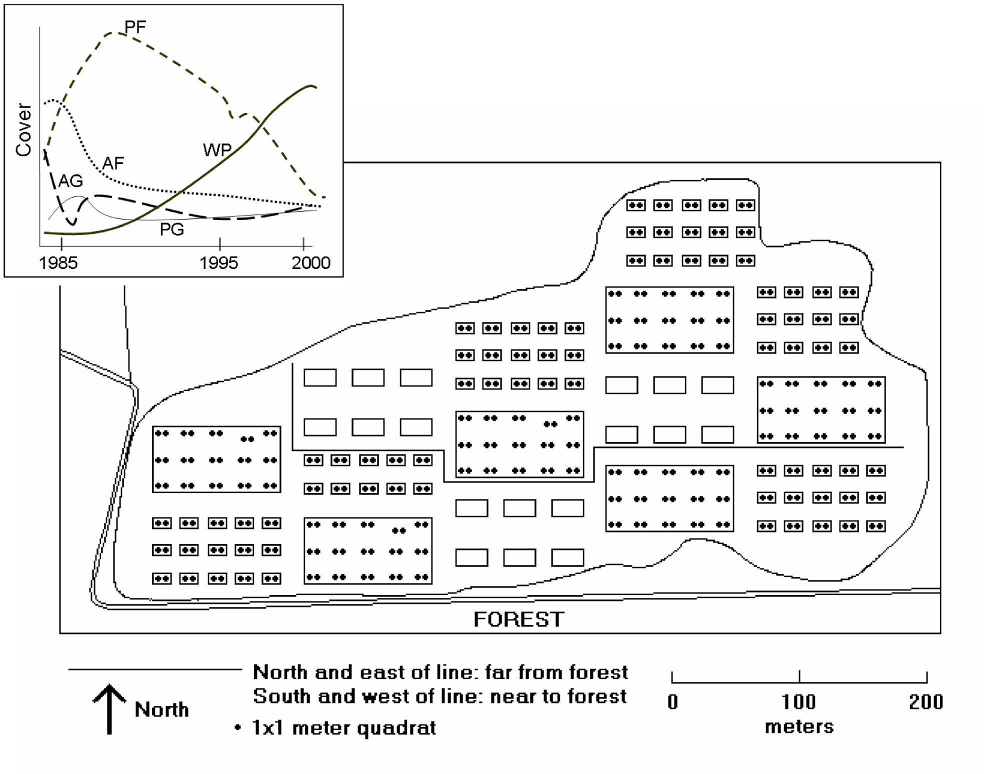
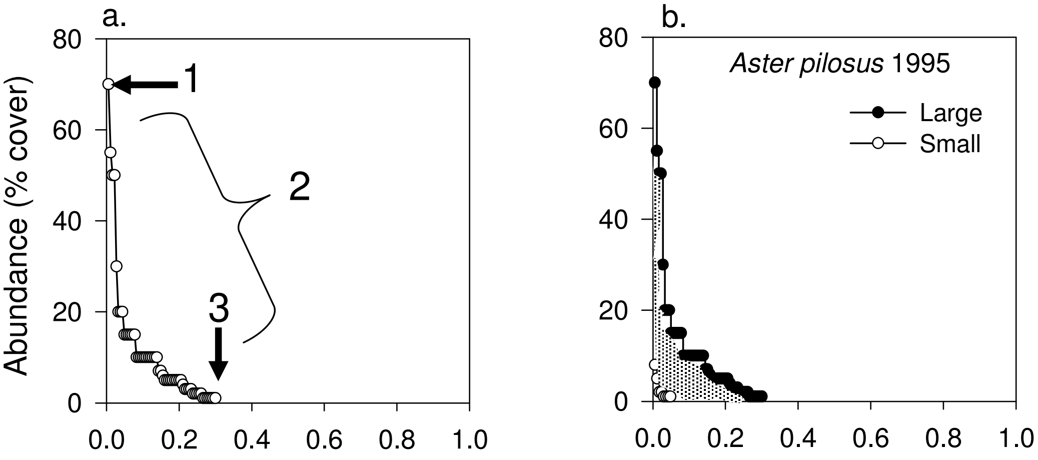


Figure 1. The experimentally fragmented landscape in northeast Kansas. Black dots represent sampling quadrats. Patches considered near versus far from the forest source on the south side are separated by a solid line. Inset: Temporal shifts in relative abundance of life history groups in the fragmentation landscape. 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 1998-2003, quadrats in large patches contained 20% more woody stems >2 m in height, compared to small patches (Cook et al. 2005).



ROAPs over successional time

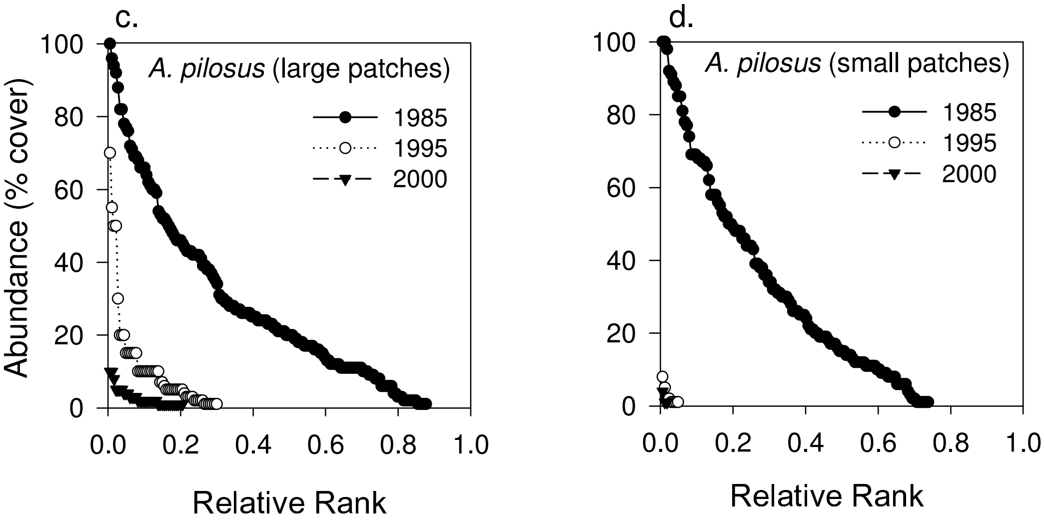


Figure 2.a) Sample Rank Occupancy-Abundance Profile (ROAP) for a single species. Local abundance was measured as percent cover in a 1-m^2 quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the number of quadrats sampled. Each quadrat in which the species was found is represented 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: *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 large patches (c) and small patches (d). For clarity, quadrats with zero abundance are not shown

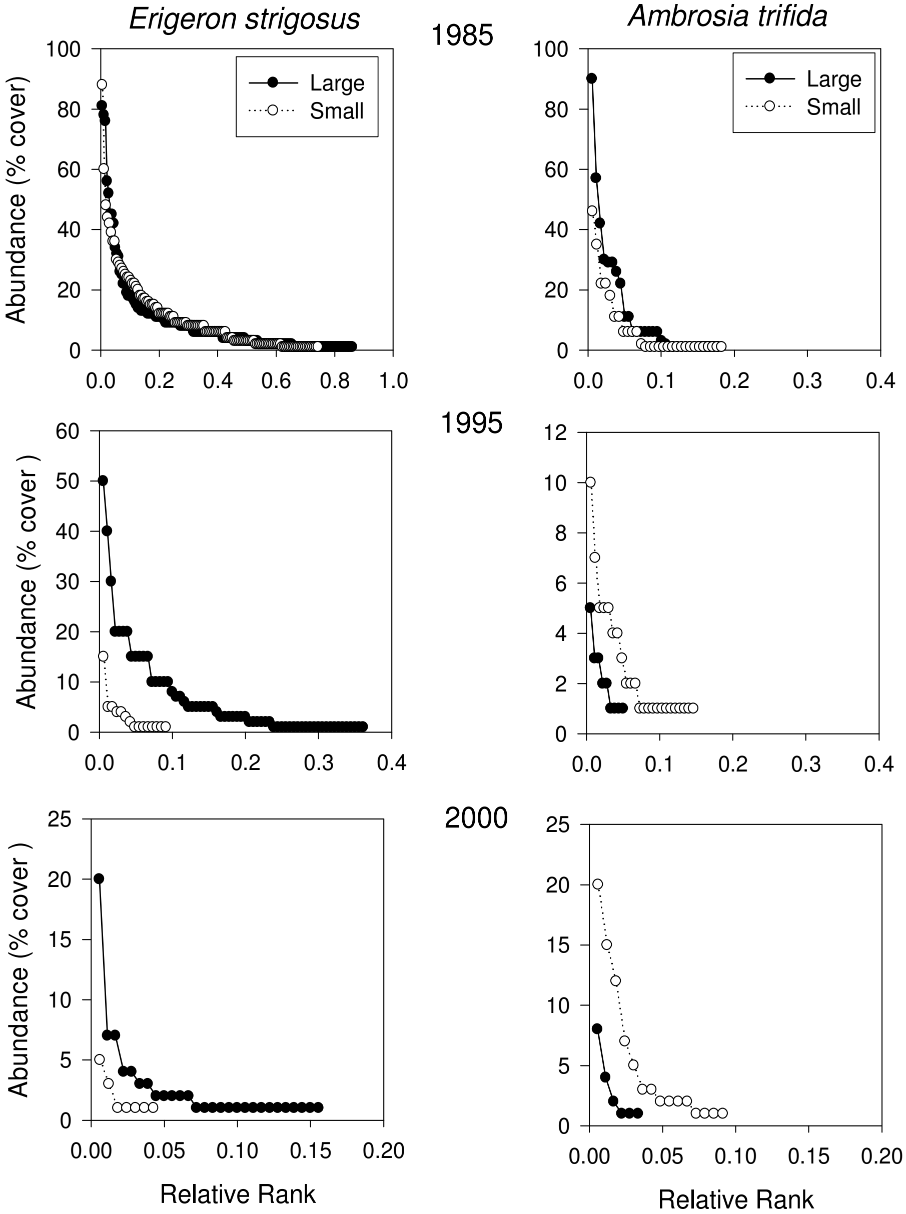


Figure 3. Examples of ROAPs comparisons between large and small patches for two species at three different time periods (1985, 1995, and 2000) during succession. Abundance was measured as percent cover in a 1-m^2 quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the total number of quadrats sampled. For both species, ROAPs on large versus 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.

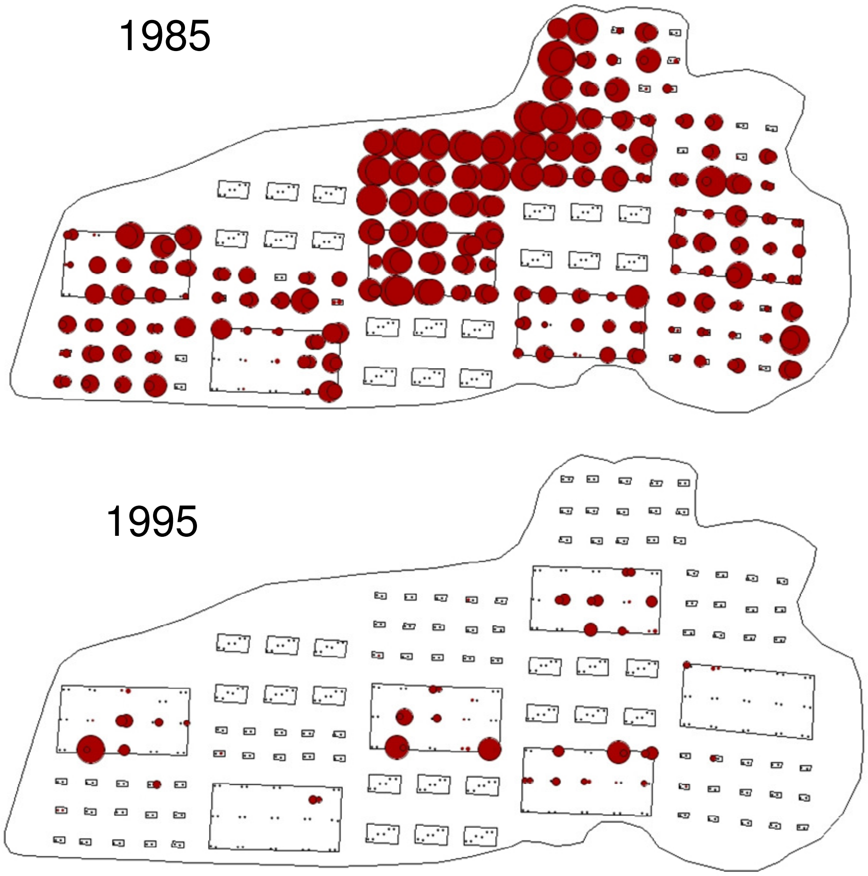


Figure 4. Visually compelling evidence for patch size effects on abundance during extinction of an early successional species. This example shows *Aster pilosus*, a species that persisted preferentially on large patches. Bubble sizes are scaled to reflect the percent cover within quadrats of *A. pilosus* 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.

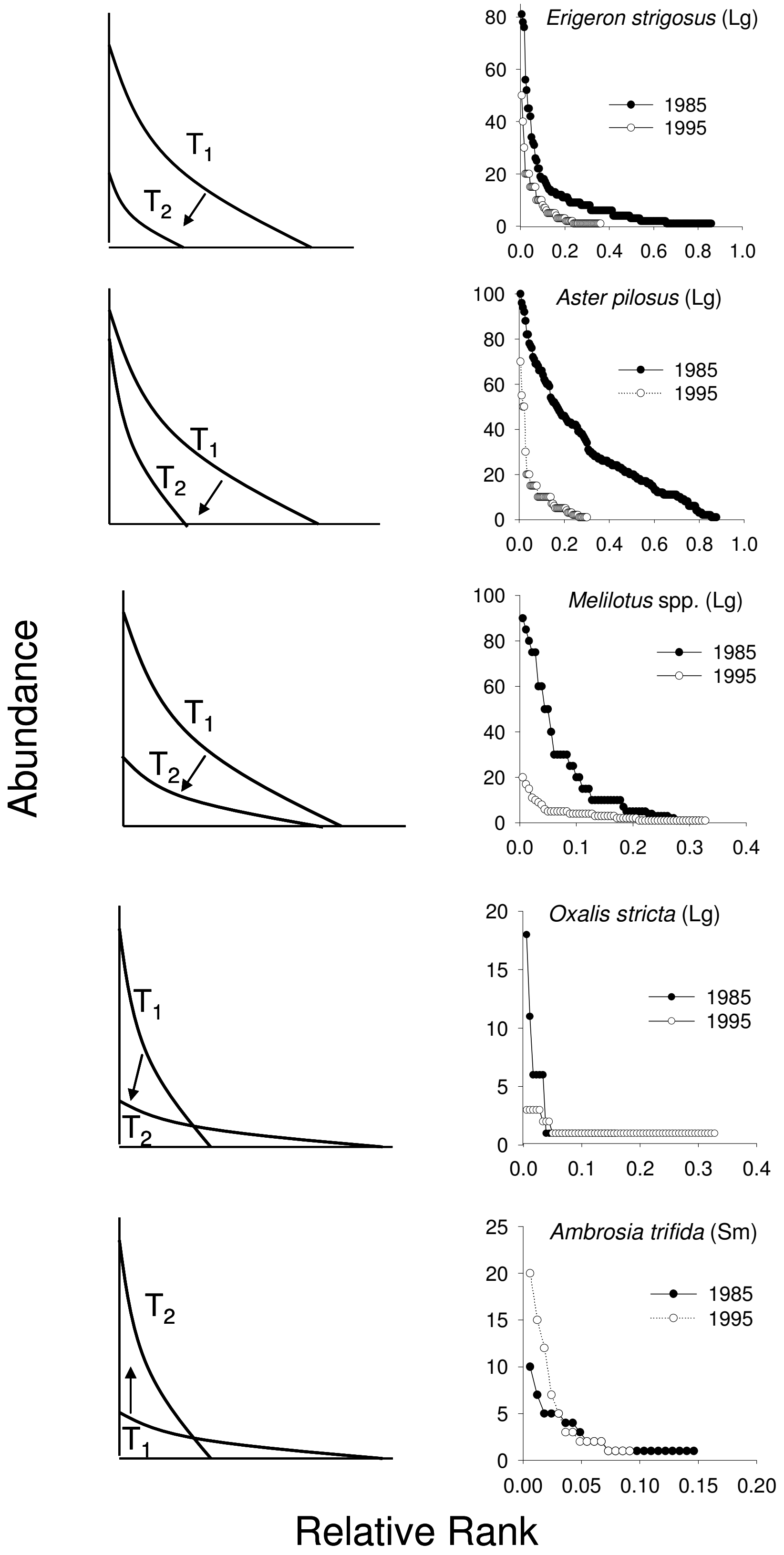

Abundance
Relative Rank
T1
T2
Erigeron strigosus (Lg)
1985
1995
0
20
40
60
80
0.0 0.2 0.4 0.6 0.8 1.0
Aster pilosus (Lg)
0
20
40
60
80
100
Melilotus spp. (Lg)
0.0 0.1 0.2 0.3 0.4
Oxalis stricta (Lg)
0
5
10
15
20
Ambrosia trifida (Sm)
25
0.00 0.05 0.10 0.15 0.20

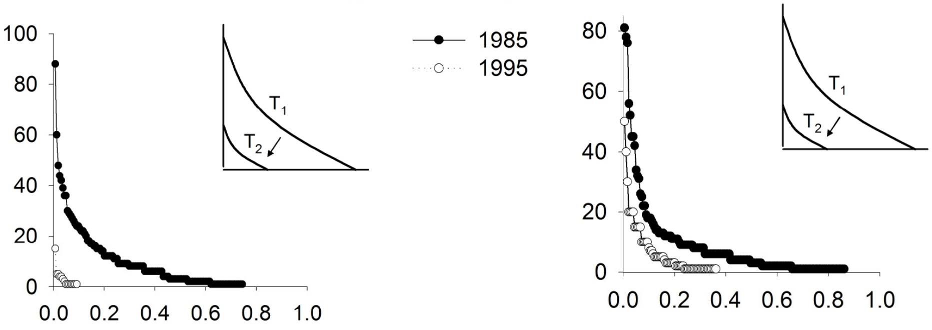
Figure 5 (previous page). Models comparing ROAPs among years depicting possible trajectories of abundance decline. T_1 and T_2 are respectively early and later snapshots in time along the trajectory. Empirical examples were selected based on visual congruence to the conceptual models; thus, examples were drawn from both large (Lg) and small (Sm) patch sizes. Collectively, they illustrate the diverse patterns of decline exhibited by early-successional species in our system. For empirical examples, abundance was measured as percent cover in a 1-m^2 quadrat. Relative rank was calculated by dividing the rank order of the quadrat by the number of quadrats sampled

Small

Large

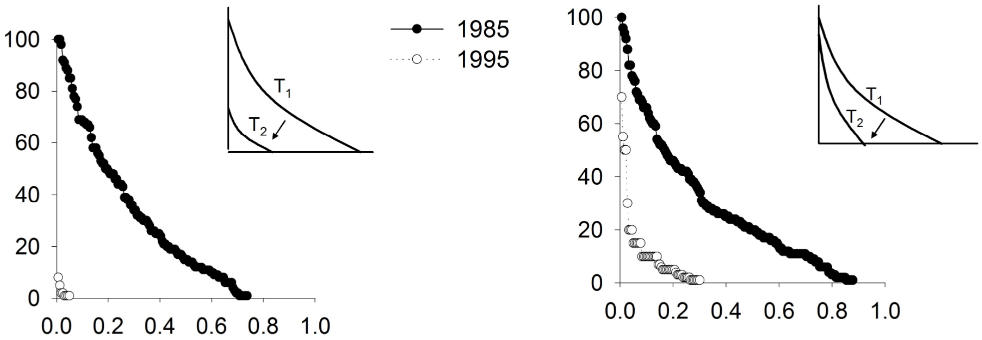
a.

Erigeron strigosus



b.

Aster pilosus



c.

Ambrosia trifida

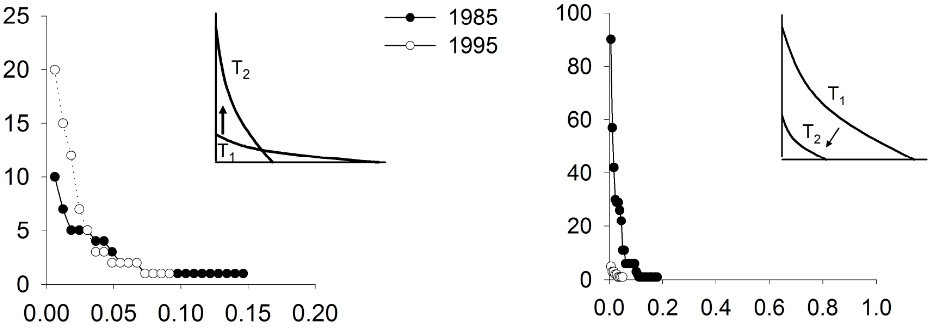


Figure 6 (previous page). Patch size effects on species declining in abundance may emerge due to a) different rates of decline on each patch size (i.e. occupancy and local abundance decline proportionally on a given patch size, but the magnitude of overall change is greater on one patch size than the 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. All plots depict abundance on the ordinate and relative rank on the abscissa. For empirical examples, abundance was measured as percent cover in a 1-m^2 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

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. (The timing of the effect depends on the timing of peak abundance for the species; species that peaked in abundance in 1985 usually showed patch size effects in 1995; ”wax-wane” species showed patch size effects in 2000. For a breakdown by year, see Appendix B). Longevity refers to the species' above-ground duration: annual (A), biennial (B), or perennial (P). Clonal spread refers to the capacity of the plant to reproduce vegetatively. Data for plant species presence (Y) or absence (N) in the matrix were collected in July 2001 (methods described in Cook et al., 2002). Direction of patch size effects are denoted by L or S depending on whether the species persisted at greater abundance on small (S) or large (L) patches; ns denotes comparisons that were not statistically significantly different.

Species	Family	Life form	Longevity	Clonal spread	Found in matrix	Persist longer on:
Ambrosia artemisiifolia L.	Asteraceae	Forb	A	N	Y	L
Aster pilosus Willd.	Asteraceae	Forb	P	Y	Y	L
Aster praelatus Poir.	Asteraceae	Forb	P	Y	Y	L
Erigeron strigosus Muhl. ex Willd.	Asteraceae	Forb	A/B	N	Y	L
Hypericum punctatum Lam.	Hypericaceae	Forb	P	Y	N	L
Lespedeza stipulacea Maxim.	Fabaceae	Forb	A	N	Y	L
Oxalis stricta L.	Oxalidacea	Forb	P	Y	Y	L
Ambrosia trifida L.	Asteraceae	Forb	A	N	N	S
Cirsium altissimum (L.) Spreng.	Asteraceae	Forb	B	N	Y	S
Helianthus annuus L.	Asteraceae	Forb	A	N	N	S
Melilotus spp.	Asteraceae	Forb	A/B	N	N	S
Apocynum cannabinum L.	Apocynaceae	Forb	P	N	N	ns
Acalypha virginica L.	Euphorbiaceae	Forb	A	N	Y	ns
Agrostis hyemalis (Walt.) B.S.P.	Poaceae	C_3 Grass	P	Y	N	ns
Juncus spp.	Junacaceae	C_3 Rush	P	N	Y	ns
Lactuca saligna L.	Asteraceae	Forb	A/B	N	Y	ns
Solidago canadensis L.	Asteraceae	Forb	P	Y	N	ns
Convolvulus arvensis L.	Convolvulaceae	Vine	P	Y	Y	ns

Appendix B. Patch size and distance effects on ROAPs for the 18 focal species broken down by year. Direction of patch size effects are denoted by L or S depending on whether the species persisted at higher abundance on small (S) or large (L) patches. Direction of distance effects are denoted according to whether a species was more prevalent on near (N) or far (F) patches. NF reflects a species for which ROAPs crossed and were significantly different, indicating higher occupancy on one patch type and higher maximum local abundance on the other.

	Patch Size			Distance	
Species	1985	1995	2000	1995	2000
Acalypha virginica	ns	ns	ns	ns	ns
Agrostis hyemalis	ns	ns	ns	ns	ns
Ambrosia artemisiifolia	**L**	ns	**L**	ns	ns
Ambrosia trifida	ns	**S**	**S**	ns	ns
Apocynum cannabinum	ns	ns	ns	ns	**N**
Aster pilosus	ns	**L**	**L**	ns	ns
Aster praealtus	ns	**L**	**L**	ns	ns
Cirsium altissimum	ns	**S**	**S**	**F**	**F**
Convolvulus arvensis	ns	ns	ns	ns	ns
Erigeron strigosus	ns	**L**	**L**	ns	ns
Helianthus annuus	**L**	**S**	ns	ns	ns
Hypericum punctatum	ns	**L**	ns	**N**	**NF**
Juncus spp.	ns	ns	ns	ns	ns
Lactuca saligna	ns	ns	ns	ns	ns
Lespedeza stipulacea	ns	**L**	ns	ns	ns
Melilotus spp	ns	ns	**S**	ns	**F**
Oxalis stricta	ns	**L**	ns	ns	ns
Solidago canadensis	ns	ns	ns	ns	ns

CHAPTER 3: Patterns of decline in North American breeding birds

Abstract.

Species extinctions typically occur following dramatic population declines; detecting these declines is therefore crucial for biodiversity conservation. Attempts to quantify local and global population declines are complicated by the fact that abundance at a single time period can be defined in terms of total abundance, local density, and occupancy. Traditional approaches to distribution-abundance patterns rely on plotting mean values for abundance against occupancy. However, mean values obscure variation in abundance across occupied sites. We used a new method called Rank Occupancy Abundance Profiles (ROAPs) to estimate declines in North American bird species. Using data from the long-term, large-scale North American Breeding Bird Survey, we quantify the magnitude of declines for 209 bird species. ROAPs allow us to partition losses in regional abundance according to the proportion of individuals lost in populations of different densities, as well as the proportion of the regional abundance lost due to local extinctions.

Nearly 20% of bird species surveyed showed statistically significantly declines in regional abundance between 1970 and 2005. The 20 bird species to experience the highest proportional losses showed declines between 48% and 89% of their initial regional population sizes. Patterns of decline varied according to initial regional abundance of the species: very abundant species experienced large proportional drops in local density, while species with low regional population sizes experienced proportionally higher losses due to local extinctions. Based on patterns we observed across species, as well as those observed in time-series data within species, we propose a new model depicting phases of decline a single species experiences as it nears extinction. Specifically, we suggest that two time lags exist as a species approaches rarity: 1) species lose individuals from intermediate-density sites prior to losing individuals from sites with the highest densities, and 2) species lose individuals from the highest density sites before local extinctions ensue (i.e. declines in occupancy). We also detected threshold regional abundances below which local populations can no longer persist. Our results emphasize the interplay between local and regional abundance as species decline. Early detection of declines could alert conservationists before the largest populations diminish. Further, monitoring schemes that record presence-absence data only will not capture declines until local extinctions occur—which we propose is at a late stage of decline.

INTRODUCTION

There is little doubt that human-induced environmental changes continue to threaten biodiversity (Sala et al. 2000; Davies et al. 2006; Pimm et al. 2006). Biodiversity loss is typically measured in units of species extinctions; the primary extinction-drivers include landscape change and habitat loss, environmental pollution, overexploitation, nutrient deposition, spread of exotic species, and changes in atmospheric composition and climate (Diamond 1984; Sala et al. 2000; Thuiller 2007). While each of these threats affects species independently, the synergism among threats may be the most influential extinction-driver of all (Mora et al. 2007;

Brook et al. 2008). Nearly 30 years ago the field of conservation biology was established to better understand and prevent extinction in the face of such anthropogenic pressures (Brussard 2000); at present, extinction risk still guides conservation management and policy (Gaston and Fuller 2007; Mace et al. 2008).

Rate of decline is a key factor for determining extinction risk. Dramatic declines alone—even prior to rarity—may warrant a species' inclusion on the International Union for Conservation of Nature's (IUCN) Red List (Mace et al. 2008). We know that for many taxa, human activities have significantly reduced the total numbers of individuals by reducing the number and average size of local populations (Hughes et al. 1997; Ceballos and Ehrlich 2002; Balmford et al. 2003; Gaston et al. 2003). In 1994, Graeme Caughley called for conservation biologists to focus resources not just on understanding the dynamics of small populations, but on "…detecting, diagnosing, and halting … population decline" (Caughley 1994). Recently, Gaston and Fuller (2007) argued that we should pay more attention to the decline of common species because they play significant roles in ecosystems, and because their declines can ultimately lead to rarity. Indeed, species with larger populations may be even more vulnerable than small ones when extrinsic threats are driving declines (Mace et al. 2008). The conceptual dichotomy between conservation research focused on extinction-prone small populations versus larger, declining populations may be somewhat artificial given that "extinction is merely the endpoint of decline" (Gaston et al. 2000). In practice, emphasizing the detection and management of declining populations may actually reduce human-induced rarity, and ultimately, species extinctions.

Attempts to quantify local and global population declines are complicated by the fact that abundance can be defined and subdivided in a number of ways. For instance, one can measure local abundance (# individuals at a single site), global abundance (total of all individuals in all populations), distributional extent (total area within a species range), or range occupancy (proportion of occupied patches within a species range). Recording multiple aspects of abundance is crucial to conservation efforts, because human-induced declines may involve the extirpation of local populations, reduced local abundances in persisting populations, or both (Hughes 1997; Rodriguez 2002; Gaston and Fuller 2007). While local abundance and occupancy are positively correlated both inter- and intra- specifically (reviewed in Gaston et al. 2000), relying on one measure does not always provide reliable estimates of the other (Conlisk et al. 2009). Furthermore, intraspecific abundance-occupancy relationships show considerably less consistency than inter-specific patterns (Gaston et al. 1998), potentially due to time-lags between changes in occupancy and local abundance (Gaston et al. 1998; Conrad et al. 2001). Recent evidence suggests that in declining species, local abundance and occupancy are decoupled (tiger moth: Conrad et al. 2001; birds: Webb et al. 2007; Zuckerberg et al. 2009), although we do not yet know the generality of this pattern.

The traditional approach to analyzing occupancy-abundance relationships involves plotting mean local abundance against occupancy (for many species at a single point in time, or for one species across time; Gaston et al. 2000). Because mean values are used to summarize local abundances, this approach lacks the resolution to detect changes in the distribution of abundance across sampling sites within a species' range. For example, mean abundance for a given number of sites can be high due to a single population harboring most individuals, or because abundance is distributed at a reduced level—but more equally—across sites. So, although changes in mean abundance are likely driven by changes in the largest populations (Gaston et al. 2000), lack of fine-scale resolution have made it challenging to detect, visually display, and statistically summarize intra-specific dynamics.

A new tool, the Rank Occupancy-Abundance Profile (ROAP; Collins et al. *in press*) provides one alternative for tracking intra-specific abundance and occupancy patterns. ROAPs, which plot densities from all sampling sites in ranked order, simultaneously display the maximum population size, the proportion of occupied plots, and the distribution of abundance across sampling points (Fig 1a; Collins et al. *in press*). Thus, no information is lost in calculating a summary statistic, and variation in abundance across sites is clearly made visible in the shape of the distribution. To avoid confusion among different aspects of abundance, hereafter we use the term regional abundance to refer to the sum total of individuals across all sites. We use the term local density or local population size to describe the number of individuals at a single site. Declines in occupancy are equivalent to local extinctions, and we use these phrases interchangeably.

Using ROAPs, we can hypothesize different patterns of declines in regional abundance as a species approaches rarity. For instance, species may decline first in occupancy due to the extirpation of local populations (e.g. in the case of catastrophic habitat destruction) (model I in Fig. 2). Alternatively, declines in local density across occupied sites may provide the first evidence of regional abundance declines (Hughes et al. 1997; Gaston et al. 1998) (model III in Fig. 2). Declines in regional abundance could also be caused by concurrent drops in local density and occupancy (model II in Fig. 2). Finally, increasing local density and decreasing occupancy (or *vice versa*) will cause ROAPs to cross (models IV and V in Fig. 2), but unless losses in one aspect of abundance overwhelms the gains in the other, declines in regional abundance are not likely to be significant.

Breeding birds are among the most visible and well-studied groups of organisms, making them ideal for addressing long-term, large-scale questions. Furthermore, the fact that they occupy diverse habitats and migrate long distances means they serve as good indicators of global changes (BirdLife International 2004). Collectively, birds have lost an estimated 20-25% of total individuals since 1500 (Gaston et al. 2003). It is likely their declines will continue in the face of human-induced global changes, with measurable negative effects on ecosystem processes such as decomposition, pollination, and seed dispersal (Şekercioğlu et al. 2004).

In this study, we use ROAPs to quantify the degree to which 209 North American (NA) bird species experience losses in local density versus occupancy, as well as how these losses influence the magnitude of regional abundance declines. Our analysis is unique because we track declines within and across species using a technique (ROAPs) which allows us to identify intermediate phases of decline. Specifically, we address the following questions: 1) What proportion of NA bird species are significantly declining when occupancy and local density are simultaneously taken into account? 2) Which contributes more to regional abundance losses: declines in occupancy (local extinctions) or declines in local density? In particular, which conceptual model (Fig. 2) best reflects patterns of decline? 3) Does initial regional abundance influence patterns of decline?

We also examine the patterns of declines for individual species at higher temporal resolution to address the question: 4) do patterns we see across many declining species inform our understanding of the trajectory a single species may take as it declines toward rarity? We addressed these questions using data from the North American Breeding Bird Survey (NABBS)

METHODS

NABBS Data

The North American Breeding Bird Survey (NABBS) currently comprises over 4100 survey routes established along secondary roads throughout the US and Canada. The number of routes has increased steadily since the monitoring program began in 1966. Surveys are conducted by volunteer naturalists, each of which drives a 39.4 km route consisting of 50 stops distributed at 0.8 km intervals. At each stop, the observer records every bird seen or heard with in a 400-m radius during a 3-minute period (Sauer et al. 2008). Data are processed and archived by the United States Geological Survey (USGS).

To calculate local density, we averaged the number of birds recorded across sampling points within each route; thus, an occupied "site" in this study is at the spatial resolution of routes (39.4 km). We also averaged local densities for each route across a five year period to minimize noise caused by different observers or sporadic population fluctuations.

To compare declines across species, we used the five-year averages that maximized the temporal extent of the study without compromising data quality or quantity (e.g. prior to 1970, too few routes were sampled to provide data comparable to later years). We therefore used 1970-1974 and 2003-2007 as our endpoints. Species were included in the sample if they had an initial regional abundance of > 40 birds, and with ranges comprising > 11 routes. Placing these constraints on the sample meant that our analyses excluded many of the rarest birds in North America (Appendix A). Our resulting sample included 209 bird species in 21 families (Appendix B).

We increased our temporal resolution to examine patterns of decline within a single species. Because our original time span did not divide evenly into 5-year increments, we analyzed data for the following years: 1976-1980, 1981-1985, 1986-1990, 1991-1995, 1996-2000, 2001-2005. Changing the endpoints for the inter-specific analyses to match these subsets would have reduced the temporal extent of the study, also reducing the magnitude of declines we observe and our ability to detect them. Thus, for all interspecific comparisons we use the extended time frame (1970:1974 to 2003:2007) and for all intra-specific patterns, we focus on ROAPs derived from data during the 5-year increments in intervening years (listed above).

ROAPs Analyses

Constructing a ROAP requires that we know the number of sites sampled and the density at each site. To determine the proportion of occupied sites, we delineated the border of each species' range using a polygon (technically, a convex hull) around all sites at which the species was detected during any of the focal years (1970-1974; 2003-2007). The number of routes within this polygon was considered the maximum number of occupiable sites ('proportional range occupancy'; Hurlbert and White 2005).

To generate a ROAP for a single species, we first ranked routes within the species' range by the density of that species at each route (i.e. local density), from highest density (rank 1) to lowest. We then plotted the local density on the ordinate against its rank on the abscissa. To standardize the abscissas for comparison among species that vary in range size (and therefore contain different numbers of routes within the range), we divided the rank by the total number of routes sampled in the landscape. This yielded a standardized abscissa we called the "relative rank."

We generated ROAPs for all bird species that met our criteria (209 spp). Regional abundance for a species in its range is the integrated area underneath the ROAP; we calculated this for each species in each time period. (It is important to note here that this value of regional abundance is the total for sampled routes, and therefore by definition an underestimate of the bird species' actual total abundance in its range). To test for significant differences between ROAPs for a single species in different time periods, we calculated D*: the integral of the difference between the two ROAPs (A+B+C in Fig. 1b; Collins et al. *in press*). D* is therefore equal to the change in regional abundance between the two time periods. If ROAPs crossed, the area between the ROAPs in all regions between crossovers was calculated and determined positive or negative relative to the initial time period (T_1). In these cases, D* reflects the sum of these integrated areas. We tested for statistical significance of *D** for each pair of ROAPs by grouping data from the two years, then re-sampling the data 1,000 times, each time randomly assigning density values to a time period without replacement. We calculated the *D** for each run. We then compared the empirical *D** to the distribution generated by our randomizations, and considered results significant at $\alpha = 0.05$. Because the abundances are in units of individual birds, D* represents the total number of birds lost or gained between the two time intervals reflected by the ROAPs.

To quantify the changes in regional abundance due to changes in maximum local density versus occupancy, we divided the area between the two ROAPs (D*) into three sections according to where the value for the intercept of the ROAP at T_2 intersects with the ROAP at T_1 (A, B, C in Fig 1b). The area in A estimates the number of birds lost or gained due to shifts in maximum local diensity between the two years. Area B reflects more uniform declines across occupied patches of intermediate densities. (Together, A and B reflect local declines in density across all populations, but for most analyses we partition the abundance to better detect the effects of global changes on local populations of different sizes). Area C estimates the number of individuals lost or gained due to changes in the proportion of occupied patches. Comparing A/(A+B+C) with C/(A+B+C) allowed us to assess the relative degree to which declines in maximum local density and declines in occupancy (local extinctions) contributed to regional abundance loss.

We should clarify here that unlike previous studies which plot mean abundance against proportion of occupied patches (e.g. Gaston et al. 2000), we do not examine percent occupancy-loss *per se*. Although shifts in occupancy are clearly visible by comparing the x-intercepts of the ROAPs at two different time periods (Fig.1b), our technique is unique in that we quantify the proportional influence, in units of individual birds, that changes in occupancy have on regional abundance declines.

All statistics were calculated using Matlab version 7.3 (R2006b).

Life history traits

Because extinction risk can vary with life history traits as well as abundance, we collected from the literature data on body size, fecundity, habitat use, and migratory behavior. We used average female body mass (g) (Dunning, 2000) as our index of body size, and mean number of eggs in a clutch as our index of fecundity (Ehrlich et al. 1988). Migratory status was designated as either long-distance (neotropical migrants), short-distance migrants (typically within the continental U.S.), or non-migratory (Sibley 2000). Preferred breeding habitat was identified as either open, forest, woodland, successional shrubland, edge (meaning forest edge), urban, or water (adapted from Peet and Bollinger (1997)).

RESULTS

Of the 209 bird species we examined, 88 showed overall declines in regional abundance from 1970:1974 to 2003:2007; 40 species (45%) showed statistically significant declines (1-tailed D* test, $p<0.05$). By chance we expect at least four species of the 90 to be statistically significant; however, that we observed 40 species, 68% of which yielded p-values less than 0.01 (Table 1) provides convincing evidence that our results are not an artifact of performing multiple tests (Moran 2003).

The 40 species with significant declines were distributed among 21 families (Table 1). Four species (Bachman's Warbler, Northern Bobwhite, Red-headed Woodpecker, and Golden-winged Warbler) were listed as near-threatened by the IUCN, while the rest are categorized as species of "least concern" (IUCN 2008).

Dramatic drops in regional abundance occurred in both common and rare species (Table 2). Birds with the highest initial regional abundances experienced greater absolute declines: four of the ten birds showing the most dramatic declines in absolute numbers had more than 20,000 individuals in the initial sample year. By contrast, relatively rare bird species (based on initial regional abundances) showed the most dramatic proportional declines: nine of the top ten most proportionally-declining species were each represented by fewer than 600 individuals in 1970-1974 (Table 2). Proportional losses were substantial: the 20 bird species showing the greatest proportional declines lost a minimum of 48% and a maximum of 87% of their sample population between 1970:1974 and 2003:2007. Six of the birds showing the greatest absolute declines were among those that also experienced dramatic proportional declines (House Sparrow, Eastern Meadowlark, Northern Bobwhite, Field Sparrow, Yellow-shafted Flicker, and Loggerhead Shrike; Table 2).

Among birds showing statistically significant declines in regional abundance, reductions in the maximum local density influenced regional abundance more than reductions in site occupancy (Fig. 3). Only six bird species lost a higher proportion of individuals due to local extinctions than due to shrinking maximum local population sizes (Fig. 2; Models I and IV). Several species experienced significant losses in regional abundance but showed little decline in maximum density or site occupancy, and thus were clustered around the origin in Fig. 3. For these species, drops in abundance were accounted for exclusively by relatively uniform declines across sites of intermediate densities (Area B in Fig. 1b).

Relative losses due to declines in the maximum density populations versus declines in occupancy varied according to initial regional abundance: the smaller the initial population size, the greater the proportion of regional abundance decline attributed to local extinctions (Figs. 3 & 4). Four of the five species showing the most substantial losses due to local extinctions (15-30%; American Black Duck, Bachman's Sparrow, Golden-winged Warbler, and Spotted Sandpiper) were among the five birds with the lowest initial regional population sizes (Fig. 4, Table 1).

Regardless of their initial regional abundance, species lost the highest proportion of individuals due to local declines in density at intermediate-density sites (Fig. 4). However, there appeared to be thresholds in population size at which reductions in maximum population sizes contribute notably to regional abundance declines (Fig. 4). Declining maximum density contributed to regional abundance declines only in species with regional population sizes of fewer than 800 individuals. Only species with regional populations of fewer than 200 showed losses due to local extinctions (Fig. 4).

DISCUSSION

Declines toward rarity are notoriously difficult to document because there are several axes along which abundances vary (Rabinowitz 1981). ROAPs offer a way to visually display local density and occupancy simultaneously, while the nonparametric D* allows us to test whether the differences we see in regional abundance (comparing two ROAPs) are statistically significant. Using this approach, we found that 40 species (19% of 209 sampled) were significantly declining. Because our analyses excluded bird species with exceptionally low regional abundances and those detected in only a few BBS routes, our estimate is definitively conservative for North American birds overall. Many of the significantly declining species are among the most abundant birds in North America. While these species are not yet rare and therefore are not targeted for protection, such substantial declines imply that anthropogenic changes have profoundly influenced bird populations in the last 30 years (Owens and Bennett 2000; Blackburn and Gaston 2002).

Interspecific patterns of decline

The relative influence of local abundance and occupancy on regional abundance depended on the initial size of the regional population. For the most common species, maximum local density and total occupancy remained relatively unaffected by regional abundance declines. Instead, moderate losses in population density across intermediate-density sites accounted for nearly 100% of declines in regional abundance (e.g. Common Grackle, Fig. 5a). That the collective effect of declines across sites was influential is no surprise; species with high regional abundances tended to have many large populations, so even marginal losses across many sites will have a large combined impact. However, that the rarest populations did not experience local extinction is less intuitive. Furthermore, the largest local populations initially resisted substantial declines. This suggests that even as regional abundance drops, large local populations might be temporarily buffered from anthropogenic threats. Although we cannot be sure of the mechanism, we might expect this result if large population size reflected superior habitat quality. If so, high birth rates (Holt et al. 1997; Freckleton et al. 2006) or individuals migrating from less favorable sites (Fretwell and Lucas 1969) may maintain high densities in the best habitats, even as extrinsic threats (e.g. pollution or loss of migratory habitat) drive down regional abundance.

Most other bird species reflected a pattern of decline consistent with model III (Figs. 2 & 3), i.e. declines in the highest-density populations had greater influence on regional abundance than declines in occupancy (e.g. Northern Mockingbird, Fig. 5a). Rodriguez (2002) found a similar pattern and suggested that processes operating in high-density bird populations were driving range-wide declines. Even if this is the case, we find it somewhat surprising that local extinctions play only small role in regional declines, given that far more sites host small populations than large ones. By contrast, local extinctions contributed substantially to declines in regionally rare species (e.g. Chuck-will's Widow and the American Black Duck; Fig. 5a).

Our results suggest that there are thresholds in regional densities at which relative contributions of occupancy and local abundance characterize the patterns of decline. The regional abundances in this study reflect the total number of birds sampled, so they are not analogous to minimum viable population sizes (MVP), or other quantitative thresholds for persistence calculated using parameter estimates for population growth and environmental factors (Gilpin and Soule 1986). Still, the qualitative result is compelling: below a threshold regional population size, small local populations cease to persist, implying a strong interaction between regional and local population processes. Although models and computer simulations by Freckleton et al. (2005) suggest such thresholds may exist, to our knowledge, we are the first to show this empirically.

As expected, some species appear to fit this pattern better than others. For example, two relatively rare species, the Evening Grosbeak and Bachman's Sparrow (outliers in Fig. 3), both lost a substantially greater proportion of their numbers due to declines in maximum population size as opposed to local extinctions. Both bird species occupied very few sites during the initial time period: the range of Bachman's Sparrow included only 42 routes, the fewest number of any species for which we detected statistical declines. Although the Evening Grosbeak's range included 128 routes, only 15% of them (~19 routes) were occupied initially. Consequently, for both species, there was little potential for occupancy-losses; individuals lost from the highest-density sites thus accounted for the majority of their declines. On the other hand, the Vesper Sparrow (a relatively common species) lost proportionally more individuals to local extinctions than to declines in maximum local density, a pattern characteristic of very rare species. Habitat loss offers one explanation for why a common species might experience proportionally high losses in site occupancy. Indeed, the Vesper Sparrow is a grassland-specialist in a region where grasslands have suffered dramatic declines due to agricultural practices (With et al. 2008)

Although initial regional abundance appears to predict relative losses in local density and occupancy, it is possible that other traits linked with density may predispose species to a particular pattern of decline. For example, we expect long-lived species and habitat-specialists to show a time lag between declines in local density and loss of occupancy (Blackburn and Gaston 1998). Similarly, large body size and low fecundity are traits typically associated with higher extinction risk

(Gaston and Blackburn 1995; Bennett and Owens 1997). Overall, the group of birds most influenced by local extinctions (also the most rare) spanned a wide range of body weights (and by association, generation times; Calder 1984), fecundities, and migration patterns, making it unlikely that any single intrinsic trait explains pronounced losses in occupancy. However, these rare bird species are all associated with discrete and isolated habitat types, such as bodies of water (Spotted Sandpiper, American Bittern, American Black Duck, Belted Kingfisher) and shrubland/forest edges (Golden-winged Warbler). Still, other habitat specialists (both water and grassland bird species) show very different patterns of decline, so it is unlikely that habitat-specialization alone explains the declines in occupancy. Indeed, it is impossible to tease apart cause and effect, as rarity may reflect intrinsic traits (habitat-specialization) or interact with extrinsic traits (habitat loss) to make species more prone to local extinctions (Blackburn and Gaston 2002; Davies et al. 2004). Finally, we should also note low detection probability may contribute to the observed local extinctions of rare bird species. However, because the sampling protocol has stayed constant across time, the relative changes in abundance should not be influenced by sampling alone.

Intraspecific phases of decline

The distinct patterns we see across species of varied abundances suggests that if we were to observe the entire temporal trajectory of decline for a single species, eventually we might see each of these patterns expressed as a phase in the decline toward rarity. Interpreting our data in this way is analogous to using a chronosequence or space-for-time substitutions for studying plant communities undergoing succession. In Fig.5, we illustrate our approach by pairing hypothesized phases of intraspecific decline over time with “snapshots in time” from species that differ in regional abundance. Below, we describe our hypothesis, provide examples from our dataset, and discuss potential caveats.

We propose that for many species, local density declines are the first indicator of regional abundance decline (Phase I, Fig. 5b). During this phase, densities of the largest populations in the range do not change significantly, nor does occupancy; rather, collective losses across many intermediate-density sites result in a substantial drop in regional abundance. We had not considered this pattern in our models *a priori* because, taken to its logical conclusion, small declines across many sites do not necessarily result in rarity (i.e. a large proportion of sites are still occupied and some of them contain large populations); consequently, this pattern is not likely to lead directly to a species’ extinction. In very common species, however, this phase may set the stage for further declines.

A noteworthy decrease in the size of a species’ largest populations signals the next phase of decline, although smaller populations also continue losing individuals (Phase II, Fig. 5b). Importantly, during this phase, there is an increase in the proportion of low-density populations in the range. Phase III is characterized by the first significant loss of regional abundance due to local extinctions; however, local population declines still contribute proportionately more to total declines than do shifts in occupancy. Finally, when a species is both locally and regionally rare (“double jeopardy;” Lawton 1993), all remaining populations are small and the primary driver of regional declines is loss of occupancy via local extinctions (Phase IV, Fig. 5). As modeled here, these phases depict simplified snapshots representing different stages in a dynamic continuum toward rarity; taken together, they provide a heuristic model (and a testable hypothesis) using ROAPs to explore declines in abundance (Fig. 5c).

Importantly, this model suggests that links between local abundance and regional occupancy jointly influence the way a species approaches rarity. For example, if the largest populations are sources for other populations in the range, declines in large populations may lead to a sort of spatial feedback effect on regional population size (Hanski 1982). Reducing the size of populations reduces the number of potential colonists, ultimately having a negative effect on occupancy (Gonzalez et al. 1998; Freckleton 2005). It is not necessary to invoke metapopulation dynamics; we might see a similar pattern if declines in habitat quality or quantity (e.g. pollution in breeding habitat or deforestation in migration habitats) reduce local abundances via vital rates (Holt et al. 1997). Resulting smaller populations would be prone to stochastic extinction (Gilpin and Soule 1986), eventually reducing occupancy across the range. As others have suggested (e.g. Holt et al. 1997, Freckleton et al. 2005), these processes likely act in concert, or concurrently in different parts of the species range. Thus, we do not suggest that ROAPs discriminate between possible mechanisms; rather, they illustrate the general of interplay between local abundance and occupancy during decline.

Testing this model explicitly would require having time series data tracking a bird species from one extreme level of abundance to another. Despite the dramatic declines we observed in our data, no single species shows all four phases that we propose in Figs. 5b and 5c. However, examining ROAPs at higher temporal resolution, we were visually able to detect a subset of the phase transitions within a single species (Figs. 6 & 7). For instance, the Northern Bobwhite's decline reflects Phases I and II: loss in regional abundance between the first two time steps is due almost entirely to a uniform decline across occupied plots, with relatively little change in maximum population sizes or number of populations. The next several time steps are characterized by systematic drops in maximum population sizes in addition to the continued reduction of local abundance across occupied plots. As local abundance declines continued over time, an increasingly higher proportion of sites contained fewer than five individuals (Fig. 6a inset). The House Sparrow provides another example, differing from the Northern Bobwhite only in the amount of time before high density populations drop dramatically.

The Loggerhead Shrike, a less common bird, illustrates the increasing influence local population extirpations have on regional abundance in Phases II and III (Fig 7a). The regional population size dwindled over time due to drops in both maximum density and occupancy. By the end of the last time step, nearly 100% of the local populations supported fewer than five individuals (Fig. 7a inset), and occupancy had dropped nearly 50%. Were we to follow the Loggerhead Shrike for three more decades, according to our hypothesis we might see the pattern expressed by the

Golden-winged Warbler (Fig. 7b), in which each time step is characterized solely by local extinctions. As a consequence, the proportion of populations with fewer than five individuals actually decreases, presumably because the sites with extremely small densities experienced local extinction. While we illustrate our point using four species, these patterns were found across our dataset, and demonstrate that species ranges tend to contract numerically before they contract spatially, pre-disposing sites to serial local extinctions, and potentially, global extinction.

Time lags

Time lags are inherent at several different phases of decline depicted in this series of conceptual models, as well as evident in our data. First, there is a time lag between initial declines in local density (Phase I) and a decline in the size of the largest populations (Phase II) (e.g. Northern Bobwhite and House Sparrow, Fig. 6). If the highest densities do not decline initially as our data show, abundance-occupancy plots which rely on mean values of abundance may not detect this lag. Recognizing this initial lag exists has significant implications for conservation: the largest populations are temporarily buffered from decline, thus early detection of declines at less-dense sites may precede efforts to save the largest populations. Intervention may prove particularly important if the largest populations are dispersal sources for other populations. In these cases, preventing their demise would be integral to maintaining regional metapopulation "rescue effects." (Cornutt 1996; Gonzalez et al. 1998; Freckleton et al. 2005).

The second lag occurs between the loss of local abundance and occupied sites (between Phase II and Phase II). Conrad et al. (2001) were the first to empirically demonstrate similar delayed losses in occupancy after drops in local abundance in a species of tiger moth. Like Conrad et al. (2001), we found that populations persisted at lower abundance prior to their extirpation (e.g. Fig. 6). Webb et al. (2007) observed that rare species of European birds tended to have right skewed distributions (i.e. most populations were small), although continued monitoring would be necessary to see if the tail of the distribution retracts due to extinctions as our model predicts. The lag also has conservation significance: if we only assess the status of species using presence-absence protocols—an increasing trend among management agencies (Marsh and Trenham 2008) —we will not detect species declines until Phase III, when regional abundance has already suffered severe losses, and local extinctions ensue.

As regional populations shrink to smaller and smaller sizes, time lags may exist between phases but will likely become less prolonged and therefore less detectable; rates of decline tend to increase when species become scarce (Fagan and Homes 2006). Thus, during Phases III and IV, conservation efforts become a priority and a challenge because regionally and locally small populations are least likely to recover from fluctuations, face the highest number of extrinsic threats (Blackburn and Gaston 2002), and are more prone to the "extinction vortex" (Gilpin and Soule 1986; Fagan and Homes 2006).

Using ROAPs to study occupancy and abundance

Relationships between local density and distribution, both inter- and intra-specific, are traditionally depicted using plots of mean abundance versus occupancy (reviewed in Gaston et al. 2000). ROAPs extend beyond this approach in several ways. First, by comparing two ROAPs from different time periods, we can visually depict the dynamics of shifting distributions of abundance across sites. Second, we can test for statistical significance in regional abundance declines that integrate both local abundance and occupancy into a single metric. Third, we can estimate the number of individuals (and therefore the proportion of the starting population) lost between two time periods. More specifically, we can partition changes in regional abundance into loss due to local declines in maximum- and intermediate-density popoulations, versus those attributed to local extinctions. Using means potentially obscures the contribution of large populations to slowing overall declines; consequently, ROAPs allowed us to identify phases and time lags in this study that had not previously been documented.

ROAPs are not spatially explicit, i.e. they do not allow us to track individual sites over time. We view this as a strength for assessing abundance at landscape and regional scales. Local abundances may shift asynchronously across the range because of local dynamics or movement of individuals among sites. ROAPs allows for local populations to change size (and therefore rank) without necessarily influencing the overall shape of the distribution, particularly in cases in which increases in population size at one location are compensated for by decreases at another. Whereas maps of population increases and decreases reflect specific regions of population change from year to year, it is difficult to assess from them the net effect that local shifts in abundance have on regional population size. ROAPs not only clearly reveal overall trends in regional abundance, but they also allow us to include the distribution of abundance across sites in our interpretations.

Conclusions

Abundancy-occupancy relationships have garnered much attention because they potentially link local and regional population ecology. In this study, we demonstrate that regional abundance predicts the degree to which species lose individuals due to declining local density versus local extinctions. Somewhat surprisingly, intermediate density sites were the first to lose abundance; large populations experienced a lagged response, as did the smallest populations. Futher, local rarity is not the only—or even the best—predictor of local extinction; rather, local populations experienced extinction when regional abundance declined. Overall, our work demonstrates that species ranges contract numerically before they do spatially, and further suggests that human threats impose on species a type of rarity ("widespread but locally rare," sensu Rabinowitz 1981) that may pre-dispose them to serial local extinctions, and ultimately, global extinction.

Reasons for such dramatic declines in North American birds are numerous, making it difficult to assign any single causal factor to these patterns. That the routes in the NABBS are located near relatively in-tact habitats, together with our observed declines in so many—and such a variety—of bird species, suggests the threats that bird species face are likely numerous, diffuse, and synergistic. Although listing species on the basis of declining abundance has stirred controversy (Mace et al. 2008), our results suggest that early detection of declining local abundance may 1) precede our ability to halt declines in a species' largest populations 2) be imperative to preventing local extinctions of sites occupied by only a few individuals. In both instances, using presence-absence data would fail to alert us until late in the trajectory toward extinction (Phase III in our model), when species are well on their way to rarity.

Table 1. All species showing significant declines between 1970:1974 and 2003:2007. Number of routes in range (see Methods) includes occupied and unoccupied routes. Initial regional abundance calculated from ROAPs; each point contained in a ROAP reflects the 5-yr average of abundance at each route. The *p*-values were derived from D* statistical tests (see Methods for details). Migratory status: 0 = non-migratory; 0.5 = short distance; 1.0 = neotropical. Habitat reflects preferred breeding habitat: open (grassland, prairies, old fields); urban; water (freshwater and/or saltwater); forest (deciduous, mixed, and/or coniferous forests); woodlands (open canopy); successional shrubland (shrubs, low-lying vegetation, ecotones).

Family	Common name	Latin name	# Routes in range	Initial abundance	p-value	Fecundity	Migratory status	Body size (g)	Habitat
Alcedinidae	Belted Kingfisher	*Megaceryle alcyon*	316	153.2	0.00025	6.5	0.5	148	water
Anatidae	American Black Duck	*Anas rubripes*	132	46.8	0.00851	9	0.5	1100	water
Anatidae	Northern Pintail	*Anas acuta*	66	57.8	0.00851	7.5	1	986	water
Apodidae	Chimney Swift	*Chaetura pelagica*	291	2652.8	0.00025	4.5	1	23.6	open
Ardeidae	American Bittern	*Botaurus lentiginosus*	205	84.4	0.01161	4.5	0.5	706	water
Ardeidae	Green Heron	*Butorides virescens*	301	339.2	0.00025	3	0.5	210	water
Caprimulgidae	Whip-poor-will	*Caprimulgus vociferus*	191	95	0.00025	2	1	50.6	forest
Caprimulgidae	Chuck-will's-widow	*Caprimulgus carolinensis*	130	218.6	0.00025	2	1	120	forest
Caprimulgidae	Common Nighthawk	*Chordeiles minor*	317	689.8	0.02274	2	1	61.5	open
Corvidae	Blue Jay	*Cyanocitta cristata*	291	4319.6	0.01818	4.5	0	86.8	forest
Cuculidae	Black-billed Cuckoo	*Coccyzus erythropthalmus*	225	160.6	0.00851	2.5	1	51.1	forest/edges
Cuculidae	Yellow-billed Cuckoo	*Coccyzus americanus*	274	1570.6	0.00025	4	1	64	successional shrubland
Emberizidae	Bachman's Sparrow	*Aimophila aestivalis*	42	51.6	0.00851	4.5	0.5	19.1	woodland
Emberizidae	White-throated Sparrow	*Zonotrichia albicollis*	63	750.4	0.01781	4.5	0.5	25.9	forest
Emberizidae	Vesper Sparrow	*Pooecetes gramineus*	278	1061	0.03120	3.5	0.5	24.9	open
Emberizidae	Field Sparrow	*Spizella pusilla*	270	2665.6	0.00025	4	0.5	12.5	open
Emberizidae	Eastern Towhee	*Pipilo erythrophthalmus*	260	2744.4	0.00025	3.5	0.5	39.3	successional shrubland/edges
Fringillidae	Evening Grosbeak	*Coccothraustes vespertinus*	128	99.6	0.00801	3.5	0.5	60	forest
Fringillidae	Pine Siskin	*Carduelis pinus*	183	266.8	0.03604	3.5	0.5	14.6	forest
Icteridae	Bobolink	*Dolichonyx oryzivorus*	168	1738.6	0.00025	5.5	1	37.1	open
Icteridae	Western Meadowlark	*Sturnella neglecta*	150	5374.6	0.00713	5	0.5	89.4	open
Icteridae	Eastern Meadowlark	*Sturnella magna*	284	9130.2	0.00025	4	0.5	76	open
Icteridae	Common Grackle	*Quiscalus quiscula*	304	22034.8	0.00025	4.5	0.5	100	open
Icteridae	Red-winged Blackbird	*Agelaius phoeniceus*	327	28186.8	0.00025	3.5	0.5	41.5	open
Laridae	Black Tern	*Chlidonias niger*	61	149.2	0.02252	3	1	65.3	water
Mimidae	Brown Thrasher	*Toxostoma rufum*	281	1376.8	0.00025	4.5	0.5	68.8	open
Mimidae	Northern Mockingbird	*Mimus polyglottos*	284	6445.6	0.01427	4	0	48.5	open

Table 1 (continued).

Family	Common name	Latin name	# Routes in range	Initial abundance	p-value	Fecundity	Migratory status	Body size (g)	Habitat
Odontophoridae	Northern Bobwhite	*Colinus virginianus*	250	7528	0.00025	14	0	178	successional shrubland
Parulidae	Golden-winged Warbler	*Vermivora chrysoptera*	107	56.4	0.01151	4.5	1	8.9	successional shrubland/edges
Parulidae	Canada Warbler	*Wilsonia canadensis*	139	89.8	0.00025	4	1	263	forest
Parulidae	Prairie Warbler	*Dendroica discolor*	194	292.6	0.02340	4	1	7.3	successional shrubland
Passeridae	House Sparrow	*Passer domesticus*	327	20571.2	0.00025	5	0	27.4	human-modified
Picidae	Red-headed Woodpecker	*Melanerpes erythrocephalus*	230	508	0.00025	4.5	0.5	71.6	forest
Picidae	Yellow-shafted Flicker	*Colaptes auratus*	286	1282.4	0.00025	6.5	0.5	129	woodland
Scolopacidae	Spotted Sandpiper	*Actitis macularius*	242	72.2	0.00651	4	1	40	water
Sturnidae	European Starling	*Sturnus vulgaris*	327	20183.6	0.04180	5	0	79.9	open
Thraupidae	Loggerhead Shrike	*Lanius ludovicianus*	239	565.4	0.00025	5.5	0.5	47.4	open
Turdidae	Veery	*Catharus fuscescens*	210	824.2	0.01069	4	1	31.2	forest
Turdidae	Wood Thrush	*Hylocichla mustelina*	249	2633.2	0.00025	3.5	1	47	forest
Tyrannidae	Least Flycatcher	*Empidonax minimus*	176	498	0.01590	4	1	10.3	forest

Table 2. The 20 bird species with the highest (a) absolute and (b) proportional declines between 1970:1974 and 2003:2007. Highlighted species are those shared among both lists.

a.

Top 20 Absolute Declines

Species	Initial abundance	# Birds lost (D*)	Total % change
House Sparrow	20571.2	-10524	-0.512
Red-winged Blackbird	28186.8	-8652	-0.307
Common Grackle	22034.8	-8219.8	-0.373
Eastern Meadowlark	9130.2	-5811.6	-0.637
Northern Bobwhite	7528	-5646.4	-0.750
European Starling	20183.6	-2774.2	-0.137
Western Meadowlark	5374.6	-2448	-0.455
Northern Mockingbird	6445.6	-1453.2	-0.225
Field Sparrow	2665.6	-1284.6	-0.482
Wood Thrush	2633.2	-1079.2	-0.410
Eastern Towhee	2744.4	-985.2	-0.359
Chimney Swift	2652.8	-728.4	-0.275
Yellow-shafted Flicker	1282.4	-711.2	-0.555
Bobolink	1738.6	-672	-0.387
Blue Jay	4319.6	-636.8	-0.147
Yellow-billed Cuckoo	1570.6	-594.4	-0.378
Brown Thrasher	1376.8	-448.4	-0.326
Loggerhead Shrike	565.4	-432.4	-0.765
Vesper Sparrow	1061	-395.2	-0.372
White-throated Sparrow	750.4	-340.2	-0.453

Top 20 Proportional Declines

b.

Species	Initial abundance	# Birds lost (D*)	Total % change
Evening Grosbeak	99.6	-86.6	-0.869
Bachman's Sparrow	51.6	-40.8	-0.791
Canada Warbler	89.8	-70.6	-0.786
Whip-poor-will	95	-74.2	-0.781
Loggerhead Shrike	565.4	-432.4	-0.765
Northern Bobwhite	7528	-5646.4	-0.750
Northern Pintail	57.8	-42	-0.727
American Black Duck	46.8	-33.6	-0.718
Pine Siskin	266.8	-181.6	-0.681
Eastern Meadowlark	9130.2	-5811.6	-0.637
Golden-winged Warbler	56.4	-33.2	-0.589
Black Tern	149.2	-86.4	-0.579
Yellow-shafted Flicker	1282.4	-711.2	-0.555
American Bittern	84.4	-45.8	-0.543
Spotted Sandpiper	72.2	-37	-0.512
House Sparrow	20571.2	-10524	-0.512
Chuck-will's-widow	218.6	-110.4	-0.505
Field Sparrow	2665.6	-1284.6	-0.482
Common Nighthawk	689.8	-328.2	-0.476
Red-headed Woodpecker	508	-234.8	-0.462

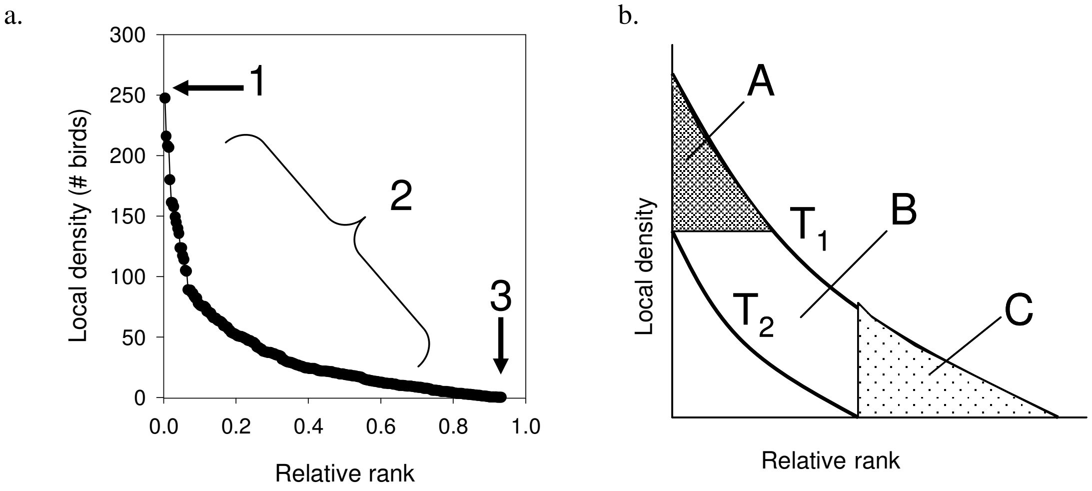


Figure 1. (a) Rank Occupancy-Abundance Profiles (ROAPs) for a single species at a single point in time. ROAPs depict the local abundance of birds (y-axis) ranked in order of their density (x-axis). Relative rank is calculated by dividing the rank value of the route by the number of routes in the range. ROAPs reveal: 1) maximum population size 2) distribution of local abundance across sites and 3) proportion of sites occupied. Each point represents the density of the species at a single sampling site. The regional abundance is the integral taken beneath the ROAP. (b) Two ROAPs from samples taken at two different time periods (T_1 and T_2). A+B+C = the total change in "regional" abundance between the two time periods. We also refer to this area as D*. A = the proportion of regional abundance decline due to drops in maximum density; B is equal to the proportion of regional abundance loss attributed to declines in local density at sites of intermediate densities; C is equal to the proportion of regional abundance loss due to decline in occupancy (local extinction).

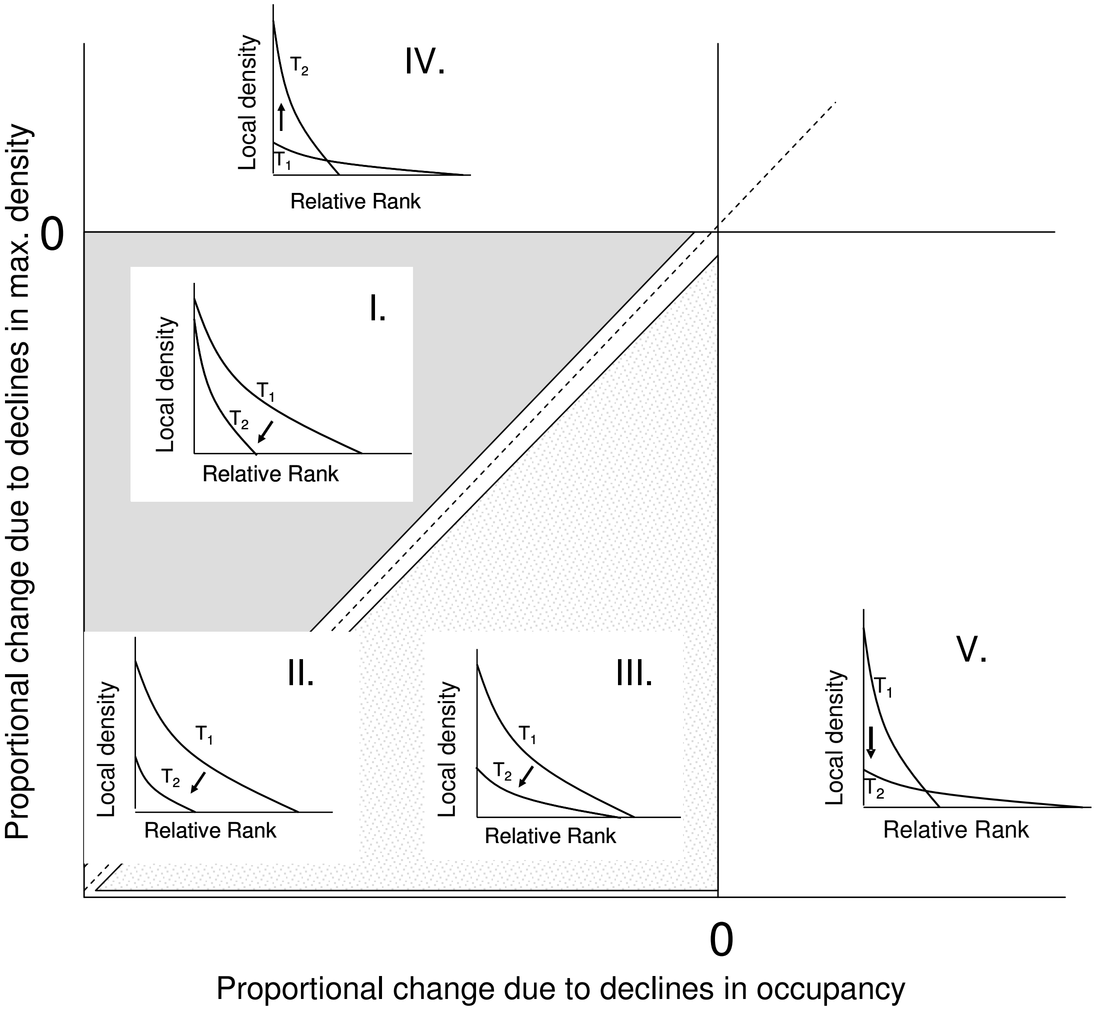


Figure 2. Axes on this plot reflect the proportional change in regional abundance due to declines in occupancy (x-axis here, calculated from area C of Fig. 1b) versus declines in maximum density (y-axis here; calculated using area A from Fig. 1b). The dotted line reflects a 1:1 change due to occupancy and maximum local density. The conceptual models depict various patterns of decline, and are situated in the portion of the plot in which we expect a species to fall depending on the relative degree to which declines in occupancy and maximum density determine regional abundance loss. (I) initial declines in occupancy, (II) concurrent declines in maximum population size and site occupancy, (III) initial declines in maximum local population sizes, (IV) declines in occupancy but an increase in maximum local abundance, and (V) declines in maximum population sizes but an increase in occupancy.

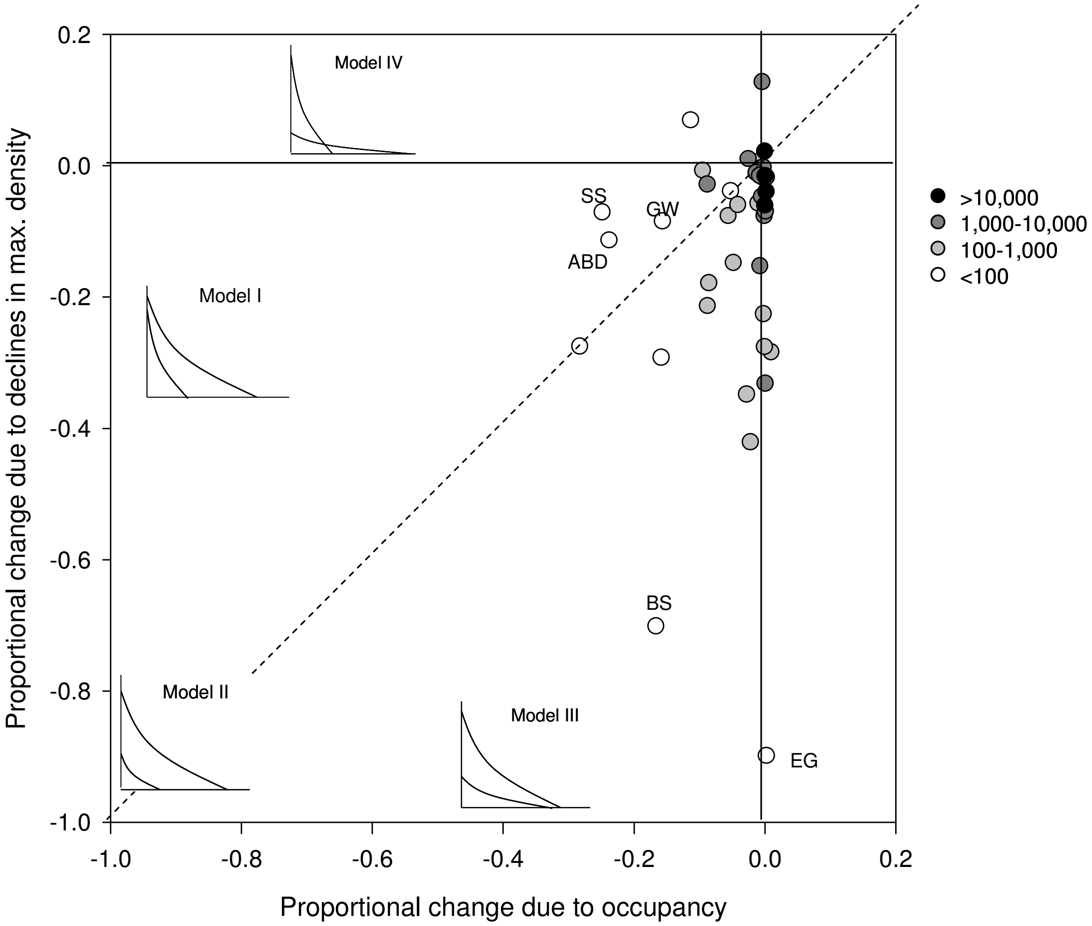


Figure 3. This plot contains only the species that showed significant declines ($p<0.05$ for D*; n=40) Axes reflect the proportional change in regional abundance due to declines in occupancy (x-axis here, calculated from area C of Fig. 1b) versus declines in maximum density (y-axis here; calculated using area A from Fig. 1b). The dotted line reflects a 1:1 change due to occupancy and maximum density. The conceptual models are situated in the portion of the plot in which we expect a species to fall depending on the relative degree to which declines in occupancy and maximum density determine regional abundance loss. Each circle represents a single species; circles are coded dark to light according to initial regional abundance of the bird species (high to low). Most species appear to best fit Model III. The rarest species tended to experience the largest losses due to local extinctions, e.g. SS=Spotted Sandpiper, GW= Golden-winged Warbler, ABD=American Black Duck, BS = Bachman's Sparrow, EG = Evening Grosbeak.

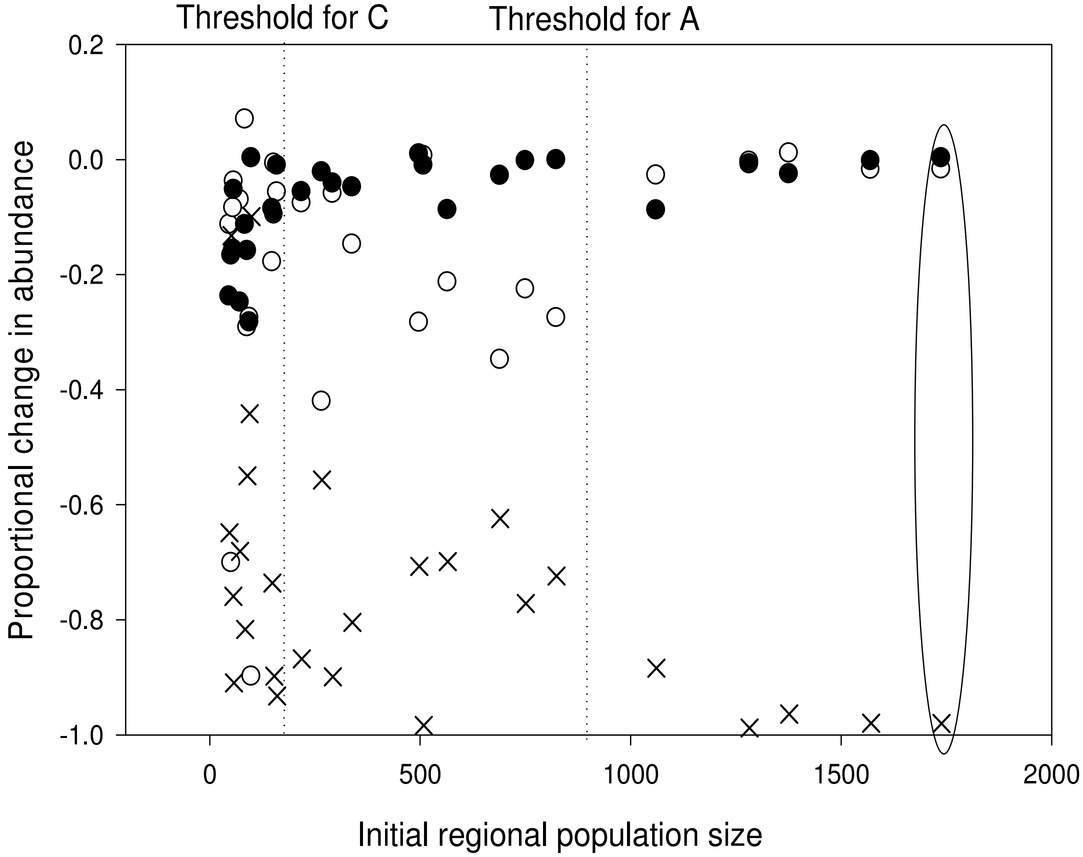


Figure 4. Initial regional population size predicts the relative contribution of declines in maximum local density and occupancy to declines in regional abundance. To demonstrate the thresholds, only 27 of 40 birds showing significant declines are shown below, excluding bird species with regional population sizes >2000 individuals.The symbols represent the proportional contribution of declines due to changes in occupancy (calculated from area C in Fig. 1b); open symbols represent the proportional contribution of declines due to drops in maximum local density (calculated from area A in Fig. 1b); X symbols represent the proportional contribution of declines across sites of intermediate abundance (calculated from area B in Fig. 1b). Because these are proportions, the values (on the y-axis) for the three symbols (e.g. those within the circle) are for a single species and total to one. When regional abundance fell below 800 individuals, we observe drops in maximum density for several bird species (Threshold for A=dotted line). The threshold for losses due to occupancy is lower: species with fewer than 200 individuals in the regional populations experience local extinctions (Threshold for C=dotted line).

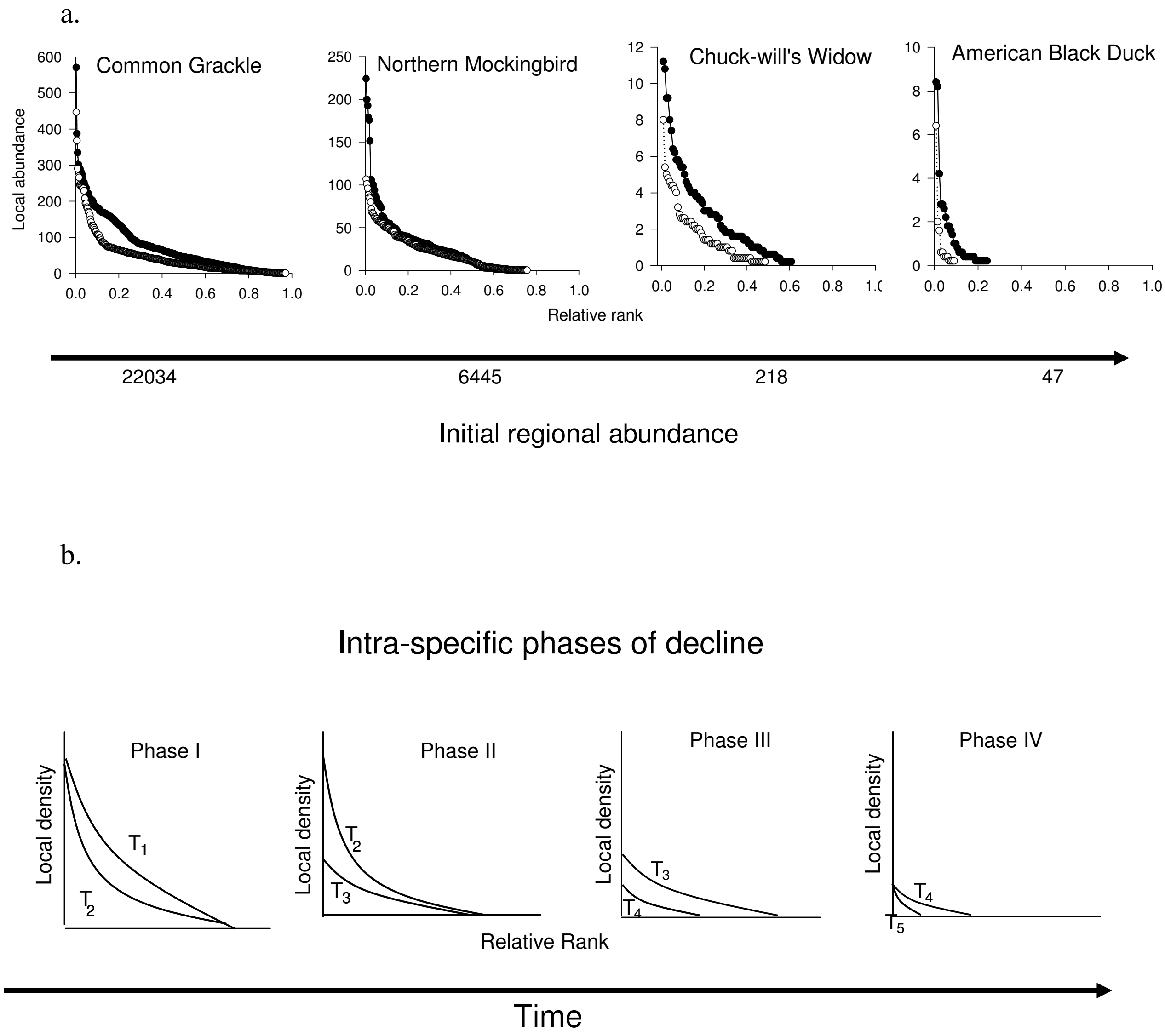


Figure 5. (a) ROAPs that depict the pattern of declines between 1970:1974 (●) and 2003:2007 (○) for four species of different initial regional abundances. Values listed below the arrow are the initial regional abundances for each species. Scale on the y-axis varies among plots to emphasize differences among plots. (b) Conceptual models using ROAPs to depict phases of decline for a single species.

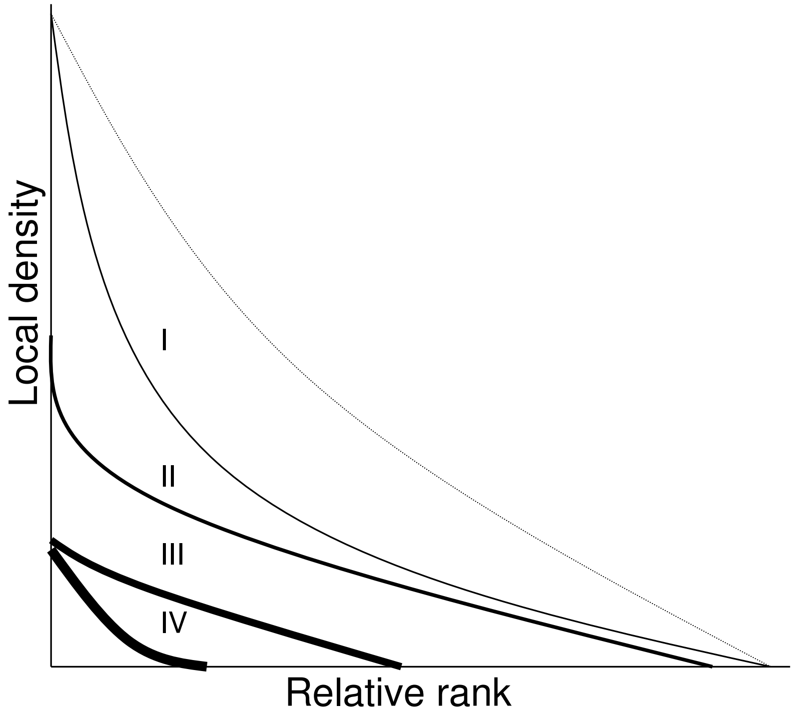


Figure 5c. A model showing what the entire series of ROAPs would look like for a single species declining toward extinction. Lines thicken over time, i.e. the thickest line represents the time series for a species closes to extinction. Phases of the model from Fig. 5b (above) are noted between the appropriate ROAPs.

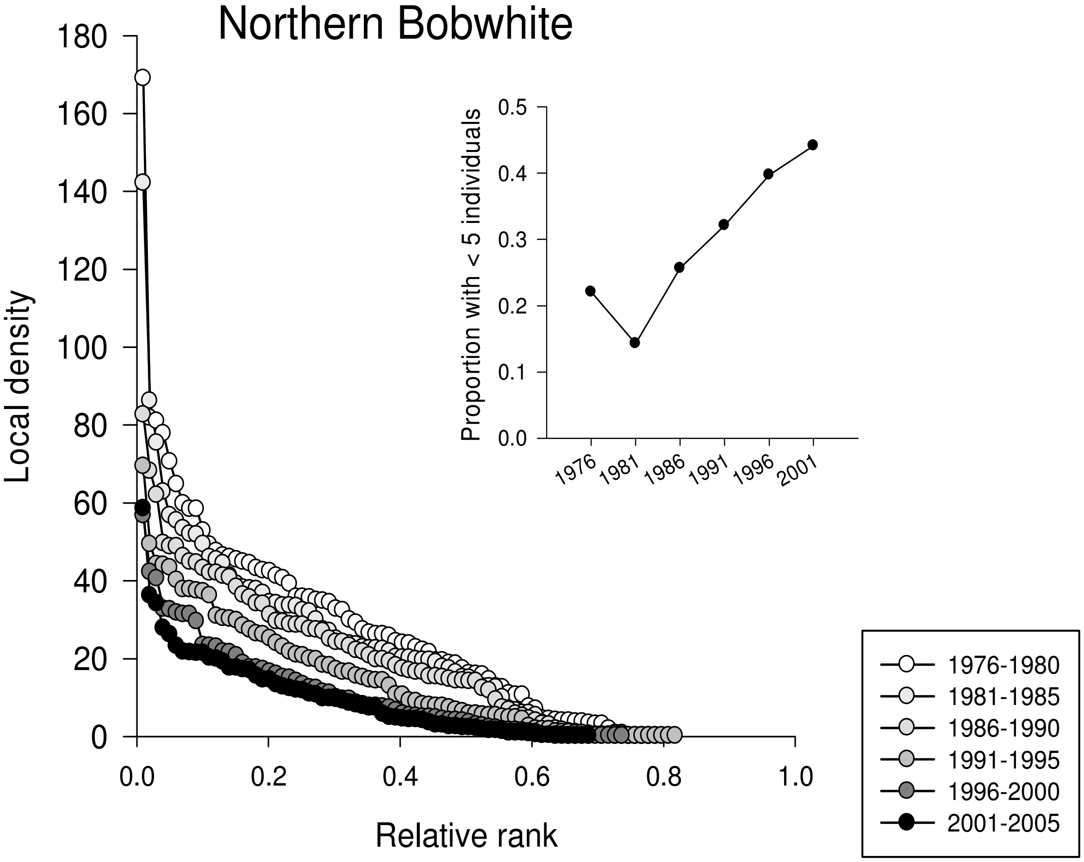


Figure 6a. Time series of ROAPs for a common species declining between 1976-2005. The earliest time period is depicted with hollow symbols, each progressive time step is filled with a darker shade. Insets show the proportion of populations comprised of fewer than 5 individual birds at each time step. The Northern Bobwhite initially shows substantial declines primarily in populations with intermediate densities (Phase I), experiences declines in populations with the highest densities (Phase II). In the last time step, local extinctions cause a decline in occupancy (Phase III).

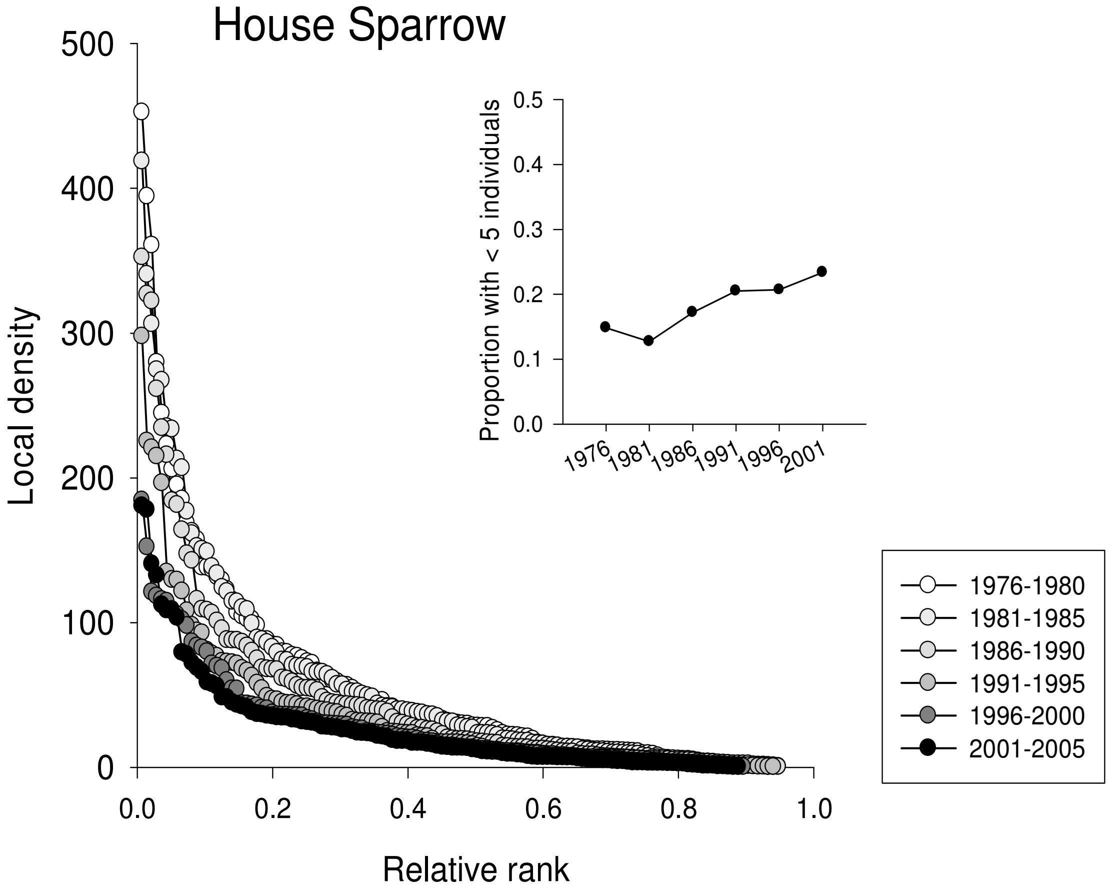


Figure 6b. Time series of ROAPs for a common species declining between 1976-2005. The earliest time period is depicted with hollow symbols, each progressive time step is filled with a darker shade. Insets show the proportion of populations comprised of fewer than 5 individual birds at each time step. The House Sparrow initially shows substantial losses in populations of intermediate densities (Phase I), then experiences declines in the populations with the highest density (Phase II).

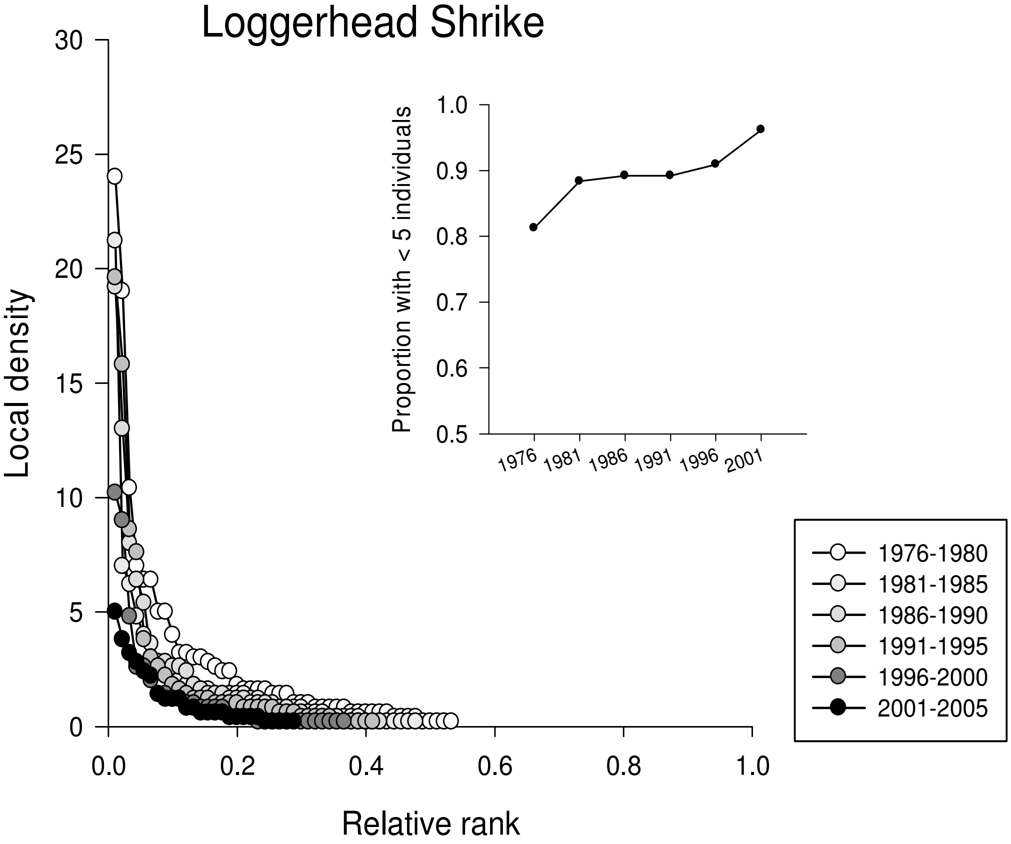


Figure 7a. Time series of ROAPs between 1976-2005 for a species with intermediate initial regional abundance. The earliest time period is depicted with hollow symbols, each progressive time step is filled with a darker shade. Insets show the proportion of populations comprised of fewer than 5 individual birds at each time step. The Loggerhead Shrike appears to match Phases II and III, initially losing maximum density, then losing occupancy as well.

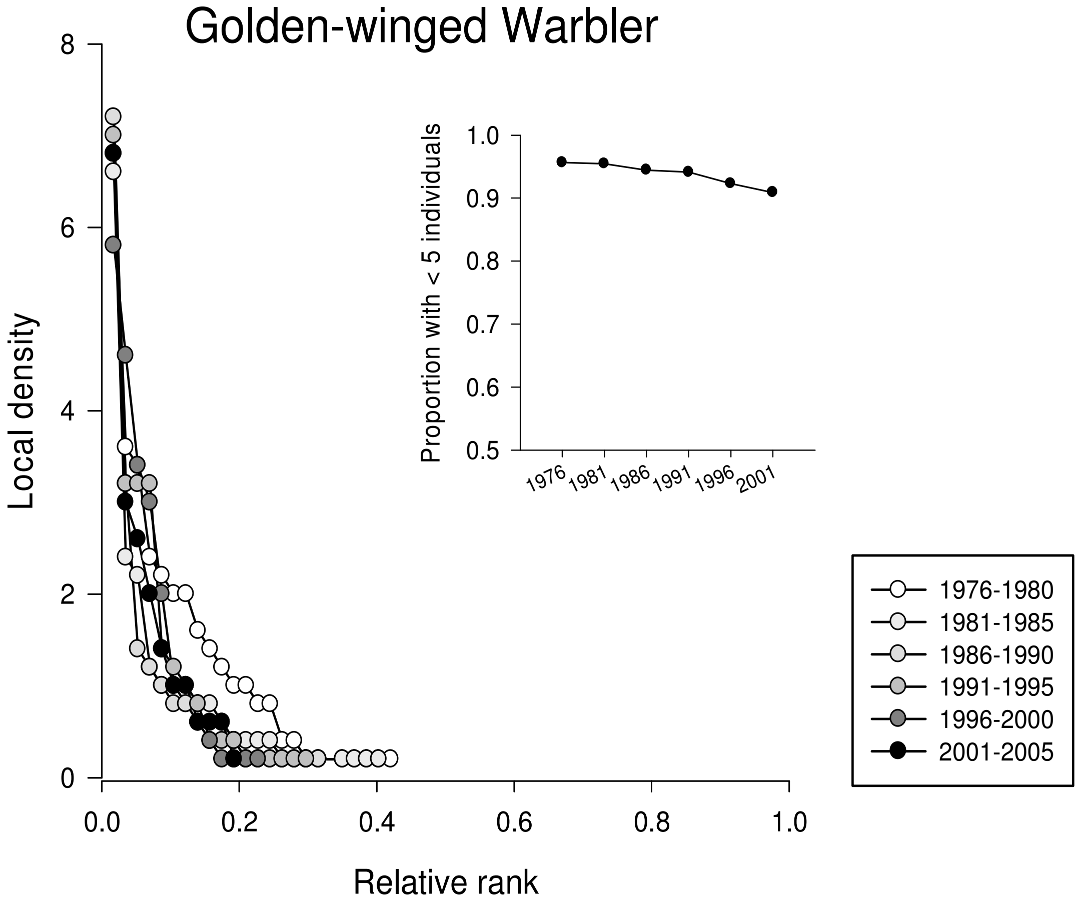


Figure 7b. Time series of ROAPs between 1976-2005 for a species with low initial regional abundance. The earliest time period is depicted with hollow symbols, each progressive time step is filled with a darker shade. Insets show the proportion of populations comprised of fewer than 5 individual birds at each time step. The Golden-winged Warbler appears to match Phase IV, experiencing local extinctions at every time step. Consequently, the proportion of populations with < 5 individuals decreases, presumably because small populations are extirpated.

Appendix A. Species discarded from analyses. Species were discarded if they were detected at fewer than 12 routes, or if their regional abundance totaled less than 40 individuals.

Species	Reason for discard	Species	Reason for discard
Tricolored Blackbird	< 12 routes	Canyon Wren	< 40 birds
Rusty Blackbird	< 12 routes	Calliope Hummingbird	< 40 birds
Chihuahuan Raven	< 12 routes	Connecticut Warbler	< 40 birds
Canyon Towhee	< 12 routes	Lewis's Woodpecker	< 40 birds
Red-cockaded Woodpecker	< 12 routes	Blue Grouse	< 40 birds
Sprague's Pipit	< 12 routes	Gray Jay	< 40 birds
Pyrrhuloxia	< 12 routes	Nelson's Sharp-tailed Sparrow	< 40 birds
Calliope Hummingbird	< 12 routes	Eastern Screech-Owl	< 40 birds
Chestnut-collared Longspur	< 12 routes	Rusty Blackbird	< 40 birds
Pinyon Jay	< 12 routes	Boreal Chickadee	< 40 birds
Bay-breasted Warbler	< 12 routes	Clark's Nutcracker	< 40 birds
Vermilion Flycatcher	< 12 routes	American Woodcock	< 40 birds
Aechmophorus spp	< 12 routes	Vermilion Flycatcher	< 40 birds
Scaled Quail	< 12 routes	Bay-breasted Warbler	< 40 birds
Lewis's Woodpecker	< 12 routes	Fox Sparrow	< 40 birds
Cactus Wren	< 12 routes	Burrowing Owl	< 40 birds
Mottled Duck	< 12 routes	Henslow's Sparrow	< 40 birds
Lesser Nighthawk	< 12 routes	Tennessee Warbler	< 40 birds
Blue Grouse	< 12 routes	Canyon Towhee	< 40 birds
Nelson's Sharp-tailed Sparrow	< 12 routes	Rufous-crowned Sparrow	< 40 birds
Connecticut Warbler	< 12 routes	Marbled Godwit	< 40 birds
Boreal Chickadee	< 12 routes	Yellow-bellied Flycatcher	< 40 birds
Tricolored Blackbird	< 12 routes	Pygmy Nuthatch	< 40 birds
Chihuahuan Raven	< 12 routes	Black-crowned Night-Heron	< 40 birds
Chestnut-collared Longspur	< 12 routes	Wood Stork	< 40 birds
Pinyon Jay	< 12 routes	Lincoln's Sparrow	< 40 birds
Scaled Quail	< 12 routes	Cassin's Finch	< 40 birds
Mottled Duck	< 12 routes	Common Tern	< 40 birds
Cactus Wren	< 12 routes	Rock Wren	< 40 birds
Lesser Nighthawk	< 12 routes	Ruffed Grouse	< 40 birds
Philadelphia Vireo	< 40 birds	Greater Prairie-Chicken	< 40 birds
Sprague's Pipit	< 40 birds	Green-tailed Towhee	< 40 birds
Northern Goshawk	< 40 birds	Curve-billed Thrasher	< 40 birds
Red-cockaded Woodpecker	< 40 birds	Cassin's Sparrow	<12routes
Blackpoll Warbler	< 40 birds		

Appendix B. List of 209 birds included in analysis. Status indicates whether net changes in regional abundance were increasing (I) or decreasing (D); however, status here reflects only the population trend, not statistically significant changes as detected by D*. Significantly declining species are displayed in Table 1.

Status	Common Name	Latin name	Family
I	Swainson's Hawk	*Buteo swainsoni*	Accipitridae
I	Northern Harrier	*Circus cyaneus*	Accipitridae
I	Red-shouldered Hawk	*Buteo lineatus*	Accipitridae
I	Red-tailed Hawk	*Buteo jamaicensis*	Accipitridae
D	Bushtit	*Psaltriparus minimus*	Aegithalidae
D	Horned Lark	*Eremophila alpestris*	Alaudidae
D	Belted Kingfisher	*Megaceryle alcyon*	Alcedinidae
D	Blue-winged Teal	*Anas discors*	Anatidae
D	Northern Pintail	*Anas acuta*	Anatidae
D	American Black Duck	*Anas rubripes*	Anatidae
D	Redhead	*Aythya americana*	Anatidae
I	Gadwall	*Anas strepera*	Anatidae
I	Wood Duck	*Aix sponsa*	Anatidae
I	Canada Goose	*Branta canadensis*	Anatidae
I	Mallard	*Anas platyrhynchos*	Anatidae
D	Chimney Swift	*Chaetura pelagica*	Apodidae
D	Green Heron	*Butorides virescens*	Ardeidae
D	Little Blue Heron	*Egretta caerulea*	Ardeidae
D	American Bittern	*Botaurus lentiginosus*	Ardeidae
I	Great Egret	*Ardea alba*	Ardeidae
I	Great Blue Heron	*Ardea herodias*	Ardeidae
I	Cattle Egret	*Bubulcus ibis*	Ardeidae
I	Cedar Waxwing	*Bombycilla cedrorum*	Bombycillidae
D	Common Nighthawk	*Chordeiles minor*	Caprimulgidae
D	Chuck-will's-widow	*Caprimulgus carolinensis*	Caprimulgidae
D	Whip-poor-will	*Caprimulgus vociferus*	Caprimulgidae
D	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Cardinalidae
D	Painted Bunting	*Passerina ciris*	Cardinalidae
I	Lazuli Bunting	*Passerina amoena*	Cardinalidae
I	Black-headed Grosbeak	*Pheucticus melanocephalus*	Cardinalidae
I	Blue Grosbeak	*Passerina caerulea*	Cardinalidae
I	Dickcissel	*Spiza americana*	Cardinalidae
I	Indigo Bunting	*Passerina cyanea*	Cardinalidae
I	Northern Cardinal	*Cardinalis cardinalis*	Cardinalidae
I	Black Vulture	*Coragyps atratus*	Cathartidae
I	Turkey Vulture	*Cathartes aura*	Cathartidae
I	Killdeer	*Charadrius vociferus*	Charadriidae
D	Common Ground-Dove	*Columbina passerina*	Columbidae

Appendix B (cont.)

Status	Common Name	Latin name	Family
D	Rock Pigeon	*Columba livia*	Columbidae
D	Band-tailed Pigeon	*Patagioenas fasciata*	Columbidae
I	Mourning Dove	*Zenaida macroura*	Columbidae
D	Blue Jay	*Cyanocitta cristata*	Corvidae
D	Black-billed Magpie	*Pica hudsonia*	Corvidae
I	Steller's Jay	*Cyanocitta stelleri*	Corvidae
I	Western Scrub-Jay	*Aphelocoma californica*	Corvidae
I	Common Raven	*Corvus corax*	Corvidae
I	Fish Crow	*Corvus ossifragus*	Corvidae
I	American Crow	*Corvus brachyrhynchos*	Corvidae
D	Yellow-billed Cuckoo	*Coccyzus americanus*	Cuculidae
D	Black-billed Cuckoo	*Coccyzus erythropthalmus*	Cuculidae
D	Field Sparrow	*Spizella pusilla*	Emberizidae
D	Eastern Towhee	*Pipilo erythrophthalmus*	Emberizidae
D	Lark Bunting	*Calamospiza melanocorys*	Emberizidae
D	Savannah Sparrow	*Passerculus sandwichensis*	Emberizidae
D	Vesper Sparrow	*Pooecetes gramineus*	Emberizidae
D	White-throated Sparrow	*Zonotrichia albicollis*	Emberizidae
D	Lark Sparrow	*Chondestes grammacus*	Emberizidae
D	Grasshopper Sparrow	*Ammodramus savannarum*	Emberizidae
D	Black-throated Sparrow	*Amphispiza bilineata*	Emberizidae
D	White-crowned Sparrow	*Zonotrichia leucophrys*	Emberizidae
D	Bachman's Sparrow	*Aimophila aestivalis*	Emberizidae
I	Spotted Towhee	*Pipilo maculatus*	Emberizidae
I	Swamp Sparrow	*Melospiza georgiana*	Emberizidae
I	Brewer's Sparrow	*Spizella breweri*	Emberizidae
I	Clay-colored Sparrow	*Spizella pallida*	Emberizidae
I	Chipping Sparrow	*Spizella passerina*	Emberizidae
I	Song Sparrow	*Melospiza melodia*	Emberizidae
I	American Kestrel	*Falco sparverius*	Falconidae
D	Pine Siskin	*Carduelis pinus*	Fringillidae
D	Evening Grosbeak	*Coccothraustes vespertinus*	Fringillidae
D	Purple Finch	*Carpodacus purpureus*	Fringillidae
D	Red Crossbill	*Loxia curvirostra*	Fringillidae
I	Lesser Goldfinch	*Carduelis psaltria*	Fringillidae
I	House Finch	*Carpodacus mexicanus*	Fringillidae
I	American Goldfinch	*Carduelis tristis*	Fringillidae
D	Bank Swallow	*Riparia riparia*	Hirundinidae
I	Violet-green Swallow	*Tachycineta thalassina*	Hirundinidae
I	Northern Rough-winged Swallo	*Stelgidopteryx serripennis*	Hirundinidae
I	Tree Swallow	*Tachycineta bicolor*	Hirundinidae
I	Purple Martin	*Progne subis*	Hirundinidae
I	Cliff Swallow	*Petrochelidon pyrrhonota*	Hirundinidae
I	Barn Swallow	*Hirundo rustica*	Hirundinidae
D	Red-winged Blackbird	*Agelaius phoeniceus*	Icteridae
D	Common Grackle	*Quiscalus quiscula*	Icteridae

Appendix B (cont.)

Status	Common Name	Latin name	Family
D	Eastern Meadowlark	*Sturnella magna*	Icteridae
D	Western Meadowlark	*Sturnella neglecta*	Icteridae
D	Bobolink	*Dolichonyx oryzivorus*	Icteridae
D	Brown-headed Cowbird	*Molothrus ater*	Icteridae
D	Orchard Oriole	*Icterus spurius*	Icteridae
D	Brewer's Blackbird	*Euphagus cyanocephalus*	Icteridae
D	Baltimore Oriole	*Icterus galbula*	Icteridae
D	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	Icteridae
I	Bullock's Oriole	*Icterus bullockii*	Icteridae
I	Boat-tailed Grackle	*Quiscalus major*	Icteridae
I	Great-tailed Grackle	*Quiscalus mexicanus*	Icteridae
D	Herring Gull	*Larus argentatus*	Laridae
D	Franklin's Gull	*Leucophaeus pipixcan*	Laridae
D	Black Tern	*Chlidonias niger*	Laridae
D	Least Tern	*Sternula antillarum*	Laridae
D	Great Black-backed Gull	*Larus marinus*	Laridae
D	Black Skimmer	*Rynchops niger*	Laridae
I	Ring-billed Gull	*Larus delawarensis*	Laridae
I	Laughing Gull	*Leucophaeus atricilla*	Laridae
I	California Gull	*Larus californicus*	Laridae
D	Northern Mockingbird	*Mimus polyglottos*	Mimidae
D	Brown Thrasher	*Toxostoma rufum*	Mimidae
I	Sage Thrasher	*Oreoscoptes montanus*	Mimidae
I	Gray Catbird	*Dumetella carolinensis*	Mimidae
D	Northern Bobwhite	*Colinus virginianus*	Odontophoridae
I	California Quail	*Callipepla californica*	Odontophoridae
D	Mountain Chickadee	*Poecile gambeli*	Paridae
I	Black-crested Titmouse	*Baeolophus atricristatus*	Paridae
I	Black-capped Chickadee	*Poecile atricapillus*	Paridae
I	Carolina Chickadee	*Poecile carolinensis*	Paridae
I	Tufted Titmouse	*Baeolophus bicolor*	Paridae
D	Yellow-breasted Chat	*Icteria virens*	Parulidae
D	Prairie Warbler	*Dendroica discolor*	Parulidae
D	Canada Warbler	*Wilsonia canadensis*	Parulidae
D	Kentucky Warbler	*Oporornis formosus*	Parulidae
D	Golden-winged Warbler	*Vermivora chrysoptera*	Parulidae
D	Cerulean Warbler	*Dendroica cerulea*	Parulidae
D	MacGillivray's Warbler	*Oporornis tolmiei*	Parulidae
D	Prothonotary Warbler	*Protonotaria citrea*	Parulidae
D	Wilson's Warbler	*Wilsonia pusilla*	Parulidae
D	Black-and-white Warbler	*Mniotilta varia*	Parulidae
I	Black-throated Blue Warbler	*Dendroica caerulescens*	Parulidae
I	Northern Waterthrush	*Seiurus noveboracensis*	Parulidae
I	Louisiana Waterthrush	*Seiurus motacilla*	Parulidae
I	Orange-crowned Warbler	*Vermivora celata*	Parulidae
I	Black-throated Gray Warbler	*Dendroica nigrescens*	Parulidae
I	Blackburnian Warbler	*Dendroica fusca*	Parulidae

Appendix B (cont.)

Status	Common Name	Latin name	Family
I	Blue-winged Warbler	*Vermivora pinus*	Parulidae
I	Yellow-throated Warbler	*Dendroica dominica*	Parulidae
I	Black-throated Green Warbler	*Dendroica virens*	Parulidae
I	Mourning Warbler	*Oporornis philadelphia*	Parulidae
I	Magnolia Warbler	*Dendroica magnolia*	Parulidae
I	Hooded Warbler	*Wilsonia citrina*	Parulidae
I	Nashville Warbler	*Vermivora ruficapilla*	Parulidae
I	Northern Parula	*Parula americana*	Parulidae
I	Pine Warbler	*Dendroica pinus*	Parulidae
I	American Redstart	*Setophaga ruticilla*	Parulidae
I	Chestnut-sided Warbler	*Dendroica pensylvanica*	Parulidae
I	Ovenbird	*Seiurus aurocapilla*	Parulidae
I	Yellow Warbler	*Dendroica petechia*	Parulidae
I	Common Yellowthroat	*Geothlypis trichas*	Parulidae
D	House Sparrow	*Passer domesticus*	Passeridae
D	Ring-necked Pheasant	*Phasianus colchicus*	Phasianidae
D	Yellow-shafted Flicker	*Colaptes auratus*	Picidae
D	Red-headed Woodpecker	*Melanerpes erythrocephalus*	Picidae
I	Ladder-backed Woodpecker	*Picoides scalaris*	Picidae
I	Red-shafted Flicker	*Colaptes auratus*	Picidae
I	Yellow-bellied Sapsucker	*Sphyrapicus varius*	Picidae
I	Hairy Woodpecker	*Picoides villosus*	Picidae
I	Pileated Woodpecker	*Dryocopus pileatus*	Picidae
I	Downy Woodpecker	*Picoides pubescens*	Picidae
I	Red-bellied Woodpecker	*Melanerpes carolinus*	Picidae
I	Pied-billed Grebe	*Podilymbus podiceps*	Podicipedidae
D	Ruby-crowned Kinglet	*Regulus calendula*	Regulidae
D	Spotted Sandpiper	*Actitis macularius*	Scolopacidae
D	Wilson's Snipe	*Gallinago delicata*	Scolopacidae
D	Willet	*Tringa semipalmata*	Scolopacidae
I	Upland Sandpiper	*Bartramia longicauda*	Scolopacidae
D	Brown-headed Nuthatch	*Sitta pusilla*	Sittidae
I	Red-breasted Nuthatch	*Sitta canadensis*	Sittidae
I	White-breasted Nuthatch	*Sitta carolinensis*	Sittidae
D	Great Horned Owl	*Bubo virginianus*	Strigidae
D	European Starling	*Sturnus vulgaris*	Sturnidae
I	Blue-gray Gnatcatcher	*Polioptila caerulea*	Sylviidae
D	Loggerhead Shrike	*Lanius ludovicianus*	Thraupidae
I	Western Tanager	*Piranga ludoviciana*	Thraupidae
I	Summer Tanager	*Piranga rubra*	Thraupidae
I	Scarlet Tanager	*Piranga olivacea*	Thraupidae
D	White-faced Ibis	*Plegadis chihi*	Threskiornithidae
I	White Ibis	*Eudocimus albus*	Threskiornithidae
D	Rufous Hummingbird	*Selasphorus rufus*	Trochilidae
I	Ruby-throated Hummingbird	*Archilochus colubris*	Trochilidae
I	Marsh Wren	*Cistothorus palustris*	Troglodytidae
I	Winter Wren	*Troglodytes troglodytes*	Troglodytidae

Appendix B (cont.)

Status	Common Name	Latin name	Family
I	Sedge Wren	*Cistothorus platensis*	Troglodytidae
I	Bewick's Wren	*Thryomanes bewickii*	Troglodytidae
I	House Wren	*Troglodytes aedon*	Troglodytidae
I	Carolina Wren	*Thryothorus ludovicianus*	Troglodytidae
D	Wood Thrush	*Hylocichla mustelina*	Turdidae
D	Veery	*Catharus fuscescens*	Turdidae
D	Swainson's Thrush	*Catharus ustulatus*	Turdidae
I	Hermit Thrush	*Catharus guttatus*	Turdidae
I	Eastern Bluebird	*Sialia sialis*	Turdidae
I	American Robin	*Turdus migratorius*	Turdidae
D	Least Flycatcher	*Empidonax minimus*	Tyrannidae
D	Scissor-tailed Flycatcher	*Tyrannus forficatus*	Tyrannidae
D	Eastern Kingbird	*Tyrannus tyrannus*	Tyrannidae
D	Olive-sided Flycatcher	*Contopus cooperi*	Tyrannidae
D	Pacific-slope Flycatcher	*Empidonax difficilis*	Tyrannidae
I	Ash-throated Flycatcher	*Myiarchus cinerascens*	Tyrannidae
I	Alder Flycatcher	*Empidonax alnorum*	Tyrannidae
I	Western Wood-Pewee	*Contopus sordidulus*	Tyrannidae
I	Willow Flycatcher	*Empidonax traillii*	Tyrannidae
I	Acadian Flycatcher	*Empidonax virescens*	Tyrannidae
I	Western Kingbird	*Tyrannus verticalis*	Tyrannidae
I	Eastern Phoebe	*Sayornis phoebe*	Tyrannidae
I	Eastern Wood-Pewee	*Contopus virens*	Tyrannidae
I	Great Crested Flycatcher	*Myiarchus crinitus*	Tyrannidae
D	Bell's Vireo	*Vireo bellii*	Vireonidae
I	Cassin's Vireo	*Vireo cassinii*	Vireonidae
I	Blue-headed Vireo	*Vireo solitarius*	Vireonidae
I	Yellow-throated Vireo	*Vireo flavifrons*	Vireonidae
I	Warbling Vireo	*Vireo gilvus*	Vireonidae
I	White-eyed Vireo	*Vireo griseus*	Vireonidae
I	Red-eyed Vireo	*Vireo olivaceus*	Vireonidae

GENERAL CONCLUSIONS

This dissertation explores the effects of anthropogenic changes on plant and bird populations, and on plant communities. Classic ecological theories provide a foundation for each chapter, while global changes provide the impetus and the context. Additionally, original conceptual models played an integral role for guiding my inquiry in each study. In Chapter 1 the model served as a predictive tool for my experiment. In Chapters 2 and 3, the models were outcomes of the study that provide hypotheses for future research. Overall, my empirical results indicate that anthropogenic environmental changes dramatically alter the relative abundance of organisms within communities, landscapes, and on the continent as a whole.

The results from my first chapter show that soil nutrient status can indirectly influence plant diversity, composition, and productivity via plant-soil mutualisms. Although mutualisms are not explicitly incorporated in most classic models of coexistence theory, I was able to assimilate AMF into a conceptual model because they play a key role in nutrient acquisition for many prairie grasses, and therefore influence competition for resources (the basis of many community models). Relying on our knowledge of our study organisms' biology—in this case, AMF—to build predictive models is an important step toward generalizing ecological outcomes to multiple ecosystems. Consequently, while the ecological result from this work suggests that AMF mediate plant community responses to phosphorus in prairies, experiments in other systems will be necessary to test the generality of the model.

Nonetheless, this chapter reinforces the growing notion that microbes profoundly influence aboveground communities.

In the second chapter, I found that landscape patch size influenced the rate and patterns of landscape-level extinction in early successional plant species. Although more plant species persisted on the large patches than on small, I observed species-specific patterns of decline (with respect to declines in occupancy versus abundance). I quantified declines using a new metric, the Rank Occupancy-Abundance Profile (ROAP), which allowed me to statistically test for concurrent declines in local abundance and occupancy. Because ROAPs provide a visual depiction of the variation in local abundances across a landscape, they may have broad application to ecologists who wish to compare shifts in abundance over time, between experimental treatments, or among species.

In Chapter 3, I applied the ROAPs technique developed in Chapter 2 to assess the magnitude and patterns of decline in North American breeding birds. The results from this chapter are alarming given that many bird species have lost over 50% (and some have lost up to 89%) of their total population size in the last 30 years. By comparing the relative declines in local density and occupancy across species, I formulated a conceptual model that hypothesizes a general pattern of decline a single species may experience over time.

Several general points emerge from my dissertation research. First, humans are having a dramatic influence on the abundance of species—evident at both local and global scales. In the case of local prairie plant communities (Chapter 1) I found that the rank of individual species in the community shifted depending on soil nutrient levels and the presence of AMF. Thus, by removing AMF—by tilling or pollution, for example—and adding nutrients, humans may alter the competitive hierarchy of a plant community, promoting a plant species from being locally rare to being locally abundant. Other human disturbances, such as habitat fragmentation, also influence species' abundances. For instance, many early-successional species declined faster on smaller patches, despite more rapid encroachment by (and higher abundance of) woody species on large patches (Chapter 2). Finally, in only 30 years, bird species have lost as much as 89% of their 1970-sized populations (Chapter 3). In essence, humans are redistributing species in the global community, inducing some to be common, while imposing rarity—and even extinction—on others.

Second, my work also shows that responses to human-induced environmental changes vary markedly among species and functional groups. In the case of nutrients at AMF, I not only observed differential responses among grass species, but also at between C_3 and C_4 grasses. My work in fragmented habitats suggested that clonal, long-lived plant species persisted longer in large patches, while short-lived plants that relied on seedbanks persisted better in small patches. Results from both studies suggest that species traits may be useful for predicting responses to global changes.

Third, effects of global changes are often indirect. For instance, in Chapter 1 I demonstrate that nutrients influence plant communities via their mutualistic fungi, AMF. In Chapter 3, I found dramatic declines in bird species that likely reflect both direct and indirect effects of global changes. The interconnectedness of ecosystems makes this general result an unsurprising one, and yet it seems that ecologists continually underestimate the degree to which cascading effects from human impacts will influence organisms and ecosystems. In part, this is because often the properties we measure –such as diversity and productivity–are integrative properties that reflect a suite of biochemical, physiological, and community-level processes. In addition, microbes likely comprise key biological players that drive indirect effects at the community and ecosystem-scale; historically, many plant ecologists appear to have lives by the old adage "out of site, out of mind." Furthermore, indirect effects may be evident only after time lags or at large spatial scales (Chapter 3).

Finally, using a combination of approaches to address global change issues at different spatial scales and different levels of ecological organization will offer more insight on the effects global changes have on ecological systems than any singular approach. For instance, measuring community properties such as diversity and productivity reveal key net responses to environmental changes. Community approaches also provide an avenue by which we can assimilate biotic interactions (such as mutualisms) and indirect effects into our theoretical and conceptual models; ultimately, this will increase their predictive power. Moreover, biodiversity and ecosystem services have direct application and value for conservation and human welfare. However, focusing solely on community metrics can obscure species-specific patterns and responses: had I only measured diversity of small patches in a fragmented landscape, I would have overlooked the species-specific extinction trajectories I observed. Similarly, examining 209 bird species individually and collectively made clear the magnitude of abundance declines that diversity metrics at a given location would not have detected. While biodiversity is often the holy grail of conservation, management efforts often target a single species. In practice, species and community approaches should complement one another.

Overall, this dissertation uses ecological theory as a framework for documenting the dramatic influences humans are having on species and communities. My hope is that the conceptual models and tools I developed provide a basis for future research in community ecology, landscape ecology, and global change biology. Boundaries separating these fields will likely dissolve in the future as ecologists continue to recognize the complexity of biotic interactions, and the connection between patterns and processes across scales of ecological organization, space, and time.

LITERATURE CITED

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology **26**, 32-46.

Anderson, M.J. 2004. PERMDISP: a FORTRAN computer program for permutational analysis of multivariate dispersions (for any two-factor ANOVA design) using permutation tests. Department of Statistics, University of Auckland, New Zealand.

Balmford, A., R.E., Green, and M. Jenkins. 2003. Measuring the changing state of nature. Trends in Ecology and Evolution **18**: 326-330.

Barkley, T.M., R.E. Brooks, and E.K. Schofield, Editors. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS, USA.

Bazzaz, F.A. 1996. Plants in Changing Environments. Cambridge University Press, Cambridge, UK.

Bennett, E.M., S.R. Carpenter, and N.F. Caraco. 2001. Phosphorus and eutrophication: a global perspective. Bioscience **51**: 227-234.

Bever, J.D. 2003. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. New Phytologist **157**, 465-473.

BirdLife International 2004. State of the World's Birds 2004: Indicators for our Changing World, Birdlife International.

Bissonette, J.A. and I. Storch. 2002. Fragmentation: is the message clear? Conservation Ecology **6**: 14. [online] URL: http://www.consecol.org/vol6/iss2/art14/.

Blackburn, T.M. and K.J. Gaston, 2002. Extrinsic factors and the population sizes of threatened birds. Ecology Letters **5**: 568-576.

Boeken, B. and M. Shachak. 1998. The dynamics of abundance and incidence of annual plant species during colonization in a desert. Ecography **21**: 63-73.

Bronstein, J.L. 1994. Conditional outcomes in mutualistic interactions. Trends in Ecology and Evolution **9**, 214-217.

Brook, B.S., N.S., Sodhi, and R.E. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology and Evolution **23**: 453-460.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. The American Naturalist **124**: 255-279.

Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of migration on extinction. Ecology **58**: 445-449.

Brown, J.H. and M.V. Lomolino. 2000. Concluding remarks: historical perspective and the future of island biogeography theory. Global Ecology and Biogeography **9**: 87-92.

Brussard, P.F. 2000. Forward. In: Genetics, Demography and Viability of Fragmented Populations eds. Young, A.G. and Clarke, G.M. Cambridge University Press, Cambridge, pp. xv-xvi.

Calder, W.A. 1984. Size, function, and life history. Harvard University Press, Cambridge, MA.

Carpenter, S.R. 2008. Phosphorus control is critical to mitigating eutrophication. Proceedings of the National Academy of Sciences **105**: 11039-11040.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **63**: 215-244.

Ceballos, G. and P.R. Ehrlich. 2002. Mammal populations losses and the extinction crisis. *Science* **296**: 904-907.

Christensen, N.L. and R.K. Peet. 1984. Convergence during secondary forest succession. Journal of Ecology **72**: 25-36.

Conrad, K.F., J.N. Perry, and I.P. Woiwod. 2001. An abundance-occupancy time-lag during the decline of an arctiid tiger moth. Ecology Letters **4**: 300-303.

Conslisk, E., J. Conslisk, B. Enquist, J. Thompson, and J. Harte. 2009. Improved abundance prediction from presence-absence data. Global Ecology and Biogeography **18**: 1-10.

Cook, W.M., K.T. Lane, B.L. Foster, and R.D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters, **5**: 619-623.

Cook, W.M., J. Yao, B.L. Foster, R.D. Holt, and L. B. Patrick. 2005. Secondary succession in an experimentally fragmented landscape: community patterns across space and time. Ecology **85**: 1267-1279.

Cornutt, J.L., S.L. Pimm, and B.A. Maurer. 1996. Population variability of sparrows in space and time. Oikos **76**: 131-144.

Cutler, N.A., L.R. Belyea, and A.J. Dubmore. 2008. The spatiotemporal dynamics of a primary succession. Journal of Ecology **96**: 231-246.

Davies, K.F., C.R. Margules, and J.F. Lawrence. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology **85**: 265-271.

Davies, R.G., C.D.L., Orme, V., Olson, G.H.Thomas, S.G. Ross, T.S. Ding, P.C. Rasmussen, A.J. Stattersfield, P.M. Bennett, T.M. Blackburn, I.P.F. Owens, and K.J. Gaston. 2006. Human impacts and the global distribution of extinction risk. Proceedings of the Royal Society *B* **273**: 2127-2133.

Daleo, P., J. Alberti, A. Canepuccia, M. Escapa, E. Fanjul, B.R. Silliman, M.D. Bertness, and O. Iribarne. 2008. Mycorrhizal fungi determine salt-marsh plant zonation depending on nutrient supply. Journal of Ecology **96,** 431-437.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK.

Debinski, D.M. and R.D. Holt. 2000. Survey and overview of habitat fragmentation experiments. Conservation Biology **14**: 342-355.

Diamond, J.M. 1984. 'Normal' extinctions of isolated populations. Pages 191-246 *in* Niteckig, M.H., editor. Extinctions. University of Chicago Press, Chicago, USA.

Dunning, J.B. Jr. (editor). 1993. CRC handbook of avian body masses. CRC Press, Inc. Boca Raton, FL. USA.

Ehrlich, P.R. and G.C. Daily. 1993. Population extinction and saving biodiversity. Ambio **22**: 64-67.

Ehrlich, P.R., D.S. Dobkin, and D. Wheye. 1988. The Birder's handbook. Simon & Schuster Inc., NY. USA.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos **77**: 248-258.

Fagan, W.F. and E.E. Holmes. 2006. Quantifying the extinction vortex. Ecology Letters **9**: 51- 60.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology Evolution and Systematics **34**: 487-515.

Foley, J.A., R. DeFries, G.P. Asner, C. Barford, G. Bonan, S.R. Carpenter, F.S. Chapin, M.T. Coe, G.C. Daily, H.K. Gibbs, J.H. Helkowski, T. Holloway, E.A. Howard, C.J. Kucharik, C. Monfreda, J.A. Patz, I.C. Prentice, N. Ramankutty, and P.K. Snyder. 2005. Global consequences of land use. Science **309**: 570-574.

Freckleton, R.P., J.A. Gill, D. Noble, and A.R.Watkinson. 2005. Large-scale population dynamics, abundance-occupancy relationships and the scaling from local to regional population size. Journal of Animal Ecology **74**: 353-364.

Freckleton, R.P., D. Noble, and T.J. Webb. 2006. Distributions of habitat suitability and the abundance-occupancy relationship. The American Naturalist **167**: 260-275.

Fretwell, S.D. and H.L. Lucas, Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica **14**: 16-36.

Freville, H., K. McConway, M. Dodd, and J. Silvertown. 2007. Prediction of extinction in plants: Interaction of extrinsic threats and life history traits. Ecology **88**: 2662-2672.

Fischer, J. and D.B. Lindenmayer, 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. Oikos **112**, 473-480.

Foster, B.L. and K. Gross. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology **79**, 2593-2602.

Fukami, T. 2004. Assembly history interacts with ecosystem size to influence species diversity. Ecology **85**, 3234-3242.

Galloway, J.N., A.R. Townsend, J.W. Erisman, M. Bekunda, Z. Cai, J.R. Freney, L.A. Martinelli, S.P. Seitzinger, and M.A. Sutton. 2008. Transformations of the nitrogen cycle: recent trends, questions, and potential solutions. Science **320**: 889-892.

Gaston, K.J. 1994. Rarity. Chapman and Hall, London, UK.

Gaston, K.J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, New York, NY, USA.

Gaston, K.J. and Kunin, W.E. 1997. Concluding comments. Pages 262-272 *in* W.E. Kunin and K.J. Gaston, editors. The Biology of Rarity. Chapman and Hall, London, UK.

Gaston, K.J., T.M. Blackburn, and R.D. Gregory, 1998. Interspecific differences in intraspecific abundance-range size relationships of British breeding birds. Ecography **21**: 149-158.

Gaston, K.J., T.M. Blackburn, J.J.D. Greenwood, R.D. Gregory, R.M. Quinn, and J.H.Lawton. 2000. Abundance-occupancy relationships. Journal of Applied Ecology **37**, 39-59.

Gaston, K.J., T.M. Blackburn, and K.K. Goldewijk. 2003. Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society. B **270**: 1293-1300.

Gaston, K.J. and R.A. Fuller. 2007. Commonness, population depletion and conservation biology. Trends in Ecology and Evolution. **23**: 14-19.

Gilpin, M.E. and M.E. Soule. 1986. Minimum viable populations: processes of species extinctions, Pages 19-34 *in* M.E. Soule, editor. Conservation Biology – the Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, USA.

Giovannetti, M. and B. Mosse. 1980. An evaluation of techniques for measuring vesicular-arbuscular mycorrhizal infection in roots. New Phytologist **84**, 489-500.

Glenn-Lewin, D.C. and E. van der Maarel. 1992. Patterns and processes of vegetation dynamics. Pages 11-44 *in* Glenn-Lewin, D.C, R.K. Peet, and T.T. Veblen, editors. Plant Succession: Theory and Prediction. Chapman and Hall, London, UK.

Goldberg, D.E. and T.E. Miller. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology **7**, 213-225.

Gonzalez, A., J.H. Lawton, F.S. Gilbert, T.M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science **281**: 2045-2047.

Gough, L., C.W. Osenberg, K.L. Gross, and S.L. Collins. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. Oikos **89**, 428-439.

Govindarajulu, M., P.E. Pfeffer, H. Jin, J. Abudaker, D.D. Douds, J.A. Allen, H. Bucking, P.J. Lammers, and Y. Shachar-Hill. 2005. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. Nature **435**, 819-823.

Grashof-Bokdam, C.J. and Geertsema, W. 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. Journal of Biogeography **25**: 837-846.

Grime, J.P., J.M.L. Mackey, S.H. Hillier and D.J. Read. 1987. Floristic diversity in a model system using experimental microcosms. Nature **328**, 420-422.

Hanski, I. 1982. Dynamic of regional distribution: the core and satellite species hypothesis. Oikos **38**: 210-221.

Hartnett, D. C., B.A.D. Hetrick, G.W.T. Wilson, and D.J. Gibson. 1993. Mycorrhizal influence on intraspecific and interspecific neighbor interactions among co-occurring prairie grasses. Journal of Ecology **81**, 787-795.

Hartnett, D. C. and G.W.T. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prarie. Ecology **80**, 1187-1195.

Hartnett, D.C. and G.W.T. Wilson. 2002. The role of mycorrhizas in plant community structure and dynamics: lessons from the grasslands. Plant and Soil **244**, 319-331.

Holsinger, K.E. 2000. Demography and extinction in small populations. Pages 55-74 *in* A.G. Young and G.M. Clarke, editors. Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge, UK.

Holt, R.D. 1992. A neglected facet of island biogeography: the role of internal spatial dynamics in area effects. Theoretical Population Biology **41**: 354-371.

Holt, R.D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77-88 *in* R.E. Ricklefs and D. Schluter, editors. Species Diversity in Ecological Communities. University of Chicago Press, Chicago, IL, USA.

Holt, R.D., G.R. Robinson, and M.S. Gaines. 1995. Vegetation dynamics in an experimentally fragmented landscape. Ecology **76**: 1610-1624.

Holt, R.D., J.H Lawton, K.J. Gaston and T.M. Blackburn. 1997. On the relationship between range size and local abundance: back to basics. Oikos **78**: 183-190.

Holt, A.R. and K.J. Gaston. 2003. Interspecific abundance-occupancy relationships of British mammals and birds: is it possible to explain the residual variation? Global Ecology and Biogeography **12**: 37-46.

Holyoak, M., M.A. Leibold, N. Mouquet, R.D. Holt, and M.F. Hoopes. 2005. Metacommunities: A framework for large-scale community ecology. Pages 1-31 *in* M. Holyoak, M.A. Leibold, R.D. Holt, editors. Metacommunities. University of Chicago Press, Chicago, IL , USA.

Horn, H.H. 1981. Succession. Pages 253-271 *in* R.M. May, editor. Theoretical Ecology: Principles and Applications. Blackwell, Oxford, UK.

Hughes, J.B., G.C. Daily, and P.R. Ehrlich. 1997. Population diversity: its extent and extinction. *Science* **278**: 689-692.

Hurlbert, A.H. and E.P. White, 2007. Ecological correlates of geographical range occupancy in North American birds. Global Ecology and Biogeography **16**: 764-773.

Janos, D. P. 1980. Mycorrhizae influence tropical succession. Biotropica **12**, 56-64.

Johnson, N.C. 1993. Can fertilization of soil select less mutualistic mycorrhizae? Ecological Applications **3**, 749-757.

Johnson, N.C., J.H. Graham, and F.A. Smith. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytologist **135**, 575-585.

Johnson, N.C., J. Wolf, and G.W. Koch. 2003a. Interactions among mycorrhizae, atmospheric CO_2, and soil N impact plant community composition. Ecology Letters **6**, 532-540.

Johnson, N.C., D.L. Rowland, L. Corkidi, L.M. Egerton-Warburton, and E.B. Allen. 2003b. Nitrogen enrichment alters mycorrhizal allocation at five mesic to semiarid grasslands. Ecology, **87**, 1895-1908.

Johnson, N.C., J.D. Hoeksema, J.D. Bever, V.B. Chaudhary, C. Gehring, J. Klironomos, R. Koide, M.R. Miller, J. Moore, P. Moutoglis, M. Schwartz, S. Simard, W. Swenson, J. Umbanhowar, G.W.T. Wilson, and C. Zabinski. 2006. From Lilliput to Brobdingnag: extending models of mycorrhizal function across scales. BioScience **56**, 889-900.

Johnson, N.C., Rolwand, D.L., Corkidi, L., and Allen, E.B. 2008. Plant winners and losers during grassland N-eutrophication differ in biomass allocation and mycorrhizas. Ecology **89**, 2868-2878.

Joshi, J., P. Stoll, H.P. Rusterholz, B. Schmid, C. Dolt, and B. Baur. 2006. Small-scale experimental habitat fragmentation reduces colonization rates in species-rich grasslands. Oecologia **148**: 144-152.

Kardol, P., T. M. Bezemer, and W. H. van der Putten. 2006. Temporal variation in plant-soil feedback controls succession. Ecology Letters **9**: 1080-1088.

Keddy, P.A. 1992. Assembly and response rules, two goals for predictive community ecology. Journal of Vegetation Science **3**: 157-164.

Klironomos, J. N., J. McCune, M. Hart, and J. Neville. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. Ecology Letters **3**, 137-141.

Klironomos, J.N. 2003. Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology **84**, 2292-2301.

Koide, R.T. 1991. Nutrient supply, nutrient demand and plant response to mycorrhizal infection. New Phytologist **117**, 365-386.

Koide, R.T. and M. Li. 1989. Appropriate controls for vesicular-arbuscular mycorrhiza research. New Phytologist **111**, 35-44.

Koske, R.E. and J.N. Gemma. 1989. A modified procedure for staining roots to detect mycorrhizas. Mycological Research **92**, 486-488.

MacArthur, R.H. and E.O.Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ, USA.

Mace, G.M., N.J. Collar, K.J. Gaston, C. Hilton-Taylor, H.R. Akçakaya, N. Leader-Williams, E.J. Milner-Gulland, and S.N. Stuart. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology **22**: 1424-1442.

Margules, C.R. 1996. Experimental fragmentation. Pages 128-137 *in* J. Settel, C.R. Margules, P. Poschlod, and K. Henle, editors. Species survival in fragmented landscapes. Kluwer Academic, Dordecht, The Netherlands.

Marsh, D.M. and P.C. Trenham. 2008. Current trends in plant and animal population monitoring. Conservation Biology **22**: 647-655.

McArdle, B.H. and M.J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology **82**: 290-297.

McGonigle, T.P. 1988. A numerical analysis of published field trials with vesicular-arbuscular mycorrhizal fungi. Functional Ecology **2**, 473-478.

Mora, C., R. Metzger, A. Rollo, and R.A. Myers. 2007. Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing environmental warming. Proceedings of the Royal Society B **274**, 1023-1028.

Moran, M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos **100**: 403-405.

Newsham, K.K., A.H. Fitter, and A.R. Watkinson. 1995. Arbuscular mycorrhiza protect an annual grass from root pathogenic fungi in the field. Journal of Ecology **83**, 991-1000.

O'Connor, P.J., S.E. Smith, F.A. Smith. 2002. Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. New Phytologist **154**, 209-218.

Ode, D.J., L.L. Tieszen, and J.C. Lerman. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. Ecology **61**, 1304-1311.

Ovaskainen, O. and I. Hanski, 2004. Metapopulation dynamics in highly fragmented landscapes. Pages 73-103 *in* I. Hanskii, and O.E. Gaggioti, editors. Ecology, Genetic, and Evolution of Metapopulations. Elsevier Inc., Boston, MA, USA.

Owens, I.P.F. and P.M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences **97**: 12144-12148.

Peer, B. D. and E.K. Bollinger. 1997. The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/271

Pickett, S.T.A, S.L. Collins, and J.J. Armesto. 1987. Models, mechanisms, and pathways of succession. The Botanical Review **53**: 335-371.

Pickett, S.T.A. and M.L. Cadenasso. 2005. Vegetation dynamics. Pages 172-198 *in* E. van der Maarel, editor. Vegetation Ecology. Blackwell Publishing, Oxford, UK.

Pimm, S.L. and R.A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. Proceedings of the National Academy of Sciences (USA) **92**: 9343-9347.

Pimm, S., P. Raven, A. Peterson, C.H. Sekercioglu, and P.R. Ehrlich. 2006. Human impacts on the rates of recent, present, and future bird extinctions. Proceedings of the National Academy of Sciences **103**: 10941-10946.

Preston, F.W. 1948. The commonness, and rarity, of species. Ecology **29**: 254-83.

Preston, F.W. 1960. Time and space and the variation of species. Ecology **41**: 785-90.

Questad, E.J. and B.L. Foster. 2007. Vole disturbances and plant diversity in a grassland metacommunity. Oecologia **153**, 341-351.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205-217 *in* H. Synge, editor. The Biological Aspects of Rare Plants Conservation. John Wiley and Sons, Chichester, UK.

Reynolds, H.L., A. Packer, J.D. Bever, and K. Clay. 2003. Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology **84**, 2281-2291.

Reynolds, H.L., A.E. Hartley, K.M. Vogelsange, J.D. Bever and P.A. Schultz. 2005. Arbuscular mycorhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. New Phytologist **167**, 869-880.

Robinson, G.R., R.D. Holt, M.S. Gaines, S. P. Hamburg, M.L. Johnson, H.S. Fitch, and E.A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. Science **257**: 524-526.

Rodriguez, A. and M. Delibes. 2002. Internal structure and patterns of contraction in the geographic range of the Iberian Lynx. Ecography **25**: 314-328.

Rodriguez, J.P. 2002. Range contraction in declining North American bird populations.Ecological Applications **12**: 238-248.

Sala, O.E., F.S. Chapin, J.J. Armesto, E. Berlow, J. Bloomsfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H.Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**: 1770-1774.

Sauer, J. R., J.E. Hines, and J. Fallon. 2008. The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. Version 5.15.2008. USGS Patuxent Wildlife Research Center.

Schoener, T.W. *In press*. The MacArthur-Wilson equilibrium model: a chronicle of theoretical modification and real-world evaluation, *in* J. Losos and R. Ricklefs, editors. Island Biogeography at 40: Impacts and Prospects. Princeton University Press, Princeton, NJ.

Schoereder, J.H., T.G. Sobrinho, C.R. Ribas, and R.B.F. Campos. 2004. Colonization and extinction of ant communities in a fragmented landscape. Austral Ecology **29**: 391-398.

Şekercioğlu, C.H., G.C. Daily, and P.R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences **101**: 18042-18047.

Sibley, D.A. 2000. The Sibley Guide to Birds. Chanticleer Press, Inc. New York, USA.

Smith, S. and Read, D. 1997. *Mycorrhizal symbiosis*, Academic Press, London, UK.

Sylvia, D.M. and N.H. Neal. 1990. Nitrogen affects the phosphorus response of VA mycorrhiza. New Phytologist **115**, 303-310.

Stocklin, J. and M. Fischer. 1999. Plants with longer-lived seeds have lower local extinction rates in grassland remnants 1950-1985. Oecologia **120**: 539-543.

Schweiger, E.W., J.E. Diffendorfer, R.D. Holt, R. Pierotti, and M.S. Gaines. 2000. The interaction of habitat fragmentation, plant, and small mammal succession in an old field. Ecological Monographs **70**: 383-400.

Taylor, L.R. 1961. Aggregation, variance and the mean. Nature **189**: 732-735.

Thuiller, W. 2007. Climate change and the ecologist. Science **448**: 550-552.

Tilman, D., R.M. May, C.L. Lehman, and M.A. Nowak. 1994. Habitat destruction and the extinction debt. Nature **371**: 65-66.

Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. 1985. The Resource-Ratio Hypothesis of Plant Succession. American Naturalist **125**, 827-852.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs **57**, 189-214.

Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey, USA.

Tylianakis, J.M., R.K. Didham, J. Bascompte, and D.A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters **11**, 1351-1363.

Urcelay, C. and S. Diaz. 2003. The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity. Ecology Letters **6**, 388-391.

Van der Hiejden, M.G.A. 2002. Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search of underlying mechanisms and general principles. Pages 243-265 *in* van der Hiejden, M.G.A. and I.R. Sanders, editors. Mycorrhizal Ecology. Ecological Studies 157. Springer-Verlag, Heidelberg.

Van der Hiejden, M.G.A. 2004. Arbuscular mycorrhizal fungi as support systems for seedling establishment in grassland. Ecology Letters **7**, 293-303.

Van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I.R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature **396**, 69-72.

Van der Hiejden, M.G.A., Bardgett, R.D., and van Straalen, N.M. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters **11**, 296-310.

Vogelsang, K.M., H.L. Reynolds, and J.D. Bever. 2006. Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system. New Phytologist **172**, 554-562.

Wardle, D.A., R.D. Bardgett, J.N. Klironomos, H. Setala, W.H. Van der Putten, and D.H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science **304**, 1629-1633.

Warner, R.R. and P.L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. The American Naturalist **125**: 769-787.

Wassen, M.J., H.O. Venterink, E.D. Lapshina, and F. Tanneberger. 2005. Endangered plants persist under phosphorus limitation. Science **437**, 547-550.

Webb, T.J., D. Noble, and R.P. Freckleton. 2007. Abundance-occupancy dynamics in a human dominated environment: linking interspecific and intraspecific trends in British farmland and woodland birds. Journal of Animal Ecology **76**: 123-134.

Wilson, G. W. T., and D.C. Hartnett. 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. American Journal of Botany **85**, 1732-1738.

Wilson, J.B., T.C.E. Wells, I.C. Trueman, G. Jones, M.D. Atkinson, M.J. Crawley, M.E. Dodds, and J. Silvertown. 1996. Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. Journal of Ecology **84**: 527-538.

With, K.A., A.W. King, and W.E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. Biological Conservation **141**: 3152-3167.

World Resources Institute 1998. A guide to world resources 1998-1999: Environmental change and human health. World Resources Institute, Washington D.C.

Yao, J., R.D. Holt, P.M. Rich, and W.S. Marshall. 1999. Woody plant colonization in an experimentally fragmented landscape. Ecography **22**: 715-728.

Zuckerberg, B., W.F. Porter, and K. Corwin. 2009. The consistency and stability of abundance-occupany relationships in large-scale population dynamics. Journal of Animal Ecology **78**: 172-181.