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COMMUNITY INVASIBILITY, RECRUITMENT LIMITATION, AND GRASSLAND BIODIVERSITY

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Abstract. Plant species composition, species abundances, and species richness were strongly recruitment limited in a 4-yr experiment in which seeds of up to 54 species were added to patches of native grassland. Four field seasons after a one-time addition of seed, many added species were still present and reproducing, with plots seeded at the highest rate having species richness that was 83% greater and total plant cover that was 31% greater than controls. Total plant community cover increased significantly with the number of species added as seed, but total cover of pre-existing species was independent of the number of species added as seed, suggesting that the new species mainly filled previously ''empty'' sites.

The proportion of added species that became established was negatively correlated with initial species richness of plots, suggesting that species-rich sites were more resistant to invasion. Plot invasibility also depended on the abundances and species richness of plant functional groups in the plots, but was independent of seed size and of total plant cover. The major functional groups of plants differed in their abilities to invade as seed, with perennial grasses being the poorest invaders and herbaceous legumes being the best. Thus, local biotic interactions and recruitment dynamics jointly determined diversity, species composition, and species abundances in these native grassland communities. This supports a metapopulation-like perspective over a purely interspecific-interaction perspective or a purely regional perspective, suggesting that recruitment limitation may be more important, even on a local scale, than often recognized.

Key words: biodiversity; dispersal; empty sites; metapopulation dynamics; prairie grassland; recruitment limitation; savanna; seed addition; species richness.

INTRODUCTION

Among community ecologists, one school of thought has long held that local species abundances, community composition, and diversity are determined mainly by the interspecific biotic interactions that occur within a site (e.g., Hutchinson 1959, 1961, Paine 1966, Turelli 1981, Tilman 1982, Pimm 1991). In support of this view, experimental and observational studies have demonstrated strong effects of competition and/or predation on community structure (e.g., Schoener 1983, 1985, Connell 1983*a*, *b*, Sih et al. 1986), and major debates in the discipline have focused on the relative importance of one biotic interaction vs. another, such as competition vs. herbivory or predation, or top-down vs. bottom-up regulation (e.g., Carpenter et al. 1985, 1987, Power 1992). Although there are many forms to this view, its essential feature is the assumption that interspecific interactions limit which and how many species invade into and persist in a local community, and limit the abundance of each species in the community. Regional composition and diversity are then viewed as the summed effect of the local biotic interactions that occur throughout the region. In this perspective local interspecific biotic interactions are considered to be of great importance, and the composition of the regional species pool and the dispersal abilities of these species of lesser importance.

The regional perspective, in contrast, stresses the role of species isolation, speciation, and extinction as major controls of the regional species pool. As a first approximation, local diversity is considered to be a dispersal-dependent sampling of the broader regional species pool (e.g., Hubbell and Foster 1986, Cornell and Lawton 1992). The composition and diversity of local sites are thought to depend on stochastic dispersal events and dispersal barriers. This perspective hypothesizes that dispersal or recruitment limitation is the major factor determining local composition, abundance, and diversity (e.g., Gaines and Roughgarden 1985, Cornell and Lawton 1992).

An intermediate view is provided by the metapopulation perspective and the related theory of neighborhood competition and local dispersal. These emphasize the interplay of within-site biotic interactions and of site-to-site dispersal as controllers of both local and regional species composition and diversity (e.g., Levins 1969, 1970, Horn and MacArthur 1972, Levin and Paine 1974, Paine and Levin 1981, Hanski and Gilpin 1991, Hastings and Harrison 1994). In multi-

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species models, dispersal limitation is hypothesized to reduce the effects of local interspecific interactions by generating sites in which inferior competitors escape from competition with their superiors (e.g., Tilman 1994), or prey are freed from predation (e.g., Hassell et al. 1994). Coexistence of numerous competing species, for instance, requires interspecific trade-offs between dispersal vs. competitive ability (e.g., Horn and MacArthur 1972, Tilman 1994). Given this trade-off, local abundances of all species can, in theory, be increased, at least in the short term, by increases in their dispersal because all localities should contain some suitable sites that are presently unoccupied (Tilman 1994).

These differing but interrelated perspectives represent benchmarks on an intergrading continuum. They, and the studies upon which they are based, suggest that both dispersal and local interactions play a role in local species diversity, as is also suggested by island biogeographic theory (e.g., MacArthur and Wilson 1967). One way to determine the roles that such processes may play in a community is to test how local species composition, abundance, and diversity are influenced by dispersal, and how the invasibility of sites depends on site characteristics such as species richness. Species richness is hypothesized to influence invasibility because areas that are more species rich are assumed to have a more complete or efficient use of limiting resources, and thus be less invasible (Robinson et al. 1995).

This study was designed to determine the extent to which species composition, abundance, and diversity were limited by dispersal of species into localities; the factors, such as seed size and the plant functional traits, that influenced invasibility; and the effect of such invasions on existing species. In this experiment, seeds of different numbers of plant species were added to undisturbed native grassland. Nutrient addition experiments in this field have identified nitrogen as the only soil nutrient (of N, P, K, Ca, Mg, S, and trace metals) that significantly limits productivity and influences composition and diversity (Tilman 1987, 1988). The plots were studied for a year before seed addition to quantify initial plant species composition and abundance, species richness, the amount of bare mineral soil, the extent of recent soil disturbance by gophers, and extractable levels of soil nitrate and ammonium. These are all thought to influence invasibility of plant communities (e.g., Huntly and Inouye 1988, Robinson et al. 1995). If local interactions are the overriding factor determining local diversity, then few colonists should be successful and each successful colonist species should displace an existing species and/or cause decreased abundance of existing species. Alternatively, species richness and species abundances might increase greatly following seed addition, demonstrating strong recruitment limitation of local abundances and diversity. This would support the hypothesis that plant communities contain ''open sites'' and that these open sites are an important mechanism allowing numerous species to coexist when competing for a single resource (Tilman 1994). I tested among these alternatives by performing experimental seed additions of from 5 to 54 grassland species into replicated plots in the most species-rich herbaceous vegetation of our site, grassland openings in native savanna, and by observing responses for four field seasons after seed addition.

METHODS

This research was performed at Cedar Creek Natural History Area in a stand of native oak savanna, called Field D (Tilman 1987), that has never been cut or cultivated and has been free of domestic livestock grazing for >50 yr. It has been maintained as savanna by prescribed spring burning in two of every three years for the past 30 yr (White 1983, Tester 1989). It was burned in early May of 1991, 1993, and 1994, but not in 1992 or 1995. In August 1991, a 2 × 2 m site was chosen in each of 30 prairie openings scattered across a 2-ha portion of this savanna. Each site was divided into four adjacent 1 × 1 m plots that were examined visually to identify all vascular plant species present in each of four 50 × 50 cm subplots. The percent cover of each species was estimated using cardboard cutouts of various shapes and sizes as visual guides. Because percent cover was estimated independently for each species, and independent of canopy position, the estimates can sum to >100%. The percent cover of the most abundant species in each plot was used as a measure of species dominance in the plot. The percent covers by bare mineral soil, litter, or ground recently disturbed by plains pocket gophers (*Geomys bursarius*) were also determined for each subplot. Four soil cores, each 2.5 cm diameter and 20 cm deep, were collected per plot, extracted with 0.01 mol/L KCl, and analyzed to give the extractable soil nitrogen (NH_4 plus NO_3) concentration in each plot.

In early June 1992, seeds of from 0 to 54 different plant species were added to half of the 1 × 1 m plots. The species added as seed (Table 1) occur locally, but most are rare. Some seeds were gathered on site, but most were obtained from a local company (Prairie Restoration, Princeton, Minnesota). All seeds of a given species were thoroughly mixed prior to use. The seed addition treatments consisted of (1) a control that received no seed addition, (2) addition of seed of 5 species, (3) addition of 10 species, (4) of 15 species, (5) of 20 species, (6) of 25 species, (7) of 30 species, (8) of 35 species, (9) of 40 species, or (10) addition of all 54 species. There were six replicates per treatment, with each replicate representing a separate random draw of the appropriate number of species from the 54-species seed addition pool. Seed of each species, with dispersal structures attached, was added at 4.5 g/m^2, independent of the number of species added to a plot. Seed size (the mass of an individual seed) was

TABLE 1. Species added as seed, their life form, number of plots to which they were added, number of these in which they were present in 1991 and 1995, and their average percent cover in 1991 and 1995 across all plots to which they were and were not added as seed. The *t* tests assumed equal variance unless a variance test showed significant differences in variance.

						Cover		
							1995	
Species	Life form†	Seed mass (mg/seed)	No. plots to which added‡	No. plots present 1991§	No. plots present 1995§	1991¶	Seed added¶	Seed not added#
Achillea millefolium	PF	0.05	29	0	20	0.00	**0.59**	**0.00**
Agastache foeniculum	PF	0.23	24	0	12	0.00	**0.33**	**0.00**
Allium stellatum	PF	2.11	29	0	11	0.00	**0.18**	**0.00**
Ambrosia artemisiifolia	AF	4.02	28	1	1	0.01	0.01	0.00
Amorpha canescens	PL	2.26	24	9	8	0.77	1.07	1.94
Andropogon gerardi	PG	2.89	26	13	10	5.70	**2.09**	4.75
Anemone cylindrica	PF	1.08	28	1	25	0.00	**0.83**	**0.13**
Asclepias syriaca	PF	4.78	24	2	8	0.06	0.13	0.31
Asclepias tuberosa	PF	5.27	25	9	19	0.16	**0.56**	0.34
Asclepias verticillata	PF	2.25	27	0	8	0.00	**0.12**	**0.00**
Aster azureus	PF	0.17	24	5	13	0.78	0.78	1.32
Aster ericoides	PF	0.06	28	4	5	0.11	0.35	0.13
Aster novae-angliae	PF	0.27	24	0	0	0.00	0.00	0.00
Astragalus canadensis	PL	1.60	26	0	11	0.00	**0.32**	**0.01**
Baptisia leucantha	PL	14.80	25	0	11	0.00	**0.58**	**0.00**
Bouteloua curtipendula	PG	4.18	23	1	1	0.05	0.03	**0.00**
Celastrus scandens	PW	15.70	28	0	0	0.00	0.00	0.00
Coreopsis palmata	PF	1.41	26	0	8	0.00	**0.11**	0.32
Delphinium virescens	PF	0.52	27	0	0	0.00	0.00	0.00
Desmodium canadense	PL	4.71	28	1	23	0.37	**18.60**	**0.56**
Elymus canadensis	PG	5.46	26	0	0	0.00	0.00	0.00
Gentiana andrewsii	PF	0.05	27	0	0	0.00	0.00	0.00
Heuchera richardsonii	PF	0.05	28	0	0	0.00	0.00	0.00
Koeleria cristata	PG	0.09	23	0	4	0.00	1.70	0.10
Lespedeza capitata	PL	2.42	29	3	25	0.11	**2.13**	**0.13**
Liatris aspera	PF	2.40	27	6	15	0.20	0.27	**0.05**
Lupinus perennis	PL	24.60	24	0	18	0.00	**5.43**	**0.34**
Mimulus ringens	PF	0.01	29	0	0	0.00	0.00	0.00
Monarda fistulosa	PF	0.33	26	2	26	0.12	**3.63**	**0.09**
Nepeta cataria	PF	0.58	27	0	3	0.00	0.03	**0.00**
Oenothera biennis	BF	0.41	22	2	12	0.04	**0.98**	**0.01**
Panicum capillare	AG	0.20	29	1	1	0.01	0.28	0.19
Panicum virgatum	PG	0.90	26	0	3	0.00	0.10	0.00
Paspalum ciliatifolium	PG	0.95	27	0	0	0.00	0.00	0.00
Penstemon grandiflorus	PF	1.98	28	0	0	0.00	0.00	0.00
Petalostemum candidum	PF	1.48	24	0	5	0.00	0.14	0.01
Petalostemum purpureum	PF	1.53	26	0	14	0.00	**0.66**	**0.01**
Petalostemum villosum	PL	1.83	24	0	7	0.00	0.56	0.00
Polygonum convolvulus	AF	5.07	23	1	15	0.01	0.42	**0.01**
Potentilla arguta	PF	0.12	25	2	2	0.19	0.06	0.00
Rosa arkansana	PW	14.60	25	11	11	0.64	0.81	0.55
Rudbeckia serotina	PF	0.15	26	3	25	0.21	**5.46**	**0.08**
Schizachyrium scoparium	PG	1.80	25	3	11	1.95	3.40	1.21
Setaria lutescens	AG	4.56	23	1	3	0.01	0.03	0.00
Solidago nemoralis	PF	0.06	26	5	6	0.31	0.45	0.04
Solidago rigida	PF	0.49	28	0	2	0.00	0.04	0.00
Solidago speciosa	PF	0.20	29	0	0	0.00	0.00	0.00
Sorghastrum nutans	PG	2.28	26	23	26	24.88	**11.40**	9.88
Sporobolus heterolepis	PG	1.54	22	0	0	0.00	0.00	0.00
Stipa spartea	PG	14.80	26	6	15	0.29	**1.20**	0.57
Verbena stricta	PF	0.94	29	0	0	0.00	0.00	0.00
Veronicastrum virginicum	PF	0.04	25	0	0	0.00	0.00	0.00
Vicia villosa	AL	24.20	24	0	0	0.00	0.00	0.00
Zizia aptera	PF	2.02	27	0	10	0.00	0.22	**0.00**

† P = perennial, B = biennial, A = annual, G = grass, L = legume, F = nonlegume forb, W = woody species.

‡ Number of plots to which species was added as seed.

§ Number of seed addition plots in which the species was present in 1991 (before seed addition) or 1995.

¶ Cover of species in 1991 (before seed addition) or 1995 in plots to which seed of this species was added in 1992, with boldface values indicating that 1991 and 1995 cover percentages differ significantly ($P < 0.05$) based on a *t* test.

Cover of species in 1995 in plots to which it was not added as seed, with boldfaced values indicating that 1995 cover in seeded plots differs significantly from 1995 cover in unseeded plots, based on a *t* test.

determined by weighing a batch of 100 such seeds of each species (Table 1). To minimize accidental seed addition to a plot, only two of the four 1 × 1 m plots at each site were used, and these were diagonal to each other (i.e., nonadjacent). Treatments were randomly assigned to these 60 plots.

Seeds were manually sprinkled over the appropriate plot on a calm day. A 1 m × 1 m × 75 cm tall bottomless box contained seed within the desired plot at the time of seeding. Soil was not disturbed in any manner, but the vegetation in each plot was lightly shaken and brushed to ensure that seeds settled to the soil surface before the box was removed.

Seedlings were counted and identified to species (or to ''morphospecies'' if necessary) in early August 1992 and 1993 in the central 50 × 50 cm of each plot. In late August to early September 1992, 1993, and 1994, the same technique as in 1991 was used to determine the vascular plant species composition and percent cover in the central 50 × 50 cm of each plot. In late August 1995, the entire 1 × 1 m plot was censused just as in 1991. The change from 1991 to 1995 in the number of species present in each plot was used as an index of invasibility. For some analyses, species were grouped as grasses or forbs, or further divided into C_3 grasses, C_4 grasses, woody plants, herbaceous legumes, or nonlegume forbs.

All correlation coefficients (r) are Pearson coefficients and $N = 60$ for all correlations and regressions, unless noted otherwise. Relationships are called significant if $P < 0.05$. SAS version 6.09 (SAS 1989) was used for all analyses.

RESULTS

Initial species presence/absence.—Based on the random draws of species combinations, each of the 54 species was added as seed to between 22 and 29 of the 60 plots (Table 1). Of the 54 species added as seed in 1992, 24 species had been present in 1991 in at least one of the plots to which they were added (Table 1). Of these 24 species, 10 had been present in 1991 in at least 10% of the plots to which they were added, but only two, *Sorghastrum nutans* and *Andropogon gerardi,* had been present in 1991 in half or more of the plots.

Species establishment.—Of the 30 species that had been absent in 1991 from all plots to which they were added, 16 species became established and, on average, were present in 1995 in 34.9% of the plots to which they were added. For each species added as seed, a t test compared its 1995 abundance (cover) in plots to which it had been added with its 1995 abundance in plots to which it had not been added. Data for all plots, including those with an abundance of 0, were used. On a species-by-species basis, the cover of 19 of the 54 species was significantly increased by seed addition (t test; Table 1). In addition, the 1995 cover of each added species in a plot was compared to its cover in 1991 in those plots (t test, Table 1). This showed that 17 species were significantly more abundant in 1995 in plots to which they were added as seed than they had been in 1991. In addition to these 17 species, there were 7 other species that were absent from all plots in 1991 and were present in some plots (mean: 3.7 plots) in 1995, but not with sufficient frequency and abundance to be detectable with the t test. Initially rare (cover <0.25%) species that became common (>2% cover) after seed addition were the herbaceous legumes *Desmodium canadense, Lespedeza capitata,* and *Lupinus perennis,* and the nonlegume forb *Monarda fistula.* The nonlegume forb *Rudbeckia serotina* also became common after seed addition. The C_4 grasses *Sorghastrum nutans* and *Andropogon gerardi,* the most abundant species in 1991, were the only species to have significantly lower cover in 1995 than in 1991. However, there was no detectable difference between their abundance in 1995 in plots to which they had been added as seed vs. plots to which they had not been added (Table 1), suggesting that the 1991–1995 change was not related to seed addition.

Seedling density and final cover.—A separate analysis for each of the 54 species added as seed revealed that only 7 species had a significant correlation between their seedling density in each plot in 1992 and their 1995 abundances (covers). All of these correlations were positive. However, 28 of the 54 species had significant correlations between their 1993 seedling densities and their 1995 abundances, with all of these positive, and with 19 being highly significant ($P < 0.001$).

Functional groups, seed size and establishment.—Of the 54 species added, 11 were perennial grasses (C_3 and C_4 grasses combined). Only one of these was significantly more abundant in 1995 in plots to which its seed was added than in the other plots. Of the 28 species of nonlegume perennial forbs added, 10 were significantly more abundant in 1995 in plots to which their seed were added. Of 10 species of legumes, 6 were significantly more abundant in 1995 where their seed were added, and 3 others became established in some plots where added. A contingency table analysis revealed a significant difference among these three life history groups in the frequency with which species had significantly greater abundance in plots where added as seed ($\chi^2 = 6.02$, df = 2, $0.025 < P < 0.05$). I also tested if seed size influenced the probability (P) of establishment of each species, with $P = (N_{1995} - N_{1991})/(N_{Add} - N_{1991})$, where N_{1995} and N_{1991} are the number of seed addition plots in which a species occurred in 1995 and 1991, and N_{Add} is the number of plots to which the species was added as seed. Regression showed no significant linear ($r^2 = 0.003$, $N = 54$, $P = 0.71$) or quadratic ($r^2 = 0.003$, $N = 54$, $P = 0.92$) dependence of P on the seed sizes of the species, suggesting that interspecific differences in seed size did not explain the relative invasion successes of these 54 species. However, I did not determine if germination rates or seed

TABLE 2. Multiple regression of the effect of pre-seed-addition plot characteristics on the invasibility of plots, which was measured as the change in plot species richness from 1991 to 1995. (A) ANOVA on overall multiple regression. (B) Fitted parameter values (intercept; others are slopes) and t test for H_0 that each regression parameter differs from 0.

A) Analysis of variance

Source	df	F	P	R^2
Model	7	16.4	0.0001	0.70
Error	50			
Total	57			

B) Parameter estimates

Variable	df	Parameter estimate	t	P
Intercept	1	24.2	1.55	0.12
Species added	1	0.20	7.34	0.0001
Species richness	1	−0.77	−5.83	0.0001
Total plant cover	1	−0.078	−0.48	0.63
Bare soil	1	−0.13	−0.83	0.41
Gopher mound	1	0.10	0.41	0.69
Dominance	1	0.02	0.54	0.59
Soil $NO_3 + NH_4$	1	−4.36	−3.85	0.0003

Note: The number of species added as seed to a plot is called ''Species added.'' Species richness is plot plant species richness in 1991 (before seed addition). Gopher mound is the proportion of a plot covered by a new gopher mound in 1991. Bare soil is the proportion of a plot covered by bare mineral soil in 1991 (but not by bare mineral soil caused by a gopher mound). Dominance is the 1991 proportional cover by the most abundant species in each plot.

TABLE 3. Multiple regression of effects of pre-seed-addition plot vegetative characteristics on species invasibility following seed addition. (A) ANOVA on overall multiple regression. (B) Fitted parameter values (intercept; others are slopes) and t test for H_0 that each regression parameter differs from 0.

A) Analysis of variance

Source	df	F	P	R^2
Model	6	9.593	0.0001	0.52
Error	53			
Total	59			

B) Parameter estimates

Variable	df	Parameter estimate	t	P
Intercept	1	−2.47	−1.096	0.28
Species added	1	0.20	6.375	0.0001
C_3 grasses$_{1991}$	1	−0.01	−0.209	0.84
C_4 grasses$_{1991}$	1	0.10	3.021	0.004
Forbs$_{1991}$	1	0.09	1.338	0.19
Legumes$_{1991}$	1	−0.25	−2.181	0.03
Woody$_{1991}$	1	−0.22	−1.277	0.21

Note: Proportional abundances in 1991 of C_3 grasses, C_4 grasses, legumes, forbs, and woody plants were used as covariates with the number of species added as seed in a multiple regression in which species invasibility was the dependent variable. Species invasibility is the change in plot species richness from 1991 to 1995.

viability, which could be important covariates, differed among these species.

Plot characteristics and invasibility.—Multiple regression was used to determine the relationship between long-term invasibility and plot characteristics (species richness, disturbance by gopher mounds, bare mineral soil, total plant cover, species dominance, and extractable soil NO_3 plus NH_4). These plot characteristics, measured in 1991, the year before seed addition, were entered into a multiple regression, along with the number of species added as seed, as independent variables, with the 1991–1995 change in species richness as the dependent variable (Table 2). The increase in species richness from 1991 to 1995, which I call long-term invasibility, depends on the presence/absence of species, not their relative abundances. The multiple regression explained 70% of the variance, and thus has strong explanatory value. Long-term invasibility was significantly positively dependent on the number of species added as seed. It was significantly negatively dependent on the original species richness of the plots, suggesting that plots that were more species rich were less easily invaded. The slope of −0.77 indicates that plots containing four more species in 1991 were invaded, on average, by three fewer species. There was no detectable effect of total plant cover, gopher disturbance, bare soil, or species dominance on invasibility (Table 2). However, the experiment had little power to detect effects of soil disturbance because only a few plots had gopher mounds, the largest mound covered only 15% of that plot, and the average coverage by gopher mounds was only 0.6%. In contrast, the average cover by bare soil was 29% (range: 5.5–77%), which should have given the experiment power to detect an effect if it existed. The high cover by bare soil in this field is mainly a result of burning, which removes litter. Nearby unburned grasslands have ≈10% cover by bare soil (Inouye et al. 1987). Surprisingly, there was a significantly negative relationship between extractable soil nitrogen and invasibility (Table 2), suggesting that plots with lower levels of extractable nitrogen may be more readily invaded. Another multiple regression explored the relationships between long-term invasibility and the 1991 abundances of plant functional groups. Invasibility was not significantly dependent on the total percent covers of woody species, C_3 grasses, or nonlegume forbs, but was significantly positively correlated with 1991 C_4 grass abundance and significantly negatively correlated with 1991 legume abundance (Table 3). An additional multiple regression included all the variables of both Tables 2 and 3, but replaced total 1991 species richness with the number of species in each of the five functional groups in each plot in 1991. Of the 16 plot characteristics included, there were significant negative effects on invasibility only from species richness of legumes ($F = 6.06$, $P = 0.02$), species richness of nonlegume forbs ($F = 16.3$, $P = 0.0002$), and extractable soil nitrogen ($F_{1,57} = 16.7$, $P = 0.0002$), and a significant positive effect on invasibility only from the number of species added as seed ($F_{1,57} = 52.9$, $P < 0.001$). The overall regression had $F_{16,57} = 8.32$, $P < 0.0001$, $R^2 = 0.76$.

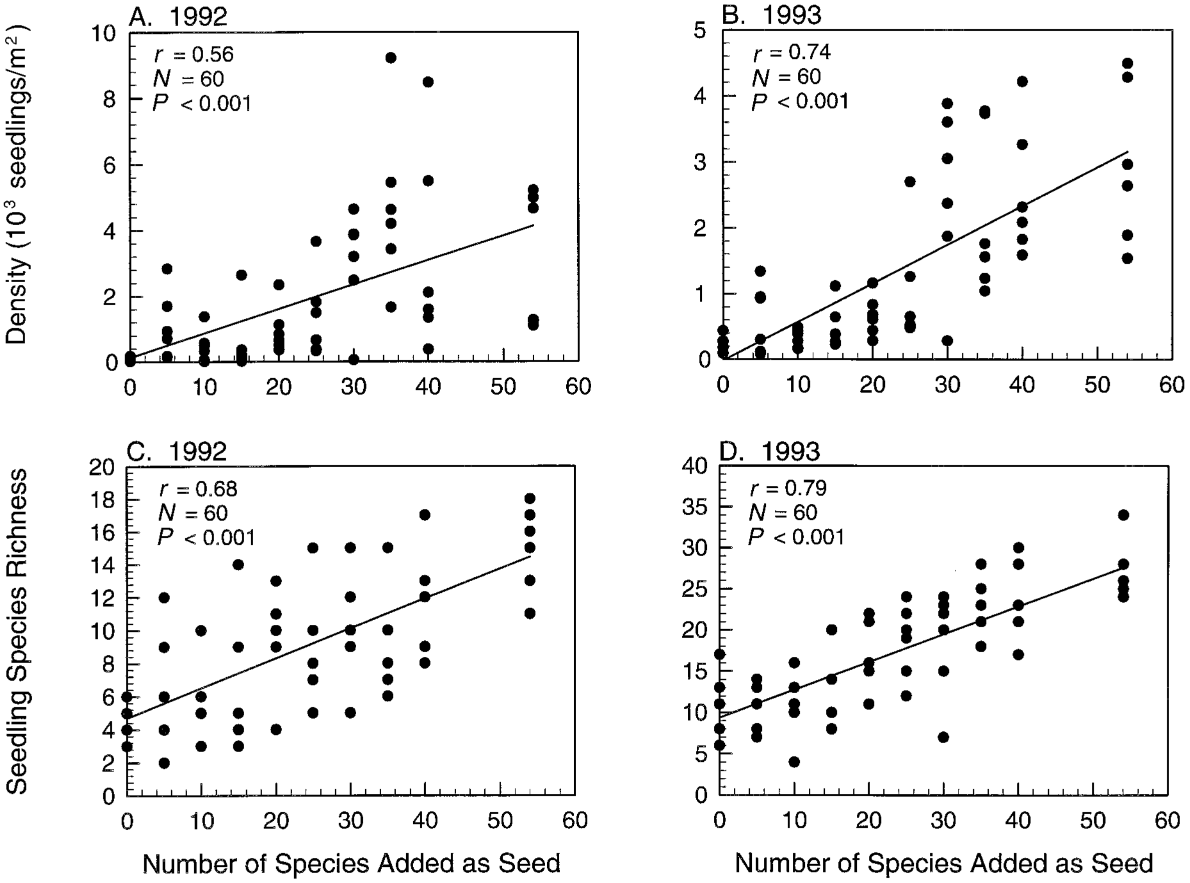

FIG. 1. Effects of the spring 1992 seed addition treatments on seedling density in 1992 and 1993 (parts A and B) and on seedling species richness in these years (parts C and D). Most seedlings were identified to species, but some could only be identified to "morphospecies."

Seedling dynamics.—Seedling densities for grasses (C_3 and C_4 grasses combined) and forbs (legumes and nonlegumes combined) increased significantly with the number of species added as seed in both 1992 and 1993 (grasses, 1992: $r = 0.44$, $P < 0.01$; 1993: $r = 0.51$, $P < 0.001$; forbs, 1992: $r = 0.47$, $P < 0.001$; 1993: $r = 0.63$, $P < 0.001$). For all taxa combined, control plots averaged 79 seedling/m^2 in 1992 and 226 seedling/m^2 in 1993, whereas plots receiving seed of all 54 species averaged 3080 seedling/m^2 in 1992 and 2970 seedling/m^2 in 1993 (Fig. 1A,B). Seedling species richness (including morphospecies) in both 1992 and 1993 was a significantly increasing function of the number of species added as seed (Fig. 1C,D).

Species richness and seed addition rate.—Species richness in 1992, 1993, 1994, and 1995 increased significantly with the number of species added (Fig. 2). On average compared to controls, plots that received the greatest number of species added as seed had 19 more species in the 2nd yr after seed addition, 16 more the 3rd yr and 13 more the 4th yr.

Total plant cover.—Total plant cover (for all species combined) increased with the number of species added as seed in 1992 (Pearson $r = 0.35$, $P < 0.01$), 1993 ($r = 0.30$, $P < 0.05$), 1994 ($r = 0.34$, $P < 0.01$), and 1995 (Fig. 3A). This was caused mainly by the additional vegetative cover of species added as seed. The total cover of added species increased significantly in 1992, 1993, 1994, and 1995 with the number of species added as seed ($P < 0.05$ for all correlations). For each plot, the 1991 summed cover of all species added as seed was subtracted from that in 1995. This change in total cover of all added species increased significantly with the number of species added as seed (Fig. 3B). On average, each added species that became established had cover in 1994 of 2.0% (i.e., occupied 200 cm^2 in a plot) and of 1.5% in 1995. Many of the added species were mature flowering individuals in 1993, 1994, and 1995. However, the total cover of the species that existed in the plots in 1991 was not significantly impacted by the increase in cover of the added species. Specifically, the 1991–1995 change in the summed covers of all species present in 1991 was not significantly dependent on the number of species added as seed (Fig.

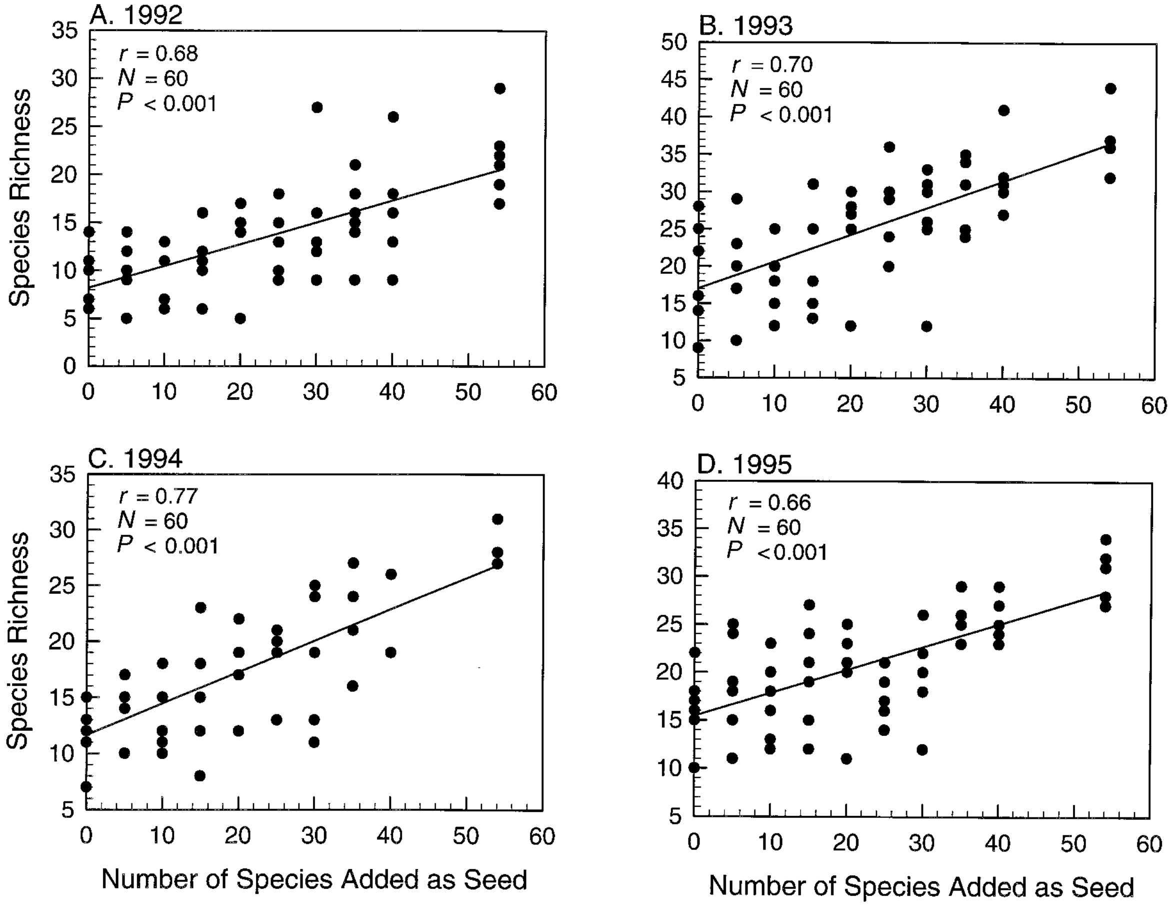

FIG. 2. Effects of the spring 1992 seed addition treatments on total vascular plant species richness per plot in (A) 1992, (B) 1993, (C) 1994, and (D) 1995. Note that the 1995 data were collected from the full 1 × 1 m plot (for direct comparison with the pre-seed-addition data of 1991), whereas the 1992, 1993, and 1994 data were from the central 0.5 × 0.5 m of each plot.

3C). Similarly, the changes in total cover of pre-existing species from 1991 to 1992, 1991 to 1993, and 1991 to 1994 were also not significantly dependent on the number of species added as seed ($P > 0.05$ for all correlations). Thus at no time was there a detectable effect of the added species on the total abundances of the pre-existing species.

Species turnover.—There was year-to-year turnover in which species were present in a plot. However, there was no significant dependence of the number of species lost from a plot from 1991 to 1995 on the number of species added as seed (Fig. 4A). The number of species gained from 1991 to 1995 increased with the number of species added as seed (Fig. 4B). The proportion of originally present species that were lost from 1991 to 1995 also was independent of the number of species added as seed (Fig. 4C) and was independent of the original species richness of the plots (Fig. 4D).

DISCUSSION

These results demonstrate that the plant species composition, abundance, and diversity of native species-rich grassland are strongly limited by recruitment. Even 4 yr after seed addition, there was a visually obvious effect of seed addition on plant composition and total plant abundance. Many species that had been absent from local sites germinated, survived, and reproduced within those sites once recruitment limitation was overcome by seed addition. Their presence reduced the amount of bare mineral soil and increased total plant cover. These results strongly support the importance of dispersal or recruitment limitation, as has been previously suggested in studies in a variety of terrestrial and aquatic communities (e.g., Elton 1958, Sagar and Harper 1960, Cavers and Harper 1967, MacArthur and Wilson 1967, Grubb 1977, 1986, Davis 1981, Gross and Werner 1982, Connell 1985, Gaines and Roughgarden 1985, Peart and Foin 1985, Fox and Fox 1986, Orians 1986, Goldberg 1987*b*, Menge and Sutherland 1987, Rejmánek 1989, Robinson et al. 1995). Thus, processes that disrupt natural dispersal dynamics, such as habitat fragmentation, should lead to changes in species abundances, including extinction, in the remaining frag-

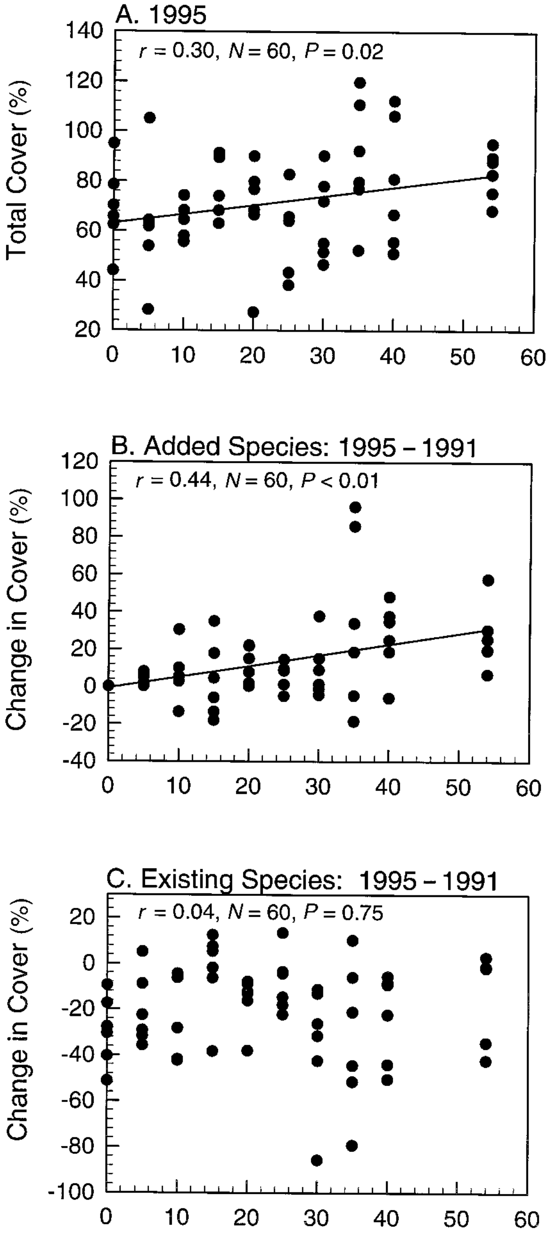

FIG. 3. Effects of the spring 1992 seed addition treatment on (A) the 1995 total cover of vascular plant species, (B) the change in total cover from 1991 to 1995 for those species added as seed in spring 1992, and (C), and the change in total cover from 1991 to 1995 for those species that existed in a plot in 1991.

ments of native ecosystems (e.g., Diamond 1972, Terborgh and Winter 1980, Usher 1988, Nee and May 1992, Tilman et al. 1994). Similarly, processes that overcome natural dispersal barriers can allow novel species to invade habitats, and thus cause marked changes in community composition, diversity, and functioning (e.g., Elton 1958, Orians 1986, Ehrlich 1989, Pimm 1989, Vitousek et al. 1987, D'Antonio and Vitousek 1992).

The ability of additional species to invade into and persist in native grasslands of Cedar Creek mimics the invasion and persistence of species during succession. Abandoned fields have low plant species richness, and are mainly dominated by Eurasian annuals. A succession of native prairie species invades and dominates these fields, but few early species are displaced (Inouye et al. 1987). Rather, there is a slow accretion of species indicating that species abundances, composition, and richness during succession are limited by dispersal (Tilman 1990, 1994). This study shows that the apparent upper bound to species richness reached in our native grassland vegetation is also dispersal or recruitment limited. Additional species from the region can persist and reproduce locally when this limitation is overcome.

Most organisms are spatially discrete entities that influence and are influenced mainly by other individuals in their immediate neighborhood (e.g., Pacala 1986*a*, *b*, Tilman 1990, 1994). Theory that incorporates this predicts that no single species or combination of species can completely occupy a spatial habitat (Tilman 1994), i.e., habitats should contain sites empty because of dispersal limitation. The results reported here demonstrate that native undisturbed grasslands contain many open sites that are invasible without causing detectable displacement of existing species, as theory predicts (Tilman 1994). If there are interspecific trade-offs between dispersal and competitive ability (e.g., Werner and Platt 1976, Platt and Weis 1977, Tilman 1990), this theory also predicts the stable coexistence of a large number of species in a homogeneous habitat (Tilman 1994). Spatially explicit versions of such theory predict that each species should occur in only a patchy subset of the sites in which it can persist (Durrett and Levin 1994*a*, *b*). This patchy distribution would limit local diversity because each species would have regions from which it was absent.

Recruitment limitation is consistent with both the metapopulation and regional perspectives. However, the results reported here suggest that interactions within sites may be important controls of invasibility and diversity. Specifically, the greater the initial plant species richness of a site, the more difficult it was for new species to invade. Furthermore, establishment differed among plant functional groups, with legumes being the best invaders in this nitrogen-limited system, perhaps because of their ability to fix N_2 or their larger seed size (Table 1). This suggests that plants that became established had to have appropriate traits relative to local conditions and to the traits of the species present in the plots. Thus, those species that became established following seed addition were a biased subset of the species added, and the number of such species that became established was influenced, in part, by the number of plant species present in the plots. This effect of interspecific interactions on species richness and com-

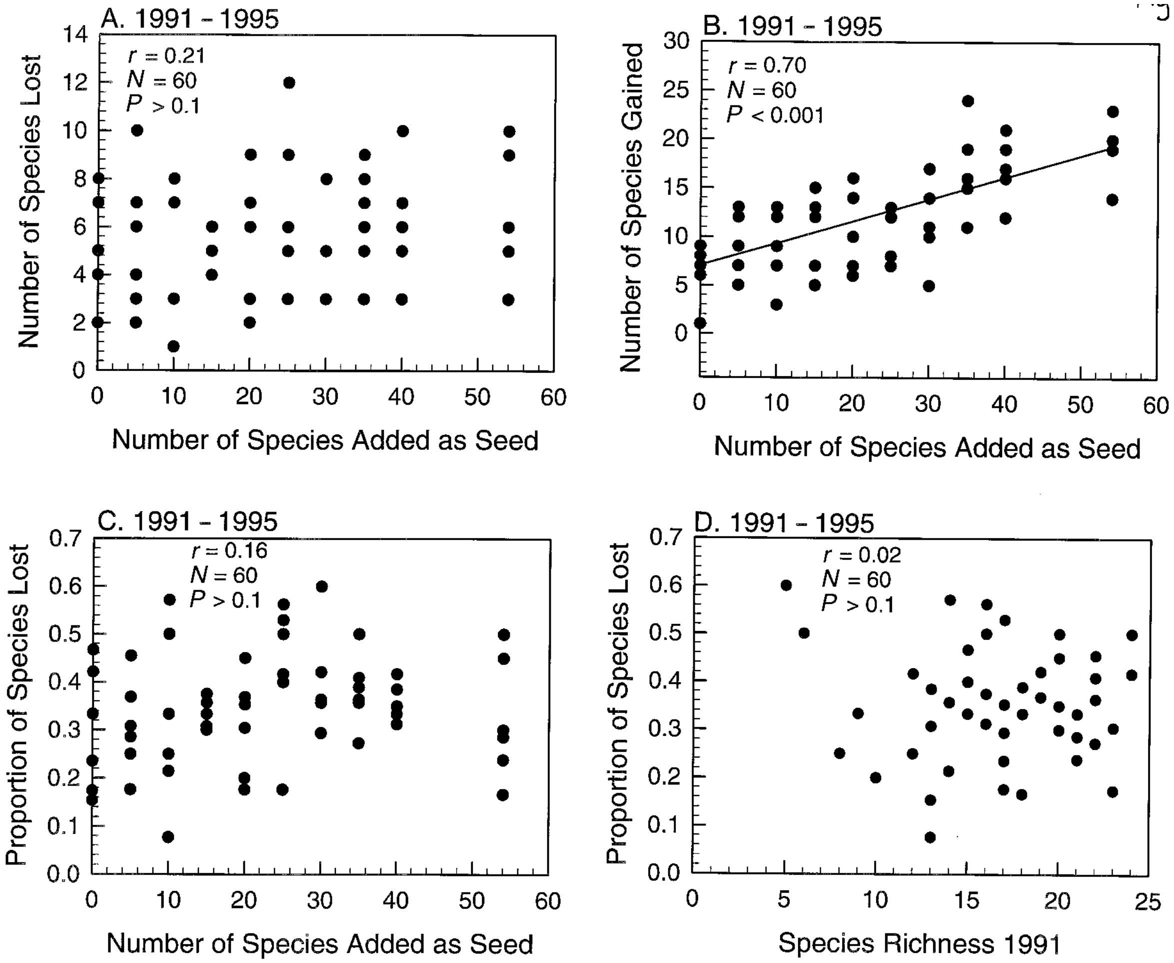

FIG. 4. Effects of the number of species added as seed in spring 1991 on (A) the number of plant species lost from 1991 to 1995 (i.e., the number of species that had been present in 1991 but were absent from that plot in 1995), (B) the number of new plant species gained in each plot, and (C) the proportion of 1991 plant species that were absent in 1995. (D) shows the relationship between the 1991 plant species richness of each plot and the proportion of plant species present in 1991 that were absent in 1995.

position is also illustrated by the dependence of invasibility on the species richness of some, but not all, functional groups. In total these results support a metapopulation-like perspective (i.e., importance of local interactions and local dispersal) over the simple species interaction perspective or the simple regional perspective. However, species richness and other plot variables were not under direct experimental control in this study, and other unmeasured but related variables may be the actual causes of the observed patterns.

The results are somewhat contradictory because invasibility was a linearly increasing function of the number of species added as seed. The increase in species richness and total plant cover caused by seed addition did not detectably limit the total species richness of the plots, i.e., species richness remained a linear function of the number of species added throughout the full range of seed addition. It may be that four growing seasons is too short a time for the increased cover of new species to cause decreased cover or local extinction of either pre-existing or added species. Alternatively it may be that local species richness can be sustained at almost double its normal level once recruitment limitation is overcome.

In studying invasion by California poppy into a winter annual grassland, Robinson et al. (1995) found that the poppy was a better invader of species-rich plots, which had higher abundances of the grass *Bromus diandrus.* Invasion success was also increased by small-mammal soil disturbances and inhibited by increased dominance of plots by a single species. In my study of invasion abilities of 54 species, invasibility was lower in plots with greater plant species richness, and independent of bare mineral soil, soil disturbance by small mammals, plot dominance by a single species, total plant cover, and seed size. However, seed size may be a more important trait for plants invading fertile soils in which seedlings must penetrate dense litter and grow up through a steep light gradient (e.g., Grime and Jeffrey 1964). Moreover, my experiment had little power to detect effects of soil disturbance. It did have power to detect effects of bare mineral soil, but found none. These unproductive grasslands are dominated by bunchgrasses, each of which is often surrounded by a ring of soil, which, though bare above ground, often has a high density of bunchgrass roots (Tilman 1989). Thus, bare mineral soil need not be indicative of an open site, but can be fully occupied belowground.

Robinson et al.'s (1995) unexpected relationship between species richness and invasibility may reflect the unique attributes of *Bromus* relative to the poppy, and the correlation between *Bromus* abundance and species richness. In contrast, by determining the responses of 54 species, the study reported here should describe a more general relationship between species richness and invasibility, though this could be better determined with direct experimental control of plant diversity. The observed relationship supports the long-standing expectation that species-poor communities should be more invasible (e.g., Elton 1958, MacArthur and Wilson 1967, Diamond and Case 1986). This is also consistent with the frequent observation that islands, which are species poor, are more readily invaded than mainland habitats (e.g., Elton 1958, Mooney and Drake 1986).

It has been hypothesized that greater species diversity would lead to more complete use of limiting resources and that the resulting lower availabilities of limiting resources would decrease invasibility by novel species (e.g., Darwin 1859, McNaughton 1993, Robinson et al. 1995). A study at Cedar Creek has found that higher plant diversity led to greater plant cover and to lower concentrations of extractable soil nitrogen both in plots where diversity was experimentally controlled, and in 1991 in the 120 plots used for the experiment reported here (Tilman et al. 1996). Although the seed addition experiment showed that more diverse plots were less readily invaded, this was not explained by the effects of diversity on extractable soil nitrogen. Rather, contrary to expectations, multiple regression showed that more nitrogen-rich plots were less readily invaded, for which I can offer no explanation. Further work is needed to determine the mechanisms whereby diversity may influence invasibility.

Although this study provides strong evidence for recruitment limitation, it does not define the life history stage or stages at which limitation occurs. The 10-fold or greater increases in seedling density following seed addition demonstrate that there are many sites in which species can successfully germinate and grow, suggesting that the major limiting stages are seed production, dispersal, and/or pregermination survival. Other studies have shown a strong interspecific trade-off between local competitive ability and seed production at Cedar Creek (Tilman and Wedin 1991*a,b*, Tilman 1990, 1994), and there is a trade-off between seed dispersal distance and seed size (e.g., Werner and Platt 1976). Seed at our site suffer mortality from insect larvae and fungi between the time of production and germination (K. Kitajima and D. Tilman, *personal observations*). Seed may be consumed by arthropods, birds, mammals, or fire. We do not know the relative importance of such factors. However, at least an order of magnitude more seedlings can become established than actually do, and some survive to be flowering adults.

Other studies have shown strong neighborhood competition in plant communities (e.g., Goldberg 1987*a,b*, Pacala and Silander 1990, Wilson and Tilman 1991). The results reported here do not diminish the importance of such processes. However, they suggest that an understanding of species composition, abundance, and diversity requires a synthesis of both the processes controlling local interactions and the processes controlling dispersal among local sites. These processes are abstracted by metapopulation-like models (e.g., Skellam 1951, Levins and Culver 1971, Horn and MacArthur 1972, Levin and Paine 1974, Hastings 1980, Hanski 1983, Tilman 1994), but such models may yield greater insights when calibrated to include the processes controlling local interactions and dispersal, and the trade-offs among these.

In total, these results demonstrate that plant species abundances and species richness are limited both by recruitment and by local biotic interactions in native grasslands. Because both local biotic interactions and regional processes interact to determine community composition, diversity, and species abundances, we must take a synthetic approach that includes both if we are to better understand community dynamics and diversity.

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