COMMUNITY ECOLOGY

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Niche differences in phenology and rooting depth promote coexistence with a dominant C$_4$ bunchgrass

Abstract Spatial and temporal niche differentiation are potential mechanisms of plant species' coexistence in many communities, including many grasslands. In a 6-year field experiment, a dominant prairie bunchgrass, *Schizachyrium scoparium*, excluded species sharing similar phenology and rooting depth, but coexisted with species differing in phenology and rooting depth. We used a series of experimental plots that differed in *S. scoparium* abundance to measure the effect of *S. scoparium* on abundances of other species and on soil nitrate concentrations across time and depth. Because we found that *S. scoparium* most strongly reduced soil nitrate levels at mid-season and at shallow depths, we hypothesized that at higher *S. scoparium* abundance, species with mid-season phenology and shallow roots would be excluded and that deep-rooted and early season species would be more likely to persist. As predicted, the proportional number and cover of species exploiting different niches than *S. scoparium* (early season and deep-rooted species) increased across the *S. scoparium* abundance gradient. This work provides novel empirical evidence for the factors that contribute to species coexistence in the field. Our study suggests that spatial and temporal niche differentiation promote species coexistence in these grasslands.

Keywords Resource competition · Invasion · Nitrogen · Nitrate · Spatiotemporal

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Introduction

Classical resource competition theory predicts that only as many species can coexist as there are limiting resources (Armstrong and McGehee 1980). Most plant communities violate this prediction. In the grasslands of Cedar Creek Natural History Area, for instance, nitrogen (N) is the major limiting nutrient (Tilman 1990), yet over 60 prairie species naturally co-occur in a typical old field (Inouye et al. 1987). The C$_4$ bunchgrass *Schizachyrium scoparium* is a dominant competitor in this system, competitively displacing other species in one-on-one competition experiments (Wedin and Tilman 1993). How, then, do so many species coexist with dominant N competitors such as *S. scoparium* in this strongly N-limited environment?

Many mechanisms have been proposed to explain how species coexist (e.g., Tilman 1988; Chesson 2000; Wright 2002). A feature common to all of these proposed mechanisms (with the exception of neutral models; Hubbell 2001; Bell 2001) is that individuals compete most strongly with individuals that are more similar to themselves, which causes intraspecific competition to be stronger than interspecific competition, leading to coexistence. This prediction assumes that species are constrained by fundamental tradeoffs, such that a superior competitor at one temperature or for one resource is necessarily a poorer competitor under other conditions or for other resources. Thus, the hypothesis that niche differences promote coexistence via interspecific tradeoffs is fundamental to almost all mechanisms of coexistence.

Two specific mechanisms often hypothesized to promote species coexistence are differences in phenology and rooting depth (Berendse 1979; Chesson 1994; Fargione and Tilman 2002). Numerous studies have documented that species differ in both phenology and rooting depth (Weaver 1958; Bratton 1976; Parrish and Bazzaz 1976; Yeaton et al. 1977; Fitter 1982, 1986; Veresoglou and Fitter 1984; Gibson 1988; McKane et al. 1990;

Mamolos et al. 1995; Jackson et al. 1996; Sun et al. 1997; Mamolos and Veresoglou 2000). At our field site, Cedar Creek Natural History Area, a ^{15}N addition study has documented such differences among six prairie species (McKane et al. 1990). However, few studies have documented the consequences of such variations for species interactions and community structure, and the hypothesis that niche differences promote species coexistence has been difficult to test in the field.

Here, we use a simple experimental approach to test the hypothesis that ''niche differentiation'' promotes coexistence. We created an experimental gradient in the abundance of a long-lived, competitively dominant species (*S. scoparium*) and allowed competitive interactions to proceed for 6 years. We then measured the effects of *S. scoparium* on the number and abundances of coexisting species, allowing us to determine which species were displaced by high abundances of *S. scoparium* and which were able to coexist with it. We classified each species as being either similar to, or niche differentiated from, *S. scoparium* based on its phenology and rooting depth. We chose to look at differences in phenology and rooting depth because *S. scoparium* is a warm-season C_4 grass that often coexists with cool-season species, and because differences in rooting depth have been hypothesized to be an important mechanism of coexistence at our site (McKane et al. 1990) and in other grasslands (Berendse 1979).

We hypothesized that increasing the abundance of a dominant species should reduce the abundance and number of similar species more than it reduces the abundance and number of niche differentiated species. Thus, the proportion of niche differentiated species is predicted to increase with increasing *S. scoparium* abundance. Our response variable, "the proportion of niche differentiated species," is a relative measure allowing us to compare the responses of niche differentiated and similar species and thus directly test our hypothesis. This response variable should not be confused with the absolute number and cover of niche differentiated species, which may be uncorrelated with the relative success of niche differentiated species and cannot be used to test our predictions.

Materials and methods

Seeds of *S. scoparium* were added to 28 plots, each 2×2 m, in a newly abandoned agricultural field in June of 1993 (Cedar Creek Long Term Ecological Research Experiment 115). Treatments were randomized among plots, which were arranged in two rows of 14. The field had been planted with annual rye since 1973 and farmed since 1896, and was disked prior to the seeding of *S. scoparium*. The seed-head material was purchased from Prairie Restorations Inc. (Princeton, MN, USA), and contained about 180 live pure seeds per gram. Seed was added by weight, with eight treatment levels: a control with no seed added and seven levels of seed addition containing approximately 15, 45, 135, 405, 1,215, 3,645, and 10,935 live seeds per m^2. There were three replicates of each seed-addition level, and seven replicates of the control. Once seed was added, no further treatments were imposed. We refer to all non *S. scoparium* species present in the experiment as nonplanted species. Possible seed sources of nonplanted species included both colonization from surrounding habitats and germination from the seed bank. The area adjacent to the experiment remained planted with winter wheat and did not contain *S. scoparium*. The seed bank and seed rain were both likely dominated by agricultural weeds common to early successional old fields.

Percent cover of all plant species in each plot was estimated visually in August 1994. More extensive data were collected in the summer of 1999, after 6 years of natural invasion. Percent cover of all species present was measured nine times during the 1999 growing season (5 May, 27 May, 14 June, 30 June, 15 July, 6 August, 25 August, 18 September, and 15 October) in two permanent 1×0.5-m subplots in each plot. Gopher mounds present at the time of subplot placement were avoided by shifting the subplots the minimal distance required to totally avoid a mound. To increase consistency, all 1999 percent cover estimates were made by one person (J.F.). Percent cover, including bare ground and litter, was estimated so as to sum to 100% for each plot. This provides a good approximation of cover in this low-productivity system with few overlapping leaves, and has the benefit of constraining errors in cover estimation.

The number of nonplanted species for a subplot was defined as the total number of nonplanted species that were ever observed during the growing season. The cover of nonplanted species was defined as the sum of the seasonal maximum cover for each nonplanted species ever observed in a plot. This estimate of nonplanted species cover can result in values greater than 100% if nonplanted species differ in the phenology of their maximum cover. We use the plot-level averages (averaged from values calculated for data from each 1×0.5-m subplot) in all analyses to avoid pseudoreplication.

Soil samples for measurement of extractable nitrate were taken eight times during the 1999 growing season (25 May, 8 June, 22 June, 7 July, 27 July, 20 August, 11 September, and 9 October 1999). Samples, consisting of two pooled 2-cm diameter cores, were taken at two different depths, 0–10 cm and 10–20 cm. From each pooled sample, a 10-g subsample was extracted for nitrate in the field using 0.01 molar KCl (a weak extractant that still fully extracts nitrate), stored in coolers until returned to the lab, shaken for 30 min, and allowed to settle overnight at 4°C. The supernatant was removed the following day, and was frozen until analyzed for nitrate on an Alpkem analyzer, which reduces nitrate to nitrite and then measures

nitrite colorimetrically. To obtain percent moisture, soil subsamples were weighed, dried to a constant weight at 65°C, then re-weighed.

We used soil nitrate concentrations as an index of the efficiency of exploitative plant competition, because plants that are efficient at acquiring nitrate should reduce concentrations of soil nitrate. Soil nitrate concentrations are a better index of exploitative competition than ammonium concentrations, because nitrate concentrations are relatively more sensitive to plant uptake (Tinker and Nye 2002, Tilman 1989) and relatively less sensitive to changes in soil exchange capacity (Tinker and Nye 2002). Thus, variations in ammonium concentration are more likely to be confounded by covariation with factors unrelated to the strength of exploitative plant competition. The possible importance of uptake of organic forms of N in this sandy, low organic matter soil is untested.

The 26 nonplanted species that occurred in the experiment were classified as having either shallow or deep roots, and as having either early or mid-season phenology (see Appendix table). These species included annuals, winter annuals, biennials, and perennials (Appendix table). The maximum rooting depth of nonplanted species in the experiment was measured by excavating three mature flowering individuals of each species from adjacent areas in the summer of 2000. We classified species as shallow rooted if their median observed rooting depth was less than 14 cm. Species with median rooting depth values greater than 14 cm were classified as deep rooted, which resulted in an approximately even split of nonplanted species into shallow- and deep-rooted categories. We selected this cutoff because ''shallow-rooted'' species obtain soil resources almost exclusively from the 0 to 10-cm range used for soil sampling, while ''deep-rooted'' species have the potential to significantly tap into the deeper soil, although we note that our ''deep-rooted'' species are not necessarily deep rooted compared to all grassland species (Sun et al. 1997).

Species were classified as either early-season or mid-season based on observed phenology. Species whose average cover over all plots in July and August was higher than at other, cooler times of the year were classified as warm (mid)-season species and all other species were classified as cool (early)-season species. *S. scoparium* was classified as a mid-season species. We assumed that differences in aboveground phenology were correlated with differences in belowground N uptake (McKane et al. 1990).

To quantify the effect of the *S. scoparium* abundance gradient, we used simple linear regressions with seasonal maximum *S. scoparium* cover as the predictor and report the estimated values of response variables for the two endpoints of this gradient: *S. scoparium* cover equal to zero (i.e., the regression intercept), and *S. scoparium* cover equal to 85.35% (the maximum observed value). Data were analyzed using JMP version 4.0.4 (SAS Institute 2001).

Results

The seed-addition treatment successfully created a gradient of *S. scoparium* abundance. In 1994, the year after sowing, percent cover of *S. scoparium* ranged from an average of 0.36% in control plots to an average of 66% in plots with the highest level of seed addition. In 1999, the year for which all response variables were measured, *S. scoparium* ranged from an average of 30% in the control plots to an average of 80% in the plots with the highest level of seed addition. Because we expect that it is the abundance of *S. scoparium* that influences coexistence, we present analyses with *S. scoparium* cover as a predictor variable rather than the amount of seed added. Analyses based on the amount of seed added yielded qualitatively similar results.

The total cover and species number of nonplanted species decreased significantly with increasing *S. scoparium* cover (Fig. 1a, b). Across the *S. scoparium* gradient, the total cover of nonplanted species decreased from 125% to 20%, while the number of nonplanted species decreased from 12 to 3 per 0.5 m^2.

Because the *S. scoparium* gradient is correlated with other factors, such as cover of nonplanted species, it is appropriate to ask whether changes in nitrate across the *S. scoparium* gradient can be attributed to *S. scoparium* alone. A model including the seasonal maximum of both *S. scoparium* cover ($P < 0.0001$) and nonplanted species cover ($P = 0.86$) showed that only the cover of *S. scoparium* was significantly associated with average soil nitrate. We ascribe observed changes in soil nitrate primarily to differences in *S. scoparium* abundance, as was intended by the design of the experiment. Further, we focus on nitrate because soil moisture increased with *S. scoparium* abundance ($P = 0.003$, $r^2 = 0.29$), so that competition for this resource could not be the mechanism by which *S. scoparium* inhibited other species.

Soil nitrate was negatively correlated with *S. scoparium* abundance, with 60% lower nitrate at the highest *S. scoparium* cover than in the absence of *S. scoparium* (0.23 and 0.57 mg/kg dry soil, respectively). However, the effects of *S. scoparium* on soil nitrate were stronger at shallow depths (Table 1, Fig. 1c) and during mid-season (Table 2, Fig. 1d).

In a multiple regression analysis, nitrate concentrations were significantly affected by the interaction between *S. scoparium* cover and depth (Table 1). *S. scoparium* reduced soil nitrate pools more strongly at shallow (0–10 cm) than at greater (10–20 cm) depths (Fig. 1c). Consequently, low *S. scoparium* abundance plots had more nitrate at shallow depths, whereas high *S. scoparium* abundance plots had more nitrate at deeper depths, with the transition occurring at about 50% cover of *S. scoparium* (Fig. 1c).

The effect of *S. scoparium* on soil nitrate varied significantly over time (Table 2). *Schizachyrium scoparium*
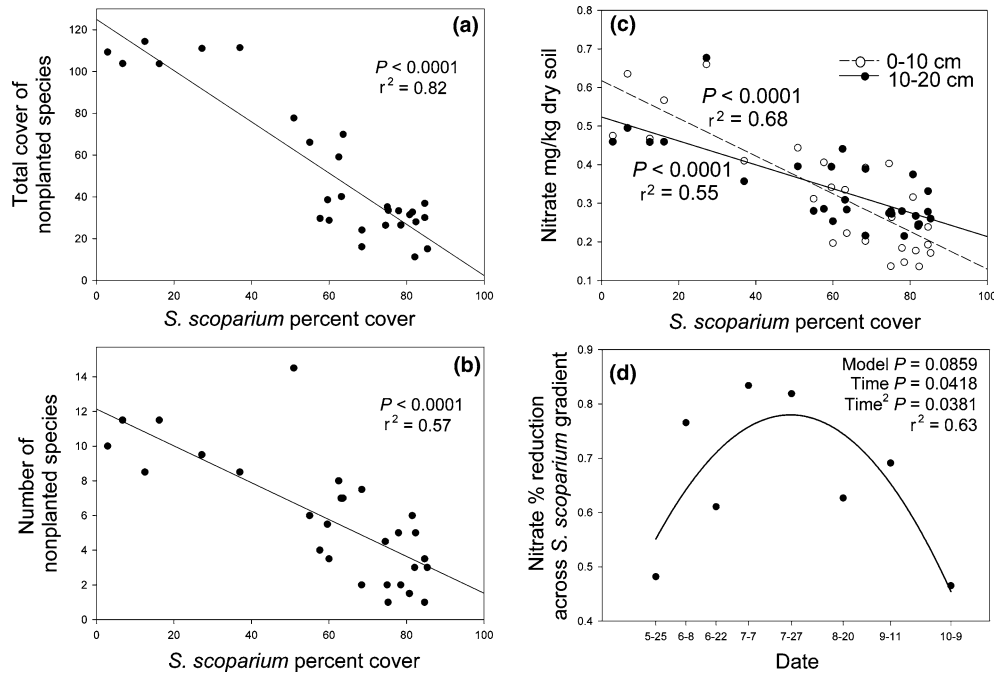
Fig. 1 Effects of *S. scoparium* abundance on nonplanted species and nitrate. **a** The cover of nonplanted species is the sum of the seasonal maximum percent cover of each species other than *S. scoparium* present in a plot. **b** The number of nonplanted species is the number of species other than *S. scoparium* that occurred in a plot over the growing season. **c** Extractable soil nitrate concentrations at different depths across the *S. scoparium* abundance gradient. **d** Effects of *S. scoparium* on soil nitrate concentrations at different times in the growing season. *Data points* show percent reduction across the *S. scoparium* gradient based on simple regressions of nitrate on *S. scoparium* for each of the eight sample dates. Percent reduction is calculated by comparing fitted soil nitrate values from the endpoints of the *S. scoparium* cover gradient (0% and 83.25%)

Table 1 ANOVA on the effects of *S. scoparium* cover and soil depth on soil nitrate concentrations

	df	F	P
S. scoparium cover	1	86.3	< 0.0001
Soil depth	1	0.35	0.558
S. scoparium cover × soil depth	1	4.34	0.042

Effects of *S. scoparium* were not constant over depth as evidenced by the significant interaction term

Table 2 Repeated measures of the effects of *S. scoparium* cover on soil nitrate concentrations (0–20 cm)

	Num df	Den df	F	P
S. scoparium cover	1	25	51.5	< 0.0001
Time	4.37	109.3	9.3	< 0.0001
S. scoparium cover × time	4.37	109.3	2.5	0.0386

Effects of the seasonal maximum *S. scoparium* cover were not constant over time as evidenced by the significant *S. scoparium* cover × time interaction term

reduced soil nitrate pools during the mid-season more strongly than during either the early or late season (Fig. 1d). Soil nitrate decreased by only 47–48% across the *S. scoparium* gradient at the beginning and end of the

season, but decreased by 83% in mid-season (Fig. 1d). A nonlinear regression analysis suggests that the effect of *S. scoparium* on shallow nitrate peaked near the end of July (Fig. 1d).

Both the species number and total percent cover of nonplanted species were positively correlated with the seasonal average nitrate levels at 0–10 cm (Fig. 2a, b). Cover of nonplanted species decreased from about 110% to 20% and species number decreased from 11 to 2 per 0.5 m², comparing the highest and lowest observed nitrate values (Fig. 2a, b).

Niche differentiation

Because *S. scoparium* more strongly reduced nitrate concentrations during the mid-season and at shallow depths, we hypothesized that species with early season phenologies and deep roots, "niche-differentiated species", would be favored in *S. scoparium* dominated communities. Conversely, those species with mid-season phenologies and shallow roots should be most strongly inhibited by *S. scoparium*. Thus, the proportion of niche differentiated species should increase as *S. scoparium* abundance increases. This prediction applies to both early season and deep-rooted species, and to both species number and cover.

Fig. 2 Nonplanted species success versus nitrate availability. See Fig. 1 for description of response variables. **a** Cover of nonplanted species. **b** Number of nonplanted species
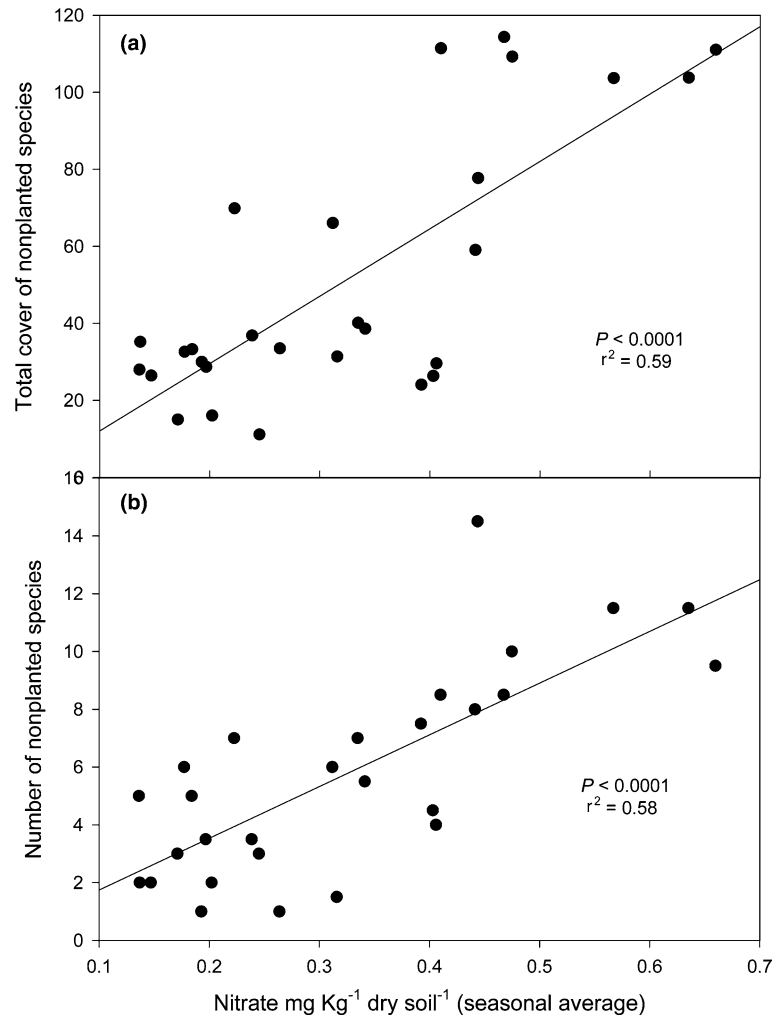
Niche differentiated species were favored as *S. scoparium* abundance increased (Fig. 3a–f), significantly increasing both their proportional cover and their proportional species number with increasing *S. scoparium* abundance. This was true for the proportion of early season species regardless of rooting depth, the proportion of deep-rooted species regardless of phenology, and the proportion of species that are both deep rooted and early season. Commensurate with these increases, there was a decrease in the proportional cover and species number of mid-season and shallow-rooted species (not shown). This is unavoidable because the shallow and deep rooted proportions sum to one and the early and late season proportions sum to one. We note that, in absolute terms, the cover and number of species in each phenology and rooting depth category decreased across the *S. scoparium* abundance gradient ($P < 0.0002$ for all eight regressions), but we emphasize that it is the proportion of cover and the proportion of the number of species that are the relevant measures for testing hypotheses about the importance of niche differentiation.

Discussion

An increase in the abundance of *S. scoparium* strongly reduced the number and cover of other species. This is consistent with *S. scoparium* being a competitive dominant, as found in previous competition experiments (Wedin and Tilman 1993) and suggested by its high abundance in late successional communities (Curtis 1959; Tilman 1988). However, the reduction of other species' number and cover was not random, but was instead biased towards species similar to *S. scoparium*, with shallow roots and mid-season phenology.

Our results show that species are much more likely to coexist with *S. scoparium* if they have early season growth or deep roots. As predicted, the proportions of species number and cover that were niche differentiated with regard to *S. scoparium* increased across the *S. scoparium* gradient (Fig. 3a–f). Specifically, the proportion of deep-rooted species, the proportion of early season species, and the proportion of species that are both deep rooted and early season increased across the
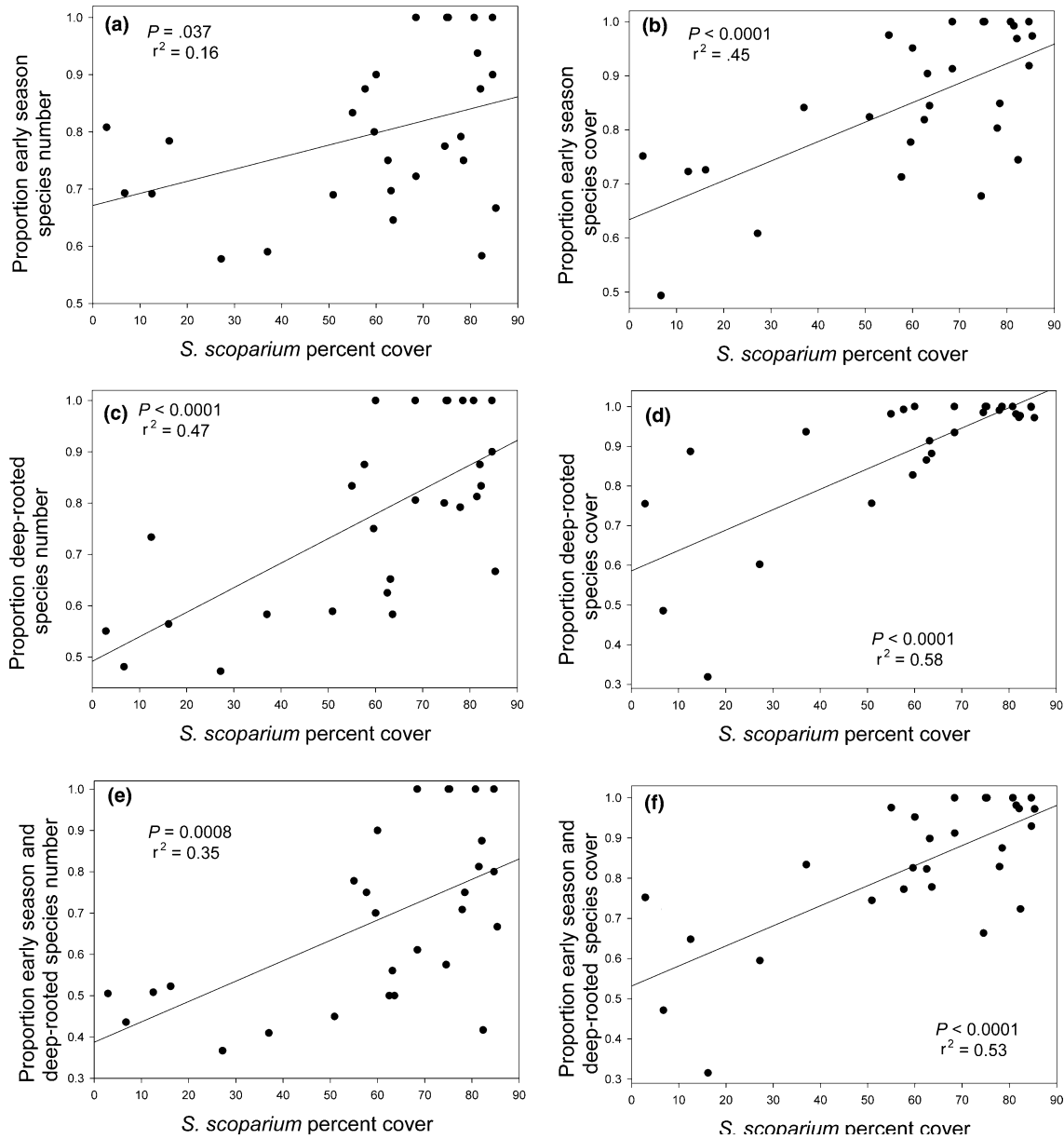
Fig. 3 Relative success of niche differentiated species increases across *S. scoparium* gradient. **a** Proportion early season species number is calculated for each plot as (number of early season species)/(total number of nonplanted species). **b** Proportion early season species cover is calculated for each plot as (cover of early season species)/(cover of all nonplanted species). **c** Proportion deep-rooted species number is calculated for each plot as (number of deep-rooted species)/(total number of nonplanted species). **d** Proportion deep-rooted species cover is calculated for each plot as (cover of deep-rooted species)/(cover of all nonplanted species). Arcsin transformations of proportion deep cover to improve non-constant variance yield similar results ($P < 0.0001$, $r^2 = 0.62$). **e** Proportion early season and deep-rooted species number is calculated for each plot as (number of early season and deep-rooted species)/(total number of nonplanted species). **f** Proportion early season and deep-rooted species cover is calculated for each plot as (cover of early season and deep-rooted species)/(cover of all nonplanted species)

S. scoparium gradient. The use of proportions controls for variation in total species number and cover and allows a direct test of the hypothesis that at higher *S. scoparium* abundances species that differ from *S. scoparium* perform relatively better than those similar to *S. scoparium*.

Our study suggests a general approach for making testable predictions about the traits of coexisting species by measuring the effect of a dominant competitor on patterns of resource availability. The correlations in our study suggest that there is strong N competition, and that the influence of *S. scoparium* on seasonal and vertical patterns of N availability strongly influences the abundance and composition of other species in the community. Specifically, as *S. scoparium* abundance increased, soil nitrate, nonplanted species number, and nonplanted species cover all decreased significantly (Fig. 1). Although these correlations do not prove cau-

sation, our interpretation of these data is consistent with previous studies at Cedar Creek demonstrating that N limits productivity, but other nutrients such as phosphorus do not (Tilman 1990) and that there is no significant competition for light (Wilson and Tilman 1993). In addition, species, including *S. scoparium*, that reduce soil nitrate concentrations dominate in competition experiments (Wedin and Tilman 1993). *Schizachyrium scoparium* has been shown to have high root:shoot biomass ratio and to maintain high root biomass in monoculture (Tilman and Wedin 1991), which presumably leads to high N uptake and is likely the primary mechanism by which *S. scoparium* reduces soil nitrate concentrations (Tilman 1989; Tilman and Wedin 1991), although other explanations such as indirect feedbacks on microbial processes via litter or soil moisture are possible (Wedin and Tilman 1990).

Schizachyrium scoparium most strongly reduced soil nitrate at shallow depths (Table 1, Fig. 1c) and during the mid-season (Table 2, Fig. 1d). We conclude that *S. scoparium* has its strongest effect on nitrate levels at mid-season based on multiple lines of evidence. First, the hypothesis of constant effect over time has been rejected ($P = 0.023$; Table 1). Second, the quadratic term in this model is a significant improvement over the linear model ($P = 0.04$), although the entire model is itself marginally nonsignificant ($P = 0.086$). However, the lack of significance may be attributable in part to the lack of power in this model, which has three fitted parameters and only eight observations. Finally, this interpretation is consistent with the mid-season phenology of *S. scoparium*.

We suggest that seasonal and rooting depth differences may be important mechanisms of coexistence in other systems when (1) there is strong belowground resource competition, (2) plants differ in their patterns of resource uptake over time and across depth. These conditions appear common. Competition has been widely documented in plant communities (Schoener 1983; Goldberg and Barton 1992; Aarssen and Epp 1990). Species in a variety of habitats have been shown to differ widely in their phenology, vertical distribution of roots, and vertical patterns of resource uptake (Bratton 1976; Parrish and Bazzaz 1976; Yeaton et al. 1977; Fitter 1982, 1986; Veresoglou and Fitter 1984; Gibson 1988; McKane et al. 1990; Mamolos et al. 1995; Jackson et al. 1996; Sun et al. 1997; Mamolos and Veresoglou 2000).

Few studies have documented the community-level consequences of these interspecific differences in phenology and rooting depth. In one study McKane et al. (1990) documented the partitioning of ^{15}N uptake by six common prairie species across the growing season and rooting depth. The three most abundant species showed distinct temporal and spatial patterns of resource acquisition. The authors suggested that species differing in their resource uptake patterns experienced reduced competition when interacting with each other, contributing to their high abundances and coexistence. In a ^{15}N addition study in tundra vegetation, McKane et al. (2002) showed that species with N-uptake patterns that mirrored N-availability patterns had higher relative abundance. Our work and these studies suggest that interspecific differences in phenology and rooting depth may play an important role in structuring plant communities.

Conclusion

Our study suggests that *S. scoparium*, via its effect on N availability, preferentially excluded competing species with similar phenology and rooting depth, thus favoring niche differentiated species. Because this dominant competitor primarily reduced available soil nitrate at shallow depths and during mid-season, other species may coexist with it based on their ability to access deeper soil resources or to grow earlier or later in the season. Such niche differentiation may help explain how species coexist in this seasonal, N-limited system.

Appendix

The appendix lists species found in the study and their phenology and rooting depth classification. B/P indicates species that exhibit both biennial and perennial life history at Cedar Creek Natural History Area. W. Annual indicates winter annual species, which germinate in the fall, overwinter as seedlings, and in the summer produce seed that germinates during the same growing season.

Species	Phenology	Rooting depth	Photo-synthetic pathway	Number of plots present	Life history
Agropyron repens	Early	Deep	C3	28	Perennial
Berteroa incana	Early	Deep	C3	12	B/P
Lychnis alba	Early	Deep	C3	16	B/P
Poa pratensis	Early	Deep	C3	14	Perennial
Polygonum convolvulus	Early	Deep	C3	16	Annual
Rudbeckia serotina	Early	Deep	C3	4	B/P
Vicia villosa	Early	Deep	C3	21	W. annual
Agrostis alba	Early	Shallow	C3	4	Perennial
Agrostis scabra	Early	Shallow	C3	2	Perennial
Crepis tectorum	Early	Shallow	C3	2	Biennial
Hedeoma hispida	Early	Shallow	C3	14	Annual
Lepidium densiflorum	Early	Shallow	C3	8	W. annual
Oxalis stricta	Early	Shallow	C3	2	Perennial
Rumex acetosella	Early	Shallow	C3	3	Perennial
Silene antirrhina	Early	Shallow	C3	4	Annual
Andropogon gerardi	Mid	Deep	C4	4	Perennial
Asclepias syriaca	Mid	Deep	C3	3	Perennial
Erigeron canadensis	Mid	Deep	C3	4	W. annual
Monarda fistulosa	Mid	Deep	C3	11	Perennial
Panicum oligosanthes	Mid	Deep	C4	2	Perennial
Petalostemum candidum	Mid	Deep	C3	1	Perennial
Sorghastrum nutans	Mid	Deep	C4	1	Perennial
Verbascum thapsus	Mid	Deep	C3	3	Biennial
Ambrosia artemisiifolia	Mid	Shallow	C3	14	Annual
Digitaria ischaemum	Mid	Shallow	C4	13	Annual
Setaria lutescens (glauca)	Mid	Shallow	C4	10	Annual

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