

Differential effects of two dominant plant species on community structure and invasibility in an old-field ecosystem

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Abstract

Aims

In this study, we examined the effects of *Solidago altissima* (hereafter *Solidago*) and two species in the genus *Verbesina*, *Verbesina virginica* and *Verbesina occidentalis* (hereafter *Verbesina*), on the structure of an old-field plant community and establishment by an invasive plant species, *Lespedeza cuneata* (hereafter *Lespedeza*).

Methods

We removed *Solidago*, *Verbesina* and both *Solidago* and *Verbesina* from 4-m² plots in an intact old-field community during two growing seasons. We then quantified the effects of these removals on richness, evenness, diversity and composition of the subdominant plant community. We also measured the total aboveground biomass and the aboveground biomass of the subdominant community. To assess how these removals affected establishment by *Lespedeza*, we planted 20 seeds in each plot and tracked seedling emergence and survival for one growing season.

Important Findings

Subdominant community evenness and Shannon diversity were higher in plots from which *Solidago* and *Verbesina* were removed

relative to control plots. However, there were no effects of dominant species removal on species richness or composition of the subdominant community. Total aboveground biomass was not affected by dominant species removal, suggesting that the community of subdominant species exhibited compensation. In fact, subdominant community biomass was greater when *Solidago*, but not *Verbesina*, was removed. Light availability was also greater in plots where *Solidago* was removed relative to control plots throughout the growing season. In addition, removal of dominant species, in particular *Solidago*, indirectly reduced the emergence, but not survival, of *Lespedeza* seedlings by directly promoting subdominant community biomass. Taken together, our results suggest that dominant old-field plant species affect subdominant community structure and indirectly promote establishment by *Lespedeza*.

Keywords: compensation • establishment • invasive
• *Lespedeza cuneata* • *Solidago* • *Verbesina*

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INTRODUCTION

Dominant species are those that comprise the greatest proportion of the production and/or resource uptake in local plant communities, thereby playing an important role in driving community dynamics and regulating ecosystem processes (Bazzaz 1996; Chapin *et al.* 2000; Dangles and Malmqvist 2004; Grime 2001; Goldberg and Barton 1992; Hector *et al.* 1999; Hooper 1998; Hooper and Vitousek 1997; Hooper *et al.* 2005; McNaughton and Wolf 1970; May 1978; Wardle

et al. 1999; Whittaker 1972). When dominant species alter the structure of the subdominant community and affect ecosystem processes, they may also influence community invasibility (Bazzaz 1996; Hobbs and Huennekke 1992; Huston and Smith 1987; Meiners *et al.* 2002). For instance, there is some evidence that dominant plant species can hinder plant invasions in grasslands and old-field communities via resource competition for limiting nutrients and/or space (Crawley *et al.* 1999; Dukes 2002; Emery and Gross 2006, 2007; Smith *et al.* 1999; Dukes 2002; Emery and Gross 2006, 2007; Smith *et al.* 2004; Wilsey and Polley 2002).

Of course, not all dominant species are equal and have equivalent effects on the rest of the community. That is, dominant species identity affects community structure and invasibility in a variety of ways. For example, Emery and Gross (2006) found that the effect of dominant species on invasibility varied among dominant species, with some dominant species having positive effects on the establishment by exotic species and others having negative effects. In their study, old-field communities that were dominated by exotic species, such as *Bromus inermis* and *Centaurea maculosa*, exhibited high susceptibility to invasion by native and nonnative seedlings, whereas communities dominated by the native species *Andropogon virginicus* had high resistance to invasion. Whether dominant plant species differentially affect structure of the subdominant community and invasibility in other systems remains an open question.

In this study, we examined whether the removal of dominant plant species in an old-field community affects community structure, ecosystem processes and invasion by a nonnative species. We removed the dominant forb species *Solidago altissima* (hereafter *Solidago*) and two species in the genus *Verbesina* (*Verbesina occidentalis* and *Verbesina virginica*, hereafter *Verbesina*), which together comprise almost half of the aboveground biomass in these old fields. We did not differentiate between *Verbesina* species in the field as they have similar life history traits and morphologies. In fact, both *Verbesina* species are perennial and have similar phenologies and occur at similar abundances across local old-field communities (Souza and Bunn, unpublished data). Specifically, we made four predictions. First, the removal of dominant plant species would increase richness, evenness and Shannon diversity and alter the composition of the community of subdominant species via release from competitive effects resulting in greater resource availability. Second, the removal of dominant plant species would alter light and soil nitrogen availability shaping compensatory responses of the subdominant species. Third, the removal of dominant species would increase resource availability and therefore promote the emergence and survivorship of the exotic species *Lespedeza*, a Rank 1 invasive species via increases of resource availability or hinder emergence and survivorship of *Lespedeza* given strong compensatory responses of the subdominant community. Fourth, the effects of species removal would depend on the identity of the dominant species given that dominant species can vary in their resource use and effects on other species.

MATERIALS AND METHODS

Study site

In spring 2005, we initiated an experiment in an old field at Oak Ridge National Environmental Research Park, near Oak Ridge, TN (35° 58'N 84° 17'W). The old-field site was used for agriculture until 1943 and is mowed each spring. The soil has a silty clay loam texture and is classified as Typic Hapludult.

Mean annual rainfall is 1322 mm and mean air temperature ranges from 2.7°C (January) to 31.2°C (July).

Solidago and *Verbesina*, which together comprise ~40% of total aboveground biomass, are the dominant species at this site and across old fields in the area. *Solidago* is an abundant and widespread species in old fields in the USA (Semple and Cook 2006). *Solidago* makes up, on average, 20% (range = 5–47%) of the aboveground biomass in old-field communities near our study site (Souza and Bunn, unpublished data). Additionally, previous work near our site has shown that *Solidago* can influence ecosystem processes such as productivity (Crutsinger *et al.* 2006) and the structure of associated arthropod communities (Crawford *et al.* 2007; Crutsinger *et al.* 2006, 2008). *Verbesina* makes up, on average, 18% (range = 0–73%) of the aboveground biomass in old-field communities near our study site (Souza and Bunn, unpublished data). However, little is known about the effects of *Verbesina* on communities and ecosystems, though it is a common genus in the eastern USA (Chappelka *et al.* 2003). In addition, ~60 subordinate herbaceous and woody native and introduced plant species, including *Lespedeza*, occur at the study site and make up the remainder of the total aboveground biomass (Souza and Bunn, unpublished data).

Experimental manipulation

Beginning in spring 2005, we manipulated the presence of *Solidago* and *Verbesina* in twenty-four 2 × 2-m plots in an existing old-field community. The plots were spaced 1 m from each other in a completely randomized plot design. The experiment was a 2 × 2 factorial design: *Solidago* (present or removed) and *Verbesina* (present or removed). We clipped the dominant species (to 1 cm from the ground) throughout the growing season (April–October), but during the peak of the growing season (July and August), target species were clipped as necessary at least every week.

On average, control plots (those from which neither *Solidago* nor *Verbesina* were removed) consisted of 156 g m⁻² of *Solidago* and 125 g m⁻² of *Verbesina*. *Solidago* made up, on average, 30% of the total biomass of control plots and *Verbesina* made up, on average, 20% of the total biomass of control plots. The removal of one codominant species did not affect the biomass or cover of the other ($P \geq 0.10$ in all cases).

Community- and ecosystem-level responses

In each of the plots, we tallied plant species richness (S) and foliar cover of each plant species present at the beginning of the experiment (June 2005) and then at the peak of the growing season in August 2006, 1 year after the initiation of the experiment (see Supplementary table S1 for species-specific foliar cover across removal treatments). We estimated species-specific foliar cover using a modified Braun-Blanquet cover class scale (Braun-Blanquet 1932). The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75% and 6 = 75–100%. We also quantified the responses of different functional groups

(forbs, graminoids, nitrogen fixers, woody species) to the removal of dominant species (see Supplementary table S2 for average foliar cover of plant functional groups across removal treatments) by summing up the total foliar cover across individuals that belonged to each functional group. We calculated the Shannon diversity index (H') from foliar cover data (August 2006) by using the median of each cover class category as our value of abundance (excluding foliar cover of *Lespedeza*, *Verbesina* and *Solidago*). We calculated evenness (J') as $H'/\ln(S)$.

In August 2006, we estimated aboveground biomass by clipping to 1 cm aboveground level all plants within a randomly placed 0.5×1 m quadrat within each experimental plot. We categorized each clipped stem into one of the following groups: *Solidago*, *Verbesina*, *Lespedeza* or subdominant species. Clipped biomass was oven-dried at 60°C for approximately 48 h and then weighed.

We measured photosynthetic photon flux density (PPFD, hereafter light availability) monthly from April to August in 2006 in each of the 24 experimental plots, as well as soil nitrogen availability. To estimate light availability, we used a line-integrating ceptometer (Decagon Accupar; Decagon Devices, Pullman, WA) with all light availability measurements made on clear days between 11 am and 2 pm. To assess the availability of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ in the soil solution, we placed mixed-bed ion-exchange resin bags in nylon stockings (H-OH form, #R231-500; Fisher Scientific International Inc., Pittsburgh, PA) at 5-cm soil depth at two locations in each of the 24 experimental plots (Hart et al. 1994). Resins were then air-dried, and 2 g of resins from each plot were extracted with 2 M KCl. Pool sizes of NO_3^- and NH_4^+ were analyzed on a Lachat AE Flow Injection Autoanalyzer (Lachat Quikchem 8000; Hach Corporation, Loveland, OH). All values expressed in this article are based on air-dried resins.

Emergence and survivorship of *Lespedeza* seedlings

In March 2006, we added 20 *Lespedeza* seeds (Ernst Conservation Seeds, Meadville, PA) to each of the 24 plots. Ten seeds were buried 1 mm deep at 7-cm spacing within each of two grids, within each plot, where each grid was located 0.5 m from the northern and southern edges of the plot. The location of each seed was marked with a painted nail so that we could track emergence and survivorship of seedlings over the course of the growing season. We censused emerged seedlings every 2 weeks between May and August 2006 and recorded both the number of seedlings that emerged and, of the seedlings that emerged, the number of seedlings that survived until August. Although seedling emergence and survival are only the first steps in invasion success, several studies support their importance in driving the distribution of species and invasions in grassland systems (Gross and Werner 1982; Foster et al. 2002).

Statistical analyses

To examine the effects of the removal of codominant species on plant community structure and on establishment by

Lespedeza, and to investigate the potential mechanisms underlying those effects, we used a Multivariate Analysis of Variance (MANOVA) model followed by a series of generalized linear models (GLMs). The MANOVA allowed us to test whether there was an overall effect of the treatments on the linear combination of response variables as a whole. In the MANOVA and GLMs, the effects were (i) *Solidago* (at two levels: present or removed) and (ii) *Verbesina* (at two levels: present or removed). The response variables in the MANOVA and GLMs were subdominant species richness, subdominant species evenness, subdominant Shannon diversity, subdominant biomass, total biomass, light and soil N availability and *Lespedeza* seedling emergence and survival. We used Tukey's HSD means separation test ($\alpha = 0.05$) to identify which treatment means differed from one another.

We used GLMs with *Solidago* and *Verbesina* as main factors and used the following covariates: biomass of the subdominant community, species richness, evenness (excluding *Lespedeza*, *Verbesina* and *Solidago*), light availability and the foliar cover of mature *Lespedeza* to test effects on emergence and survival of *Lespedeza*. We built a correlation matrix including covariates to test for significant pairwise correlations ($P < 0.05$). Finally, in the GLMs, we chose a Poisson distribution when analyzing count response variables such as subdominant species richness and *Lespedeza* seedling emergence. For proportion data such as *Lespedeza* seedling survival, we used a binomial distribution, and for the remainder variables, we used a normal distribution.

We used PRIMER (Plymouth Marine Laboratory, UK) to conduct an analysis of similarity (ANOSIM) followed by pairwise comparisons to examine the effects of dominant species on composition of the subdominant community. In the analysis, we created two main grouping factors: *Solidago* (present or removed) and *Verbesina* (present or removed). Based on species-specific foliar cover of each subdominant species, we constructed a nonmetric multidimensional scaling (NMDS) plot, a nonparametric approach, using Bray–Curtis similarity coefficients from a triangular matrix (Bray and Curtis 1957) of euclidean distances of samples within versus among removal treatments. Further, the NMDS plot can illustrate similarity and/or dissimilarity in composition between communities. We excluded one of the plots from all analyses because it contained a fast-growing autumn olive shrub (*Elaeagnus umbellata*) that was unique to that plot and substantially altered overall biomass and structure of that plot.

RESULTS

Community- and ecosystem-level responses

The MANOVA indicated that the removal treatments differed in their effects on community- and ecosystem-level processes (Wilks' $\lambda = 0.163$, degrees of freedom [df] = 7, 13, $F = 9.49$, $P < 0.001$). Because the MANOVA indicated an overall effect of the treatments, we followed the MANOVA with subsequent GLMs.

The removal of the two dominant plant taxa affected some aspects of the structure of the subdominant community. Evenness and Shannon diversity of the subdominant community were both, on average, 20% greater in *Solidago* removal plots than in plots where *Solidago* was present. Likewise, subdominant community evenness and Shannon diversity were, on average, 30% greater in *Verbesina* removal plots than in plots where *Verbesina* was present (Table 1; Fig. 1). However, the removal of dominant taxa did not affect species richness of the subdominant community (Table 1), and the ANOSIM indicated that composition of the subdominant community was also not affected by the removal of either *Solidago* (global $R = -0.084$, $P = 0.84$, Supplementary table S3) or *Verbesina* (global $R = -0.004$, $P = 0.47$, Supplementary table S3).

The responses of individual taxa to the treatments (when both dominant species were removed vs. plots where both dominant species were present) varied dramatically: cover of *Sorghum halepense* was 11× greater in removal plots (5.4%) than in control plots (0.5%); *Lonicera japonica* was 31× greater in removal plots (15.4%) than in control plots (0.5%) and *Elephantopus carolinianus* (5.9% in removal plots), *Rubus flavinanus* (17.1% in removal plots) and *Solidago gigantea* (10.4% in removal plots) were all absent in control plots, but attained relatively high cover values in the removal plots. Yet, there were no main effects of *Solidago* or *Verbesina* removal treatments on the total abundance of exotic species, in terms

Table 1: results for GLMs of effects of dominant species removal on total community biomass, subdominant biomass, subdominant richness, subdominant evenness and subdominant diversity

	df	Chi square	<i>P</i>
Total community biomass			
<i>Solidago</i> removal	1, 19	0.5971	0.4397
<i>Verbesina</i> removal	1, 19	0.2685	0.6043
<i>Solidago</i> × <i>Verbesina</i> removal	1, 19	1.5363	0.2151
Subdominant community biomass			
<i>Solidago</i> removal	1, 19	4.8260	0.0280
<i>Verbesina</i> removal	1, 19	0.0179	0.8935
<i>Solidago</i> × <i>Verbesina</i> removal	1, 19	1.4207	0.2333
Subdominant community diversity			
<i>Solidago</i> removal	1, 19	9.1606	0.0025
<i>Verbesina</i> removal	1, 19	14.6101	0.0001
<i>Solidago</i> × <i>Verbesina</i> removal	1, 19	1.3296	0.2489
Subdominant community evenness			
<i>Solidago</i> removal	1, 19	6.8047	0.0091
<i>Verbesina</i> removal	1, 19	15.701	<0.0001
<i>Solidago</i> × <i>Verbesina</i> removal	1, 19	0.9979	0.3178
Subdominant community richness			
<i>Solidago</i> removal	1, 19	1.6824	0.1946
<i>Verbesina</i> removal	1, 19	0.9592	0.3274
<i>Solidago</i> × <i>Verbesina</i> removal	1, 19	0.4538	0.5005

Significant variables ($P < 0.05$) are in bold.

of foliar cover ($F = 0.61$, $P = 0.44$, and $F = 0.32$, $P = 0.58$, respectively), as well as on the total abundance of native plant species ($F = 1.16$, $P = 0.29$, and $F = 0.41$, $P = 0.53$, respectively). We note that *L. japonica*, *R. flavinanus* and *S. halepense* are all exotic species in East Tennessee. Additionally, the abundance of woody species was 45% greater in *Solidago* removal plots than in plots where *Solidago* was present, whereas the abundance of forb species was 55% lower in *Verbesina* removal plots than in plots where *Verbesina* was present (Supplementary table S2).

Removal of dominant taxa led to compensatory responses by the subdominant species. Biomass of the subdominant community was 49% greater in plots from which *Solidago* was removed than in plots where *Solidago* was present, but did not differ in plots where *Verbesina* was removed compared to plots where *Verbesina* was present (Table 1; Fig. 2). However, there was no effect of dominant species removals on total community biomass (Table 1; Fig. 2), suggesting that subdominant species compensated for the removal of both dominant species. For instance, when both dominant species were present total community biomass was, on average, 544 g m⁻². When both

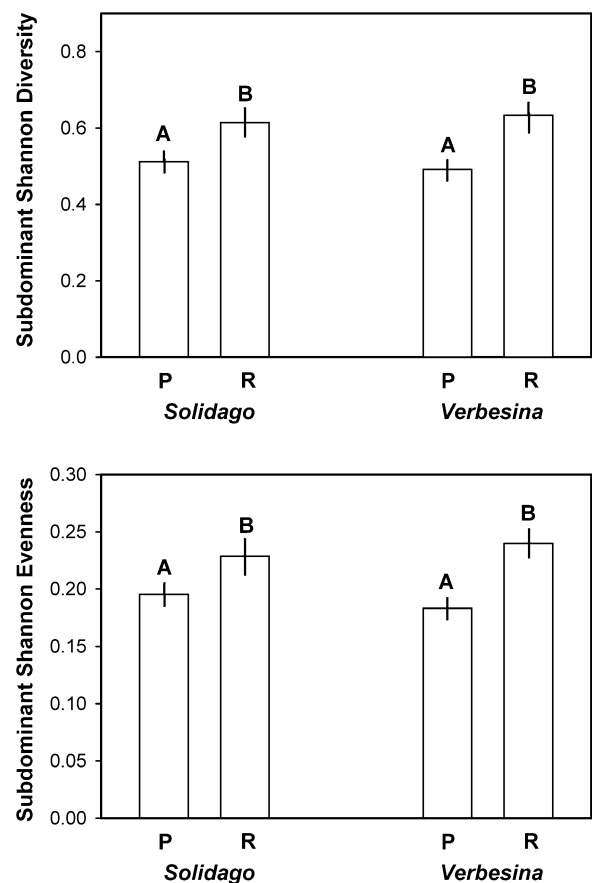


Figure 1: effect of dominant species removal on mean (\pm standard error, $n = 6$) subdominant Shannon diversity (top panel) and subdominant Shannon evenness (bottom panel). Treatments: P = no removal and R = species removal; different letters represent statistical difference at $\alpha = 0.05$ using Tukey's HSD means separation test.

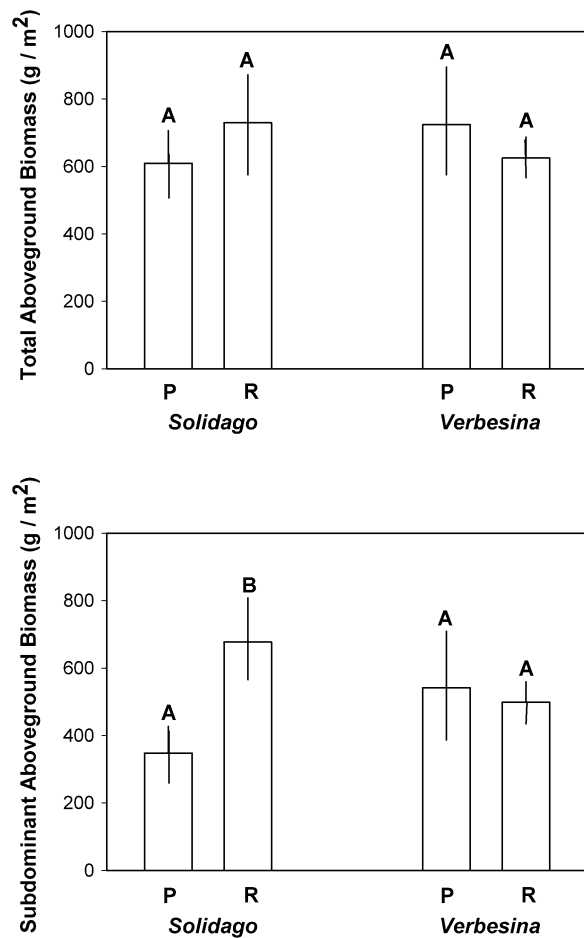


Figure 2: effect of dominant (*Solidago* and *Verbesina*) species removal on mean (\pm standard error, $n = 6$) total aboveground biomass (top panel) and subdominant aboveground biomass (bottom panel). Treatments: P = no removal and R = species removal; different letters represent statistical difference at $\alpha = 0.05$ using Tukey's HSD means separation test.

dominant species were removed, the biomass of the subdominant community was 586 g m^{-2} ($t = 0.20$, $df = 19$, $P = 0.85$).

Light availability (PPFD) was, on average, 35% greater in plots from which *Solidago* was removed when compared to plots where *Solidago* was present throughout the growing season (Table 2). Light availability in *Verbesina* removal plots differed from plots where *Verbesina* was present only during the peak of the growing season (July) (Table 2). *Verbesina* comprised a smaller proportion of the total community biomass (20%) than did *Solidago* (30%). As a result, light availability was greater in *Solidago* removal plots than in *Verbesina* removal plots when compared to plots where *Solidago* and *Verbesina* were present, respectively (because only 20% of the aboveground biomass was removed). Finally, soil nitrogen availability in the form of nitrate was not affected by the *Solidago* ($P = 0.49$) or *Verbesina* ($P = 0.20$) removal compared to plots where *Solidago* and *Verbesina* were present, respectively. Likewise, the removal of *Solidago* ($P = 0.66$) or *Verbesina* ($P = 0.09$) did not

Table 2: summary of GLMs for effects of *Solidago* and *Verbesina* removal treatments (P = dominant species present and R = dominant species removed) by date on light availability in 2006

Month	Treatment	Mean	SE	df	Chi square	P
<i>Solidago</i>						
April	P	685.29	87.1	1, 19	2.722	0.099
April	R	875.98	77.0	1, 19		
May	P	267.35	38.7	1, 19	10.028	0.002
May	R	434.32	38.8	1, 19		
July	P	198.73	46.5	1, 19	10.727	0.001
July	R	437.50	65.7	1, 19		
<i>Verbesina</i>						
April	P	802.30	70.9	1, 19	0.077	0.7809
April	R	768.72	98.0	1, 19		
May	P	309.46	37.2	1, 19	3.539	0.0599
May	R	395.72	49.8	1, 19		
July	P	227.18	49.0	1, 19	7.220	0.0072
July	R	411.42	71.5	1, 19		

SE = standard error. Values are means \pm SE. P -values ≤ 0.05 are in bold.

alter soil ammonium compared to plots where *Solidago* and *Verbesina* were present.

Emergence and survivorship of *Lespedeza* seedlings

Dominant species removal did not directly affect emergence or survival of *Lespedeza* seedlings. However, richness of subdominant species, biomass of the subdominant community and cover of mature *Lespedeza* were important covariates for seedling emergence, but not survival (Table 3). Subdominant community and biomass was negatively related to both emergence (Fig. 3) and marginally negatively related to survival (Fig. 3) of *Lespedeza* seedlings, while mature *Lespedeza* cover was positively related to seedling emergence but not survival. Finally, total community biomass was not related to the emergence of *Lespedeza* seedlings ($P = 0.52$, $F = 0.52$) but was negatively related to *Lespedeza* seedling survival ($P = 0.02$, $F = 6.47$).

DISCUSSION

Dominant species affect subdominant community structure

Both *Solidago* and *Verbesina* affected the structure of the subdominant plant community in this old-field ecosystem. In particular, evenness and Shannon diversity of the subdominant community were higher when either *Solidago* or *Verbesina* were removed relative to control plots where both species were present. The removal of each dominant species led to an increase in equitability of the remaining subdominant species, at least over the course of this experiment. Furthermore, forbs and woody plant species responded to the removal of

Table 3: summary of GLMs for effects of *Solidago* and *Verbesina* and covariates on emergence and survival of *Lespedeza* seedlings

	df	Estimate	Chi Square	P	Model P
Seedling emergence					
<i>Verbesina</i> removal	7, 15	0.0645	0.1523	0.6963	<0.0001
<i>Solidago</i> removal	7, 15	-0.0273	0.0228	0.8799	
Subdominant evenness	7, 15	2.2176	0.4321	0.5109	
Subdominant richness	7, 15	0.0839	4.4623	0.0346	
Subdominant biomass	7, 15	-0.7562	4.945	0.0262	
Light availability	7, 15	-0.0002	0.0583	0.8091	
<i>Lespedeza</i> foliar cover	7, 15	0.224	11.273	0.0008	
Seedling survival					
<i>Verbesina</i> removal	7, 15	0.1539	0.1038	0.7472	0.8887
<i>Solidago</i> removal	7, 15	0.1766	0.1219	0.7269	
Subdominant evenness	7, 15	3.9133	0.1342	0.7141	
Subdominant richness	7, 15	0.0515	0.1854	0.6667	
Subdominant biomass	7, 15	-0.748	0.6827	0.6833	
Light availability	7, 15	0.0008	0.1664	0.4086	
<i>Lespedeza</i> foliar cover	7, 15	0.126	0.4805	0.4882	

P-values ≤ 0.05 are in bold.

dominant species to a greater extent than did grasses and N-fixers, and their responses depended on which dominant species was removed. This indicates that when *Solidago* or *Verbesina* are present, they will suppress woody species (greater resource use overlap) or facilitate forb species perhaps more than they do subdominant species such as grasses and N-fixers (Supplementary table S2). The lack of responses by functionally dissimilar species, grasses and N-fixers to dominant species removal was not surprising, yet the contingency of responses by similar functional groups, woody species and forbs to dominant species removal was indeed an unexpected result.

Though the removal of dominant species affected Shannon diversity and evenness of the subdominant community, subdominant community richness and composition were not affected by either *Solidago* or *Verbesina* removal. These two community metrics, richness and composition, might take longer to respond to the removal of dominant species. If our experiment continued for several years, recruitment by new species might have been higher in the removal plots than in the control plots. Similar to our study, Schmitz (2003) found that subdominant species richness did not differ in plots where *Solidago rugosa* was abundant compared to plots where *Solidago rugosa* was low. Additionally, Munson and Lauenroth (2009) found that dominant species influenced the composition of rare subdominant species but only after 8 years of removal treatments.

Biomass of the subdominant community was affected only by removal of *Solidago*, not removal of *Verbesina*. Competition theory predicts that when a dominant species is removed from a community, the biomass of the rest of the community should increase (Tilman 1987; Whittaker 1965). In our system, the

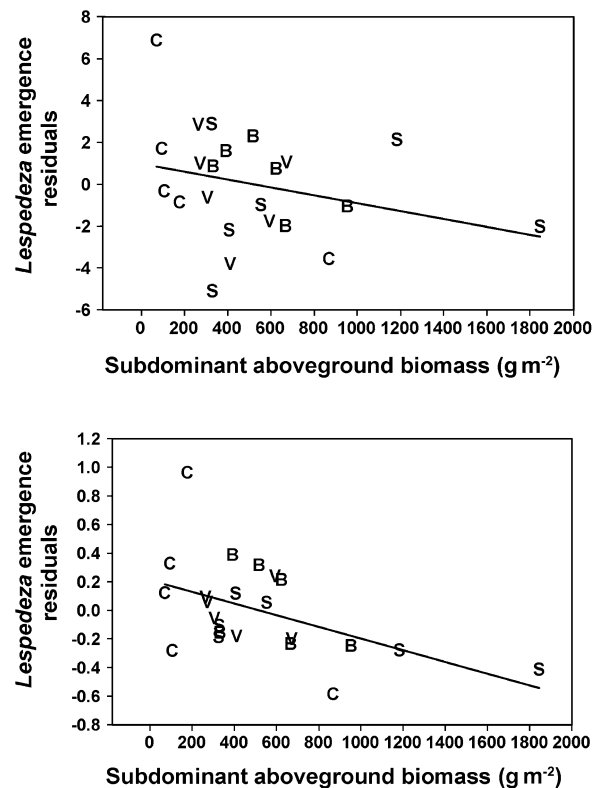


Figure 3: a plot of the residuals of *Lespedeza* emergence (top panel) and survival (bottom panel) from the GLM including the main effects (Control, *Solidago* removal, *Verbesina* removal, *Solidago* and *Verbesina* removal) and the covariates (subdominant richness and evenness and foliar cover of *Lespedeza*) against biomass of the subdominant community. The line is the best-fit linear regression. Symbols: C = control, V = *Verbesina* removed, S = *Solidago* removed and B = *Solidago* and *Verbesina* removed.

compensatory responses of the subdominant community were consistent with such a hypothesis but contingent upon the identity of the dominant species which was removed. In fact, total community biomass did not differ in either *Solidago* or *Verbesina* removals relative to controls, further supporting compensatory responses by subdominant community biomass. Although the biomass of the subdominant community did not show compensatory responses to *Verbesina* removal, we speculate that the lack of differences in total community biomass in *Verbesina* present and *Verbesina* removal plots may be due to the minimal effect of *Verbesina* species in this old-field community.

Other studies have documented similar compensatory responses (Polley *et al.* 2007; Suding *et al.* 2006; Symstad and Tilman 2001; Wardle *et al.* 1999). For instance, Polley *et al.* (2007) found that removing annual species in a prairie ecosystem led to compensatory responses of the subdominant species and consequently total community biomass did not differ between removal plots and controls. Furthermore, Suding *et al.* (2006) found that the removal of one codominant alpine species, *Deschampsia caespitosa*, altered the structure of the

subdominant community (removal increased evenness) and subdominant biomass partitioning. This suggests that the subdominant communities of plants in the tall grass prairies, alpine meadow systems and old fields are able to compensate for species loss.

Solidago indirectly limits *Lespedeza* establishment

Solidago removal led to compensatory responses of the subdominant community, which in turn negatively affected both seedling emergence and survival of *Lespedeza*. Biomass of the subdominant community was higher in *Solidago* removal plots than in plots where *Solidago* was present. In turn, total community biomass was not affected by the removal of either dominant plant species as the subdominant community compensated for dominant species loss. Previous studies (Hector et al. 1999; Hooper 1998; Naeem et al. 1994; Tilman 1996) along with ecological theory (Tilman 2004) have suggested that high-productivity communities have greater resource use complementarity than low productivity communities and are less likely to be invaded than are low productivity communities. We found that biomass of the community of subdominant species was negatively associated with invasibility. This suggests that the suite of subdominant species in this system directly compete, most likely for space rather than light availability (i.e. not statistically significant covariate in GLM model), with potential colonizing species.

Mature *Lespedeza* cover and subdominant richness were positively associated with *Lespedeza* seedling emergence but not survival. *Rhizobium* inoculum can certainly be beneficial for seedling emergence, and plots with greater mature *Lespedeza* foliar cover potentially had higher densities of soil rhizobia than did plots with few mature *Lespedeza* individuals (Acharya et al. 2006). Since *Lespedeza* is a common species in this system, the potential for facilitative effects of adults on seedlings is likely. Finally, subdominant communities with greater richness also promoted *Lespedeza* seedling emergence. This finding may indicate that factors that promote subdominant richness also promote the early establishment by *Lespedeza*.

Of course, *Lespedeza* is only one species among many non-native invasive species in this system. *Lespedeza* is a Rank 1 invasive species across many US states (Eddy and Moore 1998; Hoveland and Donnelly 1985; Sheley et al. 1999) and has been shown to alter native communities (Brandon et al. 2004; Garten et al. 2008; Price and Weltzin 2003). Moreover *Lespedeza* is the most common invasive species in this system (Souza et al., in review), and previous and ongoing work in this system has focused on *Lespedeza* (Sanders et al. 2007; Souza et al., in review). However, experiments similar to ours, focusing on the effects of dominant species on other invasive species, would be enlightening especially with a focus on the identity of dominant species. Additionally, experiments addressing the role of dominant species on community structure, ecosystem processes and invasibility could be conducted over longer temporal scales so we can make further generalizations of underlying processes structuring

communities and shaping ecosystem processes and susceptibility to biological invasions.

In sum, our study, combined with other recent species removal studies, suggests that the consequences of species loss from plant communities may be contingent on the identity of the dominant species which results in differential responses of the subdominant plant community (Bret-Harte et al. 2004; Diaz et al. 2003; Emery and Gross 2006; Suding et al. 2006; Wardle et al. 1999). Compensatory responses by the subdominant community can be a function of the identity of the dominant species. Additionally, compensatory responses by the subdominant community can shape biological invasions. Although our findings suggest that *Solidago* and *Verbesina* might promote the early establishment by *Lespedeza*, they may limit the invasion dynamics of other exotic species. In particular, the cover of three exotic species (*L. japonica*, *R. flavianus* and *S. halepense*) was significantly higher when the dominant species were removed. Future studies on the potentially diverse and differential effects of dominant species on plant community structure and function, as well as invasion dynamics, might identify generalities among ecosystems and the contingent effects of dominant species.

SUPPLEMENTARY MATERIAL

Supplementary tables S1–S3 is available at *Journal of Plant Ecology* online.

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REFERENCES

- Acharya SN, Kastelic JP, Beauchemin KA, et al. (2006) A review of research progress on cicer milkvetch (*Astragalus cicer* L.). *Can J Plant Sci* **86**:49–62.
- Bazzaz FA (1996) *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge, UK: Cambridge University Press.
- Brandon AL, Gibson DJ, Middleton BA (2004) Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biol Invasions* **6**:483–93.
- Braun-Blanquet J (1932) *Plant Sociology*. Fuller GD and Conrad HS (trans). New York: McGraw-Hill.

- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of Southern Wisconsin. *Ecol Monogr* **27**:326–49.
- Bret-Harte MS, Chapin FS III, Whorley JR, *et al.* (2000) Species and functional types affect ecosystem response to fertilization in arctic tundra. *Bull Ecol Soc Am* **81**:S61.
- Bret-Harte MS, Garcia EA, Sacer VM, *et al.* (2004) Plant and soil responses to neighbour removal and fertilization in Alaskan tussock tundra. *J Ecol* **92**:635–47.
- Chapin FS III, Zavaleta ES, Eviner VT, *et al.* (2000) Consequences of changing biodiversity. *Nature* **405**:234–42.
- Chappelka AH, Neufeld HS, Davison AW, *et al.* (2003) Ozone injury on cutleaf coneflower (*Rudbeckia laciniata*) and crown-beard (*Verbesina occidentalis*) in Great Smoky Mountains National Park. *Environ Pollut* **125**:53–9.
- Crawford KM, Crutsinger GM, Sanders NJ (2007) Host-plant genotypic diversity mediates the distribution of an ecosystem engineer. *Ecology* **88**:2114–20.
- Crawley MJ, Brown SL, Heard MS, *et al.* (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? *Ecol Lett* **2**:140–8.
- Crutsinger GM, Collins MD, Fordyce JA, *et al.* (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313**:966–68.
- Crutsinger GM, Collins MD, Fordyce JA, *et al.* (2008) Temporal dynamics in non-additive responses of arthropods to host-plant genotypic diversity. *Oikos* **117**:255–64.
- Dangles O, Malmqvist B (2004) Species richness-decomposition relationships depend on species dominance. *Ecol Lett* **7**:35–402.
- D'Antonio CM, Hughes RF, Mack M, *et al.* (1998) The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *J Veg Sci* **9**:699–712.
- Diaz S, Symstad AJ, Chapin FS III, *et al.* (2003) Functional diversity revealed by removal experiments. *Trends Ecol Evol* **18**:140–6.
- Dukes JS (2002) Species composition and diversity affect grassland susceptibility and response to invasion. *Ecol Appl* **12**:602–17.
- Eddy TA, Moore CM (1998) Effects of sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don) invasion on oak savannas in Kansas. *Trans Wis Acad Sci Arts Lett* **86**:57–62.
- Emery SM, Gross KL (2006) Dominant species identity regulates invasibility of old-field plant communities. *Oikos* **115**:549–58.
- Emery SM, Gross KL (2007) Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. *Ecology* **88**:954–64.
- Foster BL, Smith VH, Dickson TL, *et al.* (2002) Invasibility and compositional stability in a grassland community: relationships to diversity and extrinsic factors. *Oikos* **99**:300–7.
- Garten CT, Classen AT, Norby RJ, *et al.* (2008) Role of N₂-fixation in constructed old-field communities under different regimes of [CO₂], temperature, and water availability. *Ecosystems* **11**:125–37.
- Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am Nat* **139**:771–801.
- Grime JP (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. London: Wiley- Blackwell.
- Gross KL, Werner PA (1982) Colonizing abilities of biennial plant species in relation to ground cover—implications for their distributions in a successional sere. *Ecology* **63**:921–93.
- Hart SC, Nason GE, Myrold DD, *et al.* (1994) Dynamics of gross nitrogen transformations in an old-growth forest—the carbon connection. *Ecology* **75**:880–91.
- Hector A, Schmid BB, Beirkuhnlein C, *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science* **286**:1123–7.
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv Biol* **6**:324–37.
- Hooper DU (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* **79**:704–19.
- Hooper DU, Chapin FS III, Ewel JJ, *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* **75**:3–35.
- Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. *Science* **277**:1302–5.
- Hoveland SC, Donnelly ED (1985) *The Lespedezas. Forages: The Science of Grass Agriculture*. Ames, IA: Iowa State University Press.
- Huston M, Smith T (1987) Plant succession: life history traits and competition. *Am Nat* **130**:168–98.
- May RM (1978) The evolution of ecological systems. *Sci Am* **239**:160–75.
- McNaughton SJ, Wolf LL (1970) Community ordering and niche width. *Science* **170**:1335.
- Meiners SC, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography* **25**:215–23.
- Munson SM, Lauenroth WK (2009) Plant population and community responses to removal of dominant species in the shortgrass steppe. *J Veg Sci* **20**:224–32.
- Naem S, Thompson LJ, Lawler SP, *et al.* (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734–7.
- Polley HW, Wilsey BJ, Derner JD (2007) Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* **116**:2044–52.
- Price CA, Weltzin JF (2003) Managing non-native plant populations through intensive community restoration in Cades Cove, Great Smoky Mountains National Park, USA. *Restor Ecol* **11**:351–8.
- Sanders NJ, Weltzin JF, Crutsinger GM, *et al.* (2007) Insects mediate the effects of propagule supply and resource availability on a plant invasion. *Ecology* **88**:2383–91.
- Schmitz OJ (2003) Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecol Lett* **6**:156–63.
- Semple JC, Cook RE (2006) *Flora of North America*. Oxford: Oxford University Press.
- Sheley RJ, Petroff J, Borman M (1999) *Introduction to Biology and Management of Noxious Rangeland Weeds*. Corvallis, OR: Oregon State University Press.
- Smith MD, Knapp AK (1999) Exotic plant species in a C-4-dominated grassland: invasibility, disturbance, and community structure. *Oecologia* **120**:605–12.
- Smith MD, Wilcox JC, Kelly T, *et al.* (2004) Dominance not richness determines invasibility of tallgrass prairie. *Oikos* **106**:253–62.
- Suding KN, Miller AE, Bechtold H, *et al.* (2006) The consequence of species loss on ecosystem nitrogen cycling depends on community compensation. *Oecologia* **149**:141–9.

- Symstad AJ, Tilman D (2001) Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal experiment. *Oikos* **92**:424–35.
- Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol Monogr* **57**: 189–214.
- Tilman D (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc Natl Acad Sci U S A.* **101**:10854–61.
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**: 718–20.
- Wardle DA, Bonner KI, Barker GM, *et al.* (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecol Monogr* **69**:535–68.
- Whittaker RH (1965) Dominance and diversity in land plant communities—numerical relations of species express importance of competition in community function and evolution. *Science* **147**:250.
- Whittaker RH (1972) Evolution and measurements of species diversity. *Taxon* **21**:217–51.
- Wilsey BJ, Polley HW (2002) Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecol Lett* **5**:676–84.