

Selective manipulation of a non-dominant plant and its herbivores affects an old-field plant community

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Abstract Competition and herbivory can interact to influence the recovery of plant communities from disturbance. Previous attention has focused on the roles of dominant plant species in structuring plant communities, leaving the roles of subordinate species often overlooked. In this study, we examined how manipulating the density of a subordinate plant species, *Solanum carolinense*, and its insect herbivores influenced an old-field plant community in

northern Florida following a disturbance. Five years following the disturbance, the initial densities of *S. carolinense* planted at the start of the experiment negatively influenced total plant cover and species diversity, and the cover of some grasses (e.g., *Paspalum urvillei*) and forbs (e.g., *Rubus trivialis*). Selectively removing herbivores from *S. carolinense* increased *S. carolinense* abundance (both stem densities and cover), increased the total cover of plants in the surrounding plant community, and affected plant community composition. Some plant species

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increased (e.g., *Digitaria ciliaris*, *Solidago altissima*) and others decreased (e.g., *Paspalum notatum*, *Cynodon dactylon*) in cover in response to herbivore removal. Herbivore effects on plant community metrics did not depend on *S. carolinense* density (no significant herbivory by density interaction), suggesting that even at low densities, a reduction of *S. carolinense* herbivores can influence the rest of the plant community. The recovery of the plant community was context dependent, depending on site- and plot-level differences in underlying environmental conditions and pre-disturbance plant community composition. We demonstrate that the density of and herbivory on a single subordinate plant species can affect the structure of an entire plant community.

Keywords Context-dependency · Competition · Density manipulation · Plant communities · Recovery · Selective removal

Introduction

The recovery of plant communities following a disturbance is influenced by an array of biotic factors (Gleason 1927; Clements 1938; Connell and Slayter 1977; Diamond 1975). For example, competition for resources has long been considered an important biotic force structuring plant communities (Hairston et al. 1960). However, herbivores can also influence plant community structure through direct plant mortality and more importantly, indirectly by altering the competitive ability of plants (Crawley 1989; Louda et al. 1990; Huntly 1991). For instance, herbivore damage to a competitively dominant plant species can weaken its competitive effect on other species, potentially increasing plant diversity by allowing subordinate (non-dominant) species to grow and persist (Carson and Root 1999). Alternatively, damage to a subordinate species can exacerbate the negative effects of dominant competitors on the subordinate plant's growth, potentially reducing overall diversity (Kim et al. 2013).

While the separate and combined effects of competition and herbivory have been repeatedly demonstrated to be important for structuring plant communities (reviewed by Chase et al. 2002; Hambäck and Beckerman 2003), it is unclear which members of a community can influence diversity

patterns. Past studies often relate changes in plant diversity to changes in the competitive ability of the dominant plant species (Crawley and Pacala 1991; Carson and Root 2000) leaving the contribution of subordinate species overlooked (but see Bach 1994). This focus on dominant species is presumably because they have the largest direct effects on other members of the plant community (Armesto and Pickett 1985; Keddy 1990). However, in these studies, the densities of both the dominant and subordinate species typically vary simultaneously, making it difficult to assess the contribution of subordinate species to overall community structure (Connell 1983; Firbank and Watkinson 1990; Inouye 2001). Similarly, in herbivore removal experiments, plant communities are compared in the presence and absence of herbivores, and any differences in community composition are thought to arise from changes in the competitive ability of dominant plants. However, these studies generally use blanket removal techniques where herbivores are removed from all plant species with the use of fences, cages, or insecticides (Crawley 1989; Crawley and Pacala 1991). Because blanket removals affect herbivores on both dominant and subordinate species, these studies cannot rule out the possibility that subordinate species are also influencing plant communities. The contribution of subordinate species to community-level processes can be assessed by selectively manipulating their densities and associated herbivores while not manipulating other plant species, and following changes in plant community structure. By ignoring the role of subordinates, we are not getting a full picture of how herbivory and competition interact to influence plant communities.

In this study, we took advantage of an existing five-year experiment designed to examine the effects of herbivores on the demography of a native weed, *Solanum carolinense* (Underwood and Halpern 2012), to ask how competition by a non-dominant plant, *S. carolinense*, and herbivory on, *S. carolinense*, influences the surrounding old-field plant community (i.e., other non-*S. carolinense* members of the local plant community). To ensure the establishment of *S. carolinense*, this experiment was begun by disking plots and spraying with herbicide. This major disturbance to the pre-existing plant community was followed by planting of *S. carolinense* in plots at a range of densities. In half of these plots, *S. carolinense* was

sprayed with insecticide to remove insect herbivores, while other plant species were allowed to establish on their own and grow without insecticide. By assessing the composition of the plant community after 5 years of ongoing herbivory treatments, we were able to ask the following questions: (1) Can the selective removal of herbivores on individuals of a subordinate plant species influence the surrounding plant community? (2) Does the initial density manipulation of a subordinate species after a disturbance influence the rest of the plant community? (3) Do herbivore removal and density manipulations interact? That is, does the absence of *S. carolinense* herbivores accentuate the effects of *S. carolinense* density on the surrounding members of the plant community? Or does selectively removing herbivores from *S. carolinense* only have effects in high-density plots where the insecticide intensity (and subsequent herbivore reduction) is highest?

Methods

Study system

Our study took place in abandoned agricultural fields (hereafter “old-fields”) at the North Florida Research and Education Center in Quincy, Florida (30.54, –84.59°). These sites are characterized by annual and perennial plant species including grasses (e.g., *Digitaria ciliaris* and *Paspalum notatum*), forbs (e.g., *Sida spinosa* and *Commelina communis*), and some legumes (e.g., *Cassia obtusifolia*). Prior to the study, fields were mowed twice per year. Our selective herbivore removal experiment focused on *S. carolinense* (Carolina horsenettle), a perennial herbaceous plant native to the eastern United States. *Solanum carolinense* reproduces both sexually and asexually, and is commonly found in old-fields throughout the region at densities of 0.3–8.1 individuals/m² (T. Kim unpublished data). At our study location, recruitment occurs primarily through the growth of underground horizontal rhizomes rather than by seed (N. Underwood unpublished data) and before the start of our study, *S. carolinense* was rare in both fields and the experimental plots. *Solanum carolinense* is a relatively minor component of old-field vegetation (mean 5.3–11 % cover; T. Kim unpublished data) and therefore is well suited for understanding the effects of non-dominant plants on diversity patterns and the role of

herbivores in mediating those effects. In this region, *S. carolinense* is fed on by many specialist (e.g., *Manduca sexta*, *Leptinotarsa juncta*, and *Epitrix fuscula*) and generalist (e.g., *Spodoptera exigua*, *Melanoplus* and *Aptenopedes spp.*, Kim 2012) herbivores and damage can vary in intensity (16–62 % leaf damage; Kim et al. 2013). *Solanum carolinense* herbivory can influence both vegetative and sexual reproduction (Wise and Sacchi 1996), but it can also influence competition between *S. carolinense* and other old-field plant species (Kim et al. 2013) and is a function of the local neighborhood composition (Kim and Underwood 2015).

Study design

The 40 plots in this experiment were initially designed to examine density dependence in herbivore effects on the demography of *S. carolinense* (Underwood and Halpern 2012). All 40 experimental plots were established in March 2007 in two different old-fields (20 plots per field). The two fields (hereafter “sites”) were separated by 750 m of rural old-field land cover. Plots were established with five initial planting densities of *S. carolinense* (0.65, 2.77, 11.11, 22.68, and 30.86 stems/m² (as described in Underwood and Halpern 2012), allowing us to examine the effects of the initial planting densities of *S. carolinense* on plant community structure (i.e., the abundance, diversity, and composition of other species within the plot). Insect herbivores were selectively removed from *S. carolinense* in 20 of the plots by spraying all *S. carolinense* stems with 0.13 % carbaryl insecticide. This allows us to examine the effect of *S. carolinense* herbivory on plant community structure. To avoid confounding plot area and *S. carolinense* density, two different plot sizes were used for each density/spray treatment combination (plots varied in area from 1.6 to 98.4 m²). However, by logistical necessity, smaller plots were associated with higher initial densities (Appendix 1). For each plot area and density combination, an insecticide-sprayed and a control plot were paired and established next to each other (to reduce environmental heterogeneity) but pairs were randomly assigned to positions within a site. This design was balanced and the design was the same at each of the two sites.

Establishment and maintenance of treatments

Before planting, plots were disturbed by disking and then sprayed with the broad-spectrum herbicide

Glyphosate (Roundup, The Scotts Company LLC, Marysville, OH, USA) to remove existing plant cover and minimize surviving seeds and roots. The few “wild” *S. carolinense* stems that re-emerged in experimental plots after the herbicide treatment were individually treated with herbicide again during the first growing season. Insects were removed from *S. carolinense* in half of the plots by spraying with Carbaryl (22 ml of Sevin Concentrate per 3.785 l, GardenTech, Lexington, KY, USA), a common insecticide targeting leaf chewing insects. Carbaryl has been shown to have little to no effect on plant growth (Simms and Rausher 1987; Murthy and Raghu 1990; Lau and Strauss 2005) and binds to soil (Gunasekara et al. 2008). *Solanum carolinense* in control plots were sprayed with an equal amount of water. Plants were sprayed at close range (5–10 cm from each *S. carolinense* stem) to minimize drift to neighboring plants (mean area sprayed per plant = 28.2 cm × 26.4 cm), although it is possible that plants immediately adjacent to *S. carolinense* received incidental spray. Spraying was performed every 2 weeks during the growing season (April–October) for 5 years (2007–2011).

Data collection

In August 2011, we surveyed plants using 50 cm diameter hoops. The number of hoops per plot was scaled with plot size (5–13 hoops placed at fixed sampling locations; small plots were near the maximum number of non-overlapping hoops that would fit in a plot, larger plots had more hoops, Pearson $r = 0.95$). Within each hoop, we estimated the percent cover of each plant species and bare ground (at intervals of 0–5, 6–20, 21–40, 61–80, 81–100 %), and counted the number of *S. carolinense* stems, our measure of density. After assessing the community within each hoop, we inspected the entire plot area and noted any rare species that were not captured in our hoops. Such rare species were assigned a cover of 0.2 %, a cover value slightly lower than the lowest occurring species recorded from our hoop measurements (0.23 %). Plant cover for each species was averaged across hoops within each plot.

We define the surrounding old-field plant community as the non-*S. carolinense* members of the plant community within a plot. We thus excluded *S.*

carolinense cover from our calculations of species richness, diversity, and composition. Species richness was the number of plant species in each plot. Total cover was used as a surrogate for plant abundance, and was estimated as the sum of each species’ percent cover, excluding *S. carolinense*. Shannon-Weiner diversity (hereafter “diversity”) was calculated for each plot using the mean percent cover of each species. Differences in plant community composition among plots were characterized using Bray-Curtis dissimilarity, which was based on mean cover.

Data analysis

We used four separate generalized linear models (GLMs) to examine how *S. carolinense* cover, species richness, total cover, and diversity of the surrounding plant community responded to the insecticide treatment, initial planting densities of *S. carolinense*, and their interactions. We also included three covariates. First, we included “plot size” in the models to account for area effects as we sampled larger areas in larger plots. Second, we included “site” as a covariate to account for underlying differences in environmental conditions between the two fields, such as edaphic factors or past land-use practices. Lastly, we used an index of prior plant species composition at the scale of individual plots to account for the effects of spatial variation in pre-disturbance plant species composition and/or environmental conditions within each site. Plant composition within each plot prior to disturbance was estimated from high-resolution digital orthographic imagery acquired in March 2004, 3 years before the start of the experiment. There was no other experiment performed at our sites between 2004 and 2007, our initial planting date, thus our sites remained undisturbed during this period except for occasional mowing. Three spectral bands (green, blue, and infrared) were included in a principal components analysis (PCA) in order to generate a single-band image representing the spectral radiance across multiple ranges of the electromagnetic spectrum. Ordination analysis of multispectral imagery can be used in this way to characterize plant community composition in a continuous fashion, rather than using discrete classes (Schmidtlein et al. 2007). The mean of the first-axis PCA scores corresponding to each plot area was used as an index of prior plant composition (hereafter “prior plant cover,” Appendix 2). We

evaluated all potential two- and three-way interactions between the insecticide and density treatments and the covariates. To simplify our final model, we dropped all three-way interactions if none were significant and reran GLMs with only two-way interactions. If none of the two-way interactions were significant, we ran GLMs with only main factors. With each round of model simplification, we tested whether data met GLM assumptions (e.g., residuals normally distributed, homogeneity of variance). When necessary, we log-transformed the data.

We used a permutational MANOVA (PERMANOVA; Bray-Curtis dissimilarity) to examine how spray treatment and initial *S. carolinense* planting density influenced plant community composition. To determine which plant species were most influenced by the spray treatment and *S. carolinense* planting density, we also performed separate GLMs on the mean cover of each species within the plant communities. Again, prior plant cover, site, and plot area were included as covariates and all two- and three-way interactions were evaluated using the same model simplification procedures as the GLMs. All analyses were performed using R v3.03 (R Development Core Team 2014) and the RVAideMemoire package (Hervé 2015) for PERMANOVA.

Results

At planting, in May 2007, *S. carolinense* was the only plant species in the plots. However, other species quickly established and by August 2007 mean *S. carolinense* cover across all plots was 56.4 % and non-*S. carolinense* cover was 36.5 % (Underwood and Halpern, unpublished data). One year later in August 2008, mean *S. carolinense* cover had declined to 15.7 % (Underwood and Halpern, unpublished data) and by the end of our five-year experiment (in August 2011), *S. carolinense* was only a minor component of the vegetation in the plots (mean cover per plot was 3.4 %, corresponding to a mean *S. carolinense* density of 1.82 stems/m²). A total of 45 plant species were found in the plots (mean = 10 species per plot) and 97 % of each plot was covered with vegetation. Fourteen species, mainly grasses and particularly *P. notatum*, made up 95 % of the plant cover.

Underwood and Halpern (2012) found that insecticide reduced herbivore damage to *S. carolinense* in the first

4 years of the experiment (2007–2010). Not surprisingly, 5 years following disturbance, insecticide treatment positively influenced *S. carolinense* cover (GLM, main effect of insecticide, $F_{1,34} = 8.67$, $P < 0.01$, Table 1) and the abundance rank of *S. carolinense* (7th in insecticide plots versus 13th in control plots, Fig. 1). The initial planting density was positively correlated with the mean densities of *S. carolinense* in subsequent years, including 2011 ($t = 10.62$, $df = 38$, $P < 0.01$, Spearman $r = 0.86$) and had positive effects on *S. carolinense* cover in 2011 (main effect of density $F_{1,34} = 7.71$, $P < 0.01$, Table 1; Fig. 2).

The plant community surrounding *S. carolinense* was influenced by the initial planting density of *S. carolinense* and insecticide treatment (Table 1). Five years following disturbance, the initial density of *S. carolinense* did not influence which species were present (i.e., community composition, PERMANOVA main effect $F_{1,24} = 1.18$, $P = 0.28$) but increasing initial densities of *S. carolinense* reduced the total cover of plants (GLM, main effect $F_{1,22} = 6.55$, $P = 0.01$) and decreased Shannon diversity (GLM, interaction with plot area $F_{1,24} = 4.72$, $P = 0.04$). Reducing herbivory on *S. carolinense* sometimes influenced which species were present (i.e., community composition, PERMANOVA, interaction with site $F_{1,24} = 3.63$, $P < 0.01$, interaction with prior plant cover $F_{1,24} = 2.96$, $P = 0.02$) and increased the total cover of plants within the plots (GLM, main effect $F_{1,22} = 7.46$, $P = 0.01$). Neither insecticide nor *S. carolinense* density influenced species richness (GLM, main effect of insecticide $F_{1,34} = 0.19$, $P = 0.66$, main effect of density $F_{1,34} = 0.68$, $P = 0.23$). Although species richness is generally a saturating function of plot area, we found that richness increased linearly with area (GLM, main effect $F_{1,34} = 79.25$, $P < 0.01$). There were no effects of interactions between the initial densities of *S. carolinense* and herbivore reduction on any community metric.

The covers of different individual species of grasses and forbs, including both dominant and non-dominant species, were differentially affected by insecticide or the initial planting densities of *S. carolinense* (Figs. 2, 3; Appendix 3). For example, in the absence of *S. carolinense* herbivores, the cover of the most dominant grass *P. notatum* (mean cover 27.1 %, Fig. 3) was generally lower, but herbivore effects were context dependent (GLM, interaction with site $F_{1,24} = 5.29$, $P = 0.03$; interaction with prior plant cover

Table 1 ANOVA tables for the final models of insecticide treatment, initial *S. carolinense* planting density, prior plant cover, and site effects on *S. carolinense* cover (A) and plant community structure (total cover (B), species richness (C), diversity (D), and community composition (E)). We excluded *S. carolinense* cover from our calculations of total cover, species richness, diversity, and composition

	Type II SS	df	F	P
(A) <i>S. carolinense</i> cover				
Site	84.54	1	20.08	<0.01
Insecticide	36.51	1	8.67	<0.01
Plot area	0.28	1	0.07	0.80
Initial density	32.46	1	7.71	<0.01
Prior plant cover	4.35	1	1.03	0.31
Residuals	143.14	34		
(B) Total cover				
Site	410.20	1	2.23	0.15
Insecticide	1373.90	1	7.46	0.01
Plot area	166.20	1	0.90	0.35
Initial density	1206.90	1	6.50	0.02
Prior plant cover	290.00	1	1.58	0.22
Site: insecticide	739.20	1	4.02	0.06
Site: plot area	4.70	1	0.02	0.87
Site: initial density	19.60	1	0.11	0.74
Site: prior plant cover	131.60	1	0.71	0.40
Insecticide: plot area	333.70	1	1.81	0.19
Insecticide: initial density	29.20	1	0.16	0.69
Insecticide: prior plant cover	157.80	1	0.85	0.36
Plot area: initial density	269.40	1	1.46	0.23
Plot area: prior plant cover	0.10	1	<0.01	0.97
Initial density: prior plant cover	48.00	1	0.26	0.61
Residuals	4050.10	22		
(C) Richness				
Site	21.18	1	4.57	0.04
Insecticide	0.89	1	0.19	0.66
Plot area	79.25	1	17.10	<0.01
Initial density	6.83	1	1.48	0.23
Prior plant cover	0.70	1	0.15	0.70
Residuals	157.6	34		
(D) Shannon diversity				
Site	1.19	1	7.80	<0.01
Insecticide	0.11	1	0.78	0.38
Plot area	0.05	1	0.36	0.55
Initial density	0.11	1	0.79	0.38
Prior plant cover	1.11	1	7.48	0.01
Site: insecticide	0.03	1	0.21	0.65
Site: plot area	0.11	1	0.78	0.38
Site: initial density	0.25	1	1.72	0.20
Site: prior plant cover	0.14	1	0.99	0.32
Insecticide: plot area	<0.01	1	0.01	0.91
Insecticide: initial density	0.18	1	0.92	0.34

Table 1 continued

	Type II SS	df	F	P
Insecticide: prior plant cover	0.16	1	1.08	0.31
Plot area: initial density	0.70	1	4.72	0.04
Plot area: prior plant cover	0.11	1	0.73	0.40
Initial density: prior plant cover	0.44	1	2.96	0.10
Residuals	3.57	24		
(E) Community composition				
Insecticide	0.13	1	0.71	0.65
Plot area	0.40	1	2.20	0.05
Prior plant cover	0.78	1	4.36	<0.01
Site	0.82	1	4.56	<0.01
Initial density	0.22	1	1.18	0.28
Insecticide: plot area	0.14	1	0.78	0.59
Insecticide: prior plant cover	0.53	1	2.96	0.02
Insecticide: site	0.65	1	3.63	<0.01
Insecticide: initial density	0.17	1	0.94	0.46
Plot area: prior plant cover	0.12	1	0.67	0.65
Plot area: site	0.14	1	0.82	0.53
Plot area: initial density	0.21	1	1.19	0.31
Prior plant cover: site	0.30	1	1.69	0.11
Prior plant cover: initial density	0.16	1	0.90	0.47
Site: initial density	0.14	1	0.83	0.51
Residuals	4.30	24		

$F_{1,24} = 4.61$, $P = 0.04$, Appendix 2). In the insecticide plots, most of the other species increased in cover, including *D. ciliaris* (GLM, main effect $F_{1,34} = 4.92$, $P = 0.03$), *Solidago altissima* (GLM, interaction with site $F_{1,24} = 5.01$, $P = 0.03$, interaction with prior plant cover $F_{1,24} = 7.16$, $P = 0.01$) and *Ipomea* sp. (GLM, main effect $F_{1,34} = 7.91$, $P = 0.01$). Manipulating the starting densities of *S. carolinense* influenced the cover of some species (e.g., *Paspalum urvillei* (positive effect), *Verbena nastata* (positive effect), Fig. 2; Appendix 3) and there was a density and insecticide interaction for *Cynodon dactylon* (positive effects of density in insecticide-sprayed plots only, 3-way interaction of density, insecticide and site).

Underlying differences between sites and plot-level differences in pre-existing plant communities prior to the experiment influenced *S. carolinense* cover and community structure in 2011. Site had a significant effect on *S. carolinense* cover (GLM: main effect $F_{1,34} = 20.08$ $P < 0.01$), total cover (GLM:

interaction with insecticide $F_{1,22} = 4.01$ $P = 0.05$), Shannon diversity (GLM: main effect $F_{1,24} = 7.99$ $P < 0.01$), and community composition (PERMANOVA: main effect $F_{1,24} = 4.56$ $P < 0.01$). Prior plant cover influenced Shannon diversity (GLM: main effect $F_{1,24} = 7.47$ $P = 0.01$), and community composition (PERMANOVA: main effect $F_{1,24} = 4.56$ $P < 0.01$).

Discussion

The manipulation of a single, competitively subordinate plant species (*S. carolinense*) and its herbivores affected the surrounding plant community 5 years following a disturbance. The density manipulations affected the total cover of plants and plant diversity, while the insecticide treatment affected total plant cover and plant community composition. Richness, on the other hand, was not affected by either density or insecticide treatments. The covers of some individual

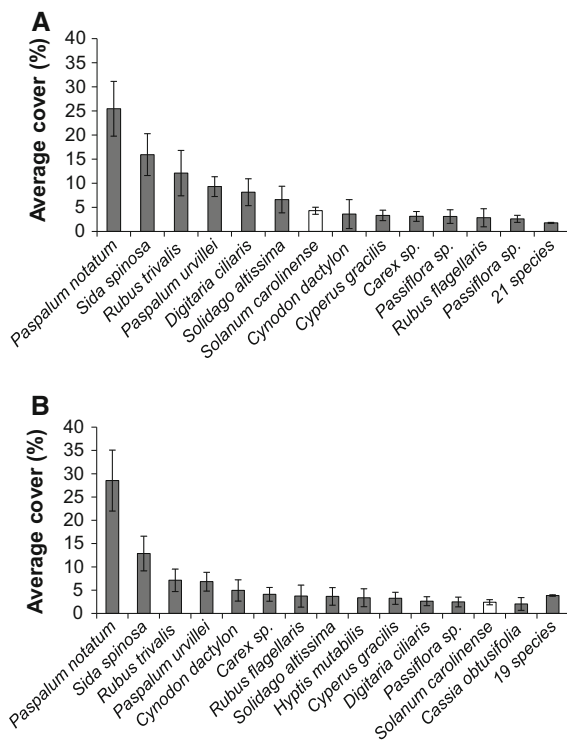


Fig. 1 The composition of the plant community in the absence (a) and presence (b) of herbivores on *S. carolinense* at the end of five-year experiment. At the start of the experiment, *Solanum carolinense* was the only plant species within the experimental plots. Five years later, 95 % of the cover was composed of a total of 14 species in insecticide-sprayed plots (a) and 13 species in control plots (b). *Solanum carolinense* (open bars) was ranked 7th overall in the absence of herbivores and 13th overall in the presence of herbivores at 4.5 % and 2.2 % cover, respectively. Error bars represent $1 \pm SE$

species (both dominant and subordinate species) were also affected by both treatments (Figs. 2, 3; Appendix 3). Bach (1994) found similar results in sand dunes where the abundances of both dominant and subordinate species varied when herbivores were removed from one plant species (*Salix cordata*); however in that study richness and diversity did not change. In our study, the effects of *S. carolinense* herbivory reduction on other members of the plant community did not depend on the density of *S. carolinense* (no interaction of planting density and insecticide), so even a small reduction of *S. carolinense* herbivores can influence the rest of the community. If other subordinate plant species have similar effects on the rest of the plant community then selective manipulation experiments with different species could reveal a larger role for subordinate species in shaping plant communities.

Potential mechanisms of plant community response to the selective removal of herbivores

Previous studies have used blanket removal experiments to evaluate the effect of herbivores on plant community structure. However, blanket removal methods do not allow us to disentangle the mechanisms by which herbivores are affecting the plant community as herbivores feeding on both dominant and subordinate plant species are affected by the herbivore manipulation. Here, we manipulated herbivores feeding on a subordinate plant species so changes to the plant community likely arise directly or indirectly via the subordinate species, or herbivores using that species. We found that herbivore removal increased the total cover of plants, altered the cover of certain plant species, and influenced plant community composition. Reducing herbivory on *S. carolinense* could affect the plant community through at least two mechanisms. First, selectively spraying *S. carolinense* with insecticide may alter herbivore damage on other plant species. Targeted insecticide could result in mortality of generalist herbivores, reducing their ability to feed on all plants in the community. If this was the case, we would expect damage to be lower in the insecticide plots versus the control plots. On the other hand, generalist herbivores could avoid sprayed plants, and instead concentrate feeding on unsprayed plants. If this was the case, we would expect damage on neighboring plants to increase, potentially resulting in reduced cover. Our results show that total plant cover increased in plots where *S. carolinense* was sprayed, which is consistent with reduced overall herbivore damage. However, some species (including the dominant grass *P. notatum*) had decreased cover in insecticide plots, suggesting that there might be some level increased feeding on non-target plants and treated plant avoidance. Although direct effects of spraying on herbivory seem likely to contribute to cases where spraying increased cover, two lines of evidence suggest that reduction in overall damage in the community does not fully explain the effects of targeted spray on the surrounding plant community. First, our detailed observations of herbivory on two common neighboring forbs (*Rubus trivialis* and *S. altissima*), showed that spraying insecticide on *S. carolinense* did not influence damage to these two species (Appendix 4, GLM, *R. trivialis* $F_{1,13} = 0.001$, $P = 0.96$, *S. altissima* $F_{1,13} = 0.308$, $P = 0.58$). Second, most damage to *S. carolinense* is

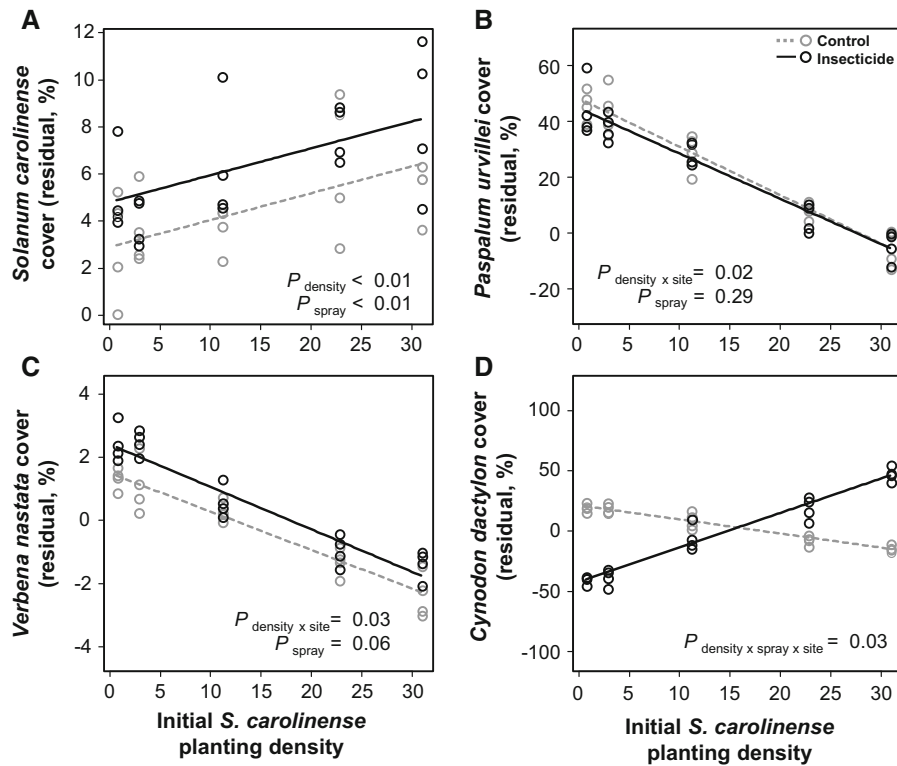


Fig. 2 The effects of the initial densities of *S. carolinense* and insecticide treatment on the mean percent cover of *Solanum carolinense* (a), *Paspalum urvillei* (b), *Verbena nastata* (c), and *Cynodon dactylon* (d). Black circles and lines are plots sprayed with insecticide (“insecticide” plots); gray circles and dotted

lines are plots sprayed with equivalent amounts of water (“control” plots). Densities are the number of *S. carolinense* ramets/m². Lines are best fit lines from linear regression. Points represent partial residuals from linear regressions (Table 1, Appendix 2)

done by specialist herbivores on Solanaceae (Wise 2007; Underwood and Halpern 2012) rather than generalists, which suggests that another mechanism may be important.

A second mechanism for the effects of spraying on plant abundances is that releasing *S. carolinense* from herbivory could have changed its competitive effects on the rest of the community (e.g., Crawley 1989; Huntly 1991; Bach 1994). In the absence of herbivores, stem densities of *S. carolinense* were higher and overall plant size was greater (Underwood and Halpern 2012). Changes in plant size and densities could have allowed *S. carolinense* to compete strongly with some other plant species for resources and space. Indeed *S. carolinense* increased in competitive ranking (to the extent that competitive effects are reflected in percent cover) from 13th place in the presence of herbivores to 7th place in the absence of herbivores, outranking other subordinate species such as *Ipomea*, *Carex*, *Hyptis mutabilis*, and *C. dactylon* (Fig. 1). In a previous study

in old-fields (Carson and Root 2000), a blanket removal of herbivores was performed and it was assumed that changes in the competitively dominant species, *S. altissima*, influenced plant community structure resulting in slower rates of succession and invasion by woody species. However, our results suggest that subordinate species were also likely influenced by the herbivore manipulation and could have contributed to changes in overall plant composition.

Potential mechanisms of plant community response to selectively adding *S. carolinense*

This experiment began with a major disturbance (disking and spraying herbicide) followed by the planting of *S. carolinense*. This gave *S. carolinense* an advantage over other plant species through preemptive competition because established *S. carolinense* could grow and use resources while other plant species were still in the process of re-establishment after the

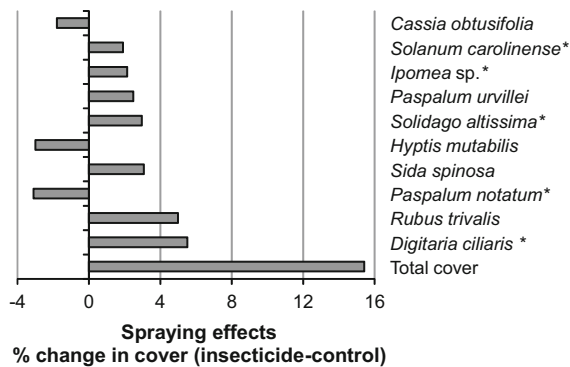


Fig. 3 Insecticide effects on the change in cover of the 10 plant species with the greatest change in cover and total cover of plants within each plot (change in mean % cover = mean % cover in insecticide-sprayed minus the mean % cover in control plots). Asterisks denote significant differences in % cover between insecticide and control plots ($P < 0.05$)

disturbance. Increasing the initial planting densities of *S. carolinense* could intensify the effect on the surrounding plant community by enhancing this advantage in establishment and thus reducing the overall cover of the surrounding plant community. There was also a negative relationship between the initial plantings of *S. carolinense* and diversity. It is unlikely that *S. carolinense* directly reduced diversity but *S. carolinense* could have reduced diversity indirectly by allowing other species to increase in dominance. Indeed there was a positive relationship between *S. carolinense* density and the cover of *P. urvillei* (grass) and *R. trivialis* (forb). It is unclear how *P. urvillei* and *R. trivialis* could benefit from increasing densities of *S. carolinense* but these effects could have affected plant species evenness and contributed to the overall change in diversity.

Plant community recovery was context dependent

Context dependencies can dominate many ecological processes (e.g., Foster et al. 2003; Cramer et al. 2008) and influence the recovery of plant communities following a disturbance. For example, we found that differences between sites were important factors influencing diversity and composition, and the cover of various plant species (Table 1). The experiment was conducted in two different fields that likely varied in abiotic factors (e.g., soil, topography) and land-use histories, which may have strongly influenced the recovery of the plant community following disturbance.

We also observed strong effects of prior plant cover on current plant community structure. Although our experimental plots were tilled and treated with herbicide at the start of the experiment, the plant community at the end of the five-year experiment was not a result of primary succession as seeds and rhizomes survived the disturbance and this legacy of the pre-disturbance plant community influenced the contemporary plant community structure. Finally, we observed significant effects of interactions between herbivory or density and site or prior plant cover on plant community composition and the cover of various plant species (Table 1; Appendix 2), suggesting that the effects of herbivory and competition in structuring plant communities may be context dependent. Similar results have been found in other studies where herbivore effects were mediated by abiotic factors (e.g., salinity Gedan et al. 2009) or land-use history (Hahn and Orrock 2015) to influence the trajectory of secondary succession. This suggests that the plant communities might not respond to biotic interactions in predictable ways and context dependency should be considered.

Conclusions

Our study supports the idea that the density and herbivory of a subordinate species can influence plant communities. Even small changes in herbivore loads, possibly through the effects of a single subordinate plant species, can have significant effects on a plant community. Our results suggest that more attention to the effects of subordinate plant species is needed and might improve our understanding of plant community structure and dynamics.

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Appendix 1

See Fig. 4.

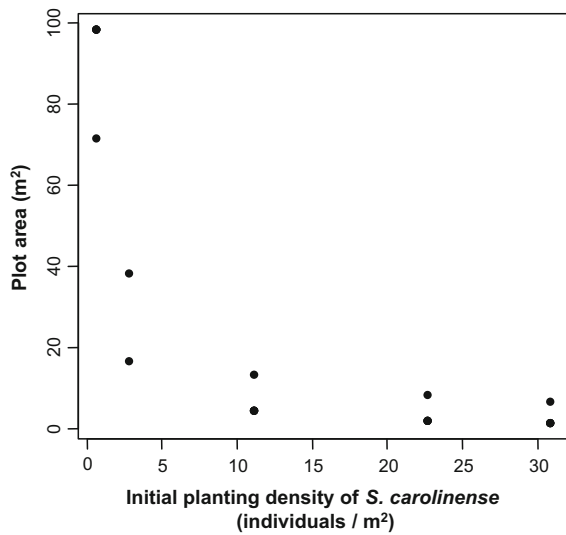


Fig. 4 For logistical reasons, plot size varied with density (Spearman $r_s = -0.948$) but to avoid completely confounding density with plot area, we used two plot sizes for each density treatment. Although this does present the possibility of spurious correlations with density and plot size, there was enough variation between the two variables to decouple their effects on plant responses. However, to ensure that spurious correlations were not present, we re-ran GLMs (see “Data analysis” in Methods), replacing the significant variable (e.g., density) with the other correlated variable (e.g., plot size) and compared model results and AICc values. If the replacement did not yield the same results and the other variable did not appear significant, we conclude that it was not a spurious correlation and that the effects are real. In all cases, the density and area effects represented in the paper were real

Appendix 2

Index of prior plant composition.

Plant composition prior to disturbance was estimated from high-resolution digital orthographic quarter quad imagery acquired in March 2004, 3 years before the start of the experiment. Different plant species, but also variation in soil and vegetation water content, can reflect light of different intensities across a range of the electromagnetic (EM) spectrum, which forms a basis for all land cover classifications (e.g., Jin et al. 2013). Accordingly, we assume that the digital number values corresponding to each 1 m² pixel represents the average spectral radiance of the individual plants within that area, and therefore the composition of plant species. Moreover, we assume underlying environmental variation potentially driving differences in prior plant cover (e.g., soil type or hydrological properties) are incorporated within radiance values. We included the three bands from the image (green, blue, and infrared) in a principal components analysis (PCA) in order to generate an image that represents spectral radiance from multiple ranges of the EM spectrum on a single band. Ordination techniques such as this can be used to characterize vegetation communities in a continuous fashion rather than forming discrete habitat classes (Schmidtlein et al. 2007). We overlaid the plot boundaries on the PCA image product and, for each plot, calculated the mean of the first-axis PCA scores

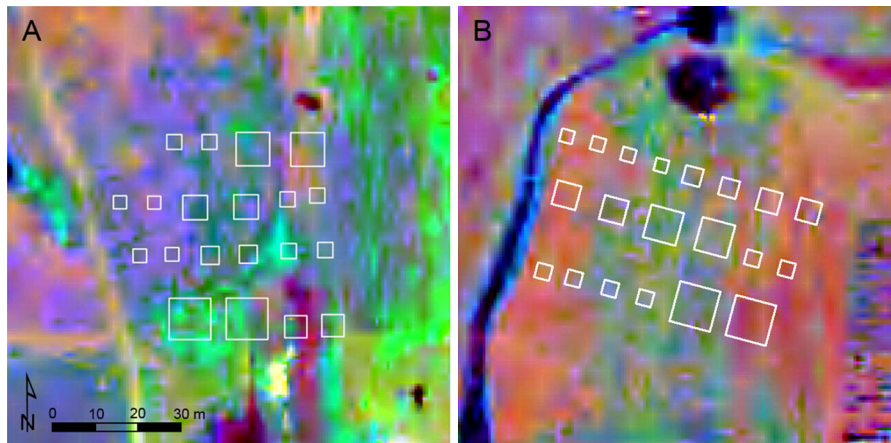


Fig. 5 PCA images illustrating differences in prior plant cover among plots in the west (a) and east (b) sites. Plot positions are outlined in white and ranged in sizes from 1.6 to 98.4 m². The five initial planting densities of *S. carolinense* within each plot were 0.65, 2.77, 11.11, 22.68, and 30.86 stems/m². This figure

depicts all three axes as a false color composite with PCA axis 1 (71.6 %) coded as red, PCA axis 2 (25.7 %) coded as blue, and PCA axis 3 (2.7 %) coded as green, but only the mean of the first-axis scores corresponding to areas within each plot was used as a covariate in our analyses “prior plant cover”

(Fig. 5). The first axis explained 71.6 % of the variation in the original three-band image. The mean for each plot was used in subsequent analyses as an index of prior plant cover.

See Fig. 5.

Appendix 3

See Table 2.

Table 2 The effects of *S. carolinense* insecticidal spray and initial planting densities on various grass (A) and forb (B) species in the surrounding plant community in 2011. Numbers in parentheses are the mean cover of each plant species

	Type II SS	df	F	P
(A) Grasses				
<i>Paspalum notatum</i> (27.1 %)				
Site	973.40	1	1.86	0.19
Insecticide	81.90	1	0.16	0.70
Plot area	301.50	1	0.58	0.46
Initial density	4.70	1	0.01	0.93
Prior plant cover	5672.50	1	10.81	<0.01
Site: insecticide	2778.00	1	5.29	0.03
Site: plot area	13.90	1	0.03	0.87
Site: initial density	3.90	1	0.01	0.93
Site: prior plant cover	891.20	1	1.70	0.20
Insecticide: plot area	169.60	1	0.32	0.58
Insecticide: initial density	1112.00	1	2.12	0.16
Insecticide: prior plant cover	2421.30	1	4.61	0.04
Plot area: initial density	232.20	1	0.44	0.51
Plot area: Prior plant cover	37.20	1	0.07	0.79
Initial density: prior plant cover	34.70	1	0.07	0.80
Residuals	12596.60	24		
<i>Paspalum urvillei</i> (8.6 %)				
Site	953.86	1	17.72	<0.01
Insecticide	62.17	1	1.16	0.29
Plot area	67.36	1	1.25	0.27
Initial density	0.26	1	0.01	0.94
Prior plant cover	298.16	1	5.54	0.03
Site: insecticide	38.68	1	0.72	0.40
Site: plot area	308.38	1	5.73	0.02
Site: initial density	369.49	1	6.87	0.02
Site: prior plant cover	100.96	1	1.88	0.18
Insecticide: plot area	3.84	1	0.07	0.79
Insecticide: initial density	7.24	1	0.14	0.72
Insecticide: prior plant cover	1.92	1	0.04	0.85
Plot area: initial density	145.71	1	2.71	0.11
Plot area: prior plant cover	247.74	1	4.60	0.04
Initial density: prior plant cover	307.14	1	5.71	0.03
Residuals	1291.81	24		

Table 2 continued

	Type II SS	df	F	P
<i>Digitaria ciliaris</i> (5.4 %)				
Site	19.89	1	0.32	0.57
Insecticide	302.95	1	4.93	0.03
Plot area	138.60	1	2.25	0.14
Initial density	166.20	1	2.70	0.11
Prior plant cover	2.11	1	0.03	0.85
Residuals	2090.46	34		
<i>Cynodon dactylon</i> (4.3 %)				
Site	386.06	1	3.83	0.07
Insecticide	0.43	1	<0.01	0.95
Plot area	39.23	1	0.39	0.54
Initial density	32.09	1	0.32	0.58
Prior plant cover	38.14	1	0.38	0.55
Site: insecticide	1.64	1	0.02	0.90
Site: plot area	53.20	1	0.53	0.48
Site: initial density	115.11	1	1.14	0.30
Site: prior plant cover	9.00	1	0.09	0.77
Insecticide: plot area	26.61	1	0.26	0.62
Insecticide: initial density	107.90	1	1.07	0.32
Insecticide: prior plant cover	51.47	1	0.51	0.49
Plot area: initial density	946.66	1	9.38	0.01
Plot area: prior plant cover	123.41	1	1.22	0.29
Initial density: prior plant cover	171.49	1	1.70	0.21
Site: insecticide:plot area	182.44	1	1.81	0.20
Site: insecticide:initial density	572.62	1	5.67	0.03
Site: insecticide:prior plant cover	4.54	1	0.05	0.84
Site: plot area:initial density	90.95	1	0.90	0.36
Site: plot area:prior plant cover	99.05	1	0.98	0.34
Site: initial density: prior plant cover	120.05	1	1.19	0.29
Insecticide: plot area: initial density	177.68	1	1.76	0.21
Insecticide: plot area: prior plant cover	13.77	1	0.14	0.72
Insecticide: initial density:prior plant cover	312.69	1	3.10	0.10
Plot area: initial density: prior plant cover	38.66	1	0.38	0.55
Residuals	1412.97	14		
(B) Forbs				
<i>Sida spinosa</i> (14.4 %)				
Site	1345.50	1	9.34	<0.01
Insecticide	91.40	1	0.64	0.43
Plot area	115.00	1	0.80	0.38
Initial density	73.30	1	0.51	0.48
Prior plant cover	819.40	1	5.69	0.02
Residuals	4899.80	34		
<i>Rubus trivalis</i> (9.6 %)				
Site	25.90	1	0.10	0.75
Insecticide	247.30	1	0.95	0.34

Table 2 continued

	Type II SS	df	F	P
Plot area	1348.10	1	5.17	0.03
Initial density	1284.10	1	4.93	0.03
Prior plant cover	62.10	1	0.24	0.63
Residuals	8866.00	34		
<i>Solidago altissima</i> (5.1 %)				
Site	27.66	1	0.25	0.62
Insecticide	64.49	1	0.59	0.45
Plot area	0.91	1	0.01	0.93
Initial density	109.80	1	1.00	0.33
Prior plant cover	44.89	1	0.41	0.53
Site:insecticide	552.47	1	5.01	0.03
Site: plot area	30.58	1	0.28	0.60
Site: initial density	21.98	1	0.20	0.66
Site: prior plant cover	254.33	1	2.31	0.14
Insecticide: plot area	66.65	1	0.60	0.44
Insecticide: initial density	65.33	1	0.59	0.45
Insecticide: prior plant cover	790.44	1	7.17	0.01
Plot area: initial density	22.40	1	0.20	0.66
Plot area: prior plant cover	2.21	1	0.02	0.89
Initial density: prior plant cover	30.73	1	0.28	0.60
Residuals	2647.51	24		
<i>Log (Passiflora sp.)</i> (2.8 %)				
Site	9.88	1	17.29	<0.01
Insecticide	0.01	1	0.01	0.92
Plot area	1.34	1	2.35	0.13
Initial density	0.00	1	<0.01	0.99
Prior plant cover	0.80	1	1.40	0.25
Residuals	19.44	34		
<i>Log (Hyptis mutabilis)</i> (1.9 %)				
Site	2.34	1	3.84	0.06
Insecticide	2.22	1	3.64	0.06
Plot area	2.85	1	4.67	0.04
Initial density	0.47	1	0.76	0.39
Prior plant cover	2.16	1	3.55	0.07
Residuals	20.71	34		
<i>Ipomea sp.</i> (1.6 %)				
Site	2.99	1	0.52	0.48
Insecticide	45.92	1	7.91	0.01
Plot area	11.45	1	1.97	0.17
Initial density	21.03	1	3.62	0.07
Prior plant cover	5.27	1	0.91	0.35
Residuals	197.34	34		
<i>Log (Verbena nastata)</i> (1.4 %)				
Site	1.30	1	2.81	0.11
Insecticide	1.81	1	3.90	0.06

Table 2 continued

	Type II SS	df	F	P
Plot area	0.01	1	0.03	0.87
Initial density	0.03	1	0.07	0.80
Prior plant cover	0.03	1	0.07	0.79
Site: insecticide	0.05	1	0.12	0.74
Site: plot area	0.71	1	1.52	0.23
Site: initial density	2.53	1	5.45	0.03
Site: prior plant cover	0.43	1	0.93	0.35
Insecticide: plot area	0.26	1	0.56	0.46
Insecticide: initial density	0.09	1	0.20	0.66
Insecticide: prior plant cover	0.39	1	0.84	0.37
Plot area: initial density	0.58	1	1.25	0.27
Plot area: prior plant cover	1.02	1	2.21	0.15
Initial density: prior plant cover	3.10	1	6.70	0.02
Residuals	11.12	24		

Appendix 4

See Table 3.

Table 3 The effects of *S. carolinense* density, insecticide spray, and site on leaf damage to *Rubus trivialis* (A) and *Solidago altissima* (B)

	Type II SS	df	F	P
(A) <i>Rubus trivialis</i>				
Insecticide	<0.01	1	0.00	0.97
Initial density	<0.01	1	0.44	0.52
Site	<0.01	1	0.89	0.36
Insecticide: initial density	<0.01	1	0.30	0.60
Insecticide: site	<0.01	1	0.03	0.86
Initial density: site	<0.01	1	0.32	0.58
Residuals	0.02	13		
(B) <i>Solidago altissima</i>				
Insecticide	<0.01	1	0.31	0.59
Initial density	<0.01	1	0.06	0.80
Site	0.01	1	4.88	0.05
Insecticide: initial density	<0.01	1	2.07	0.17
Insecticide: site	0.01	1	4.28	0.06
Initial density: site	<0.01	1	0.00	0.96

Table 3 continued

	Type II SS	df	F	P
Residuals	0.02	13		

Rubus trivialis and *S. altissima* were chosen for damage estimates because they were found in most of the experimental plots and have the potential to share generalist herbivores such as grasshoppers (*Schistocerca* sp. and *Melanoplus* sp.) and geometrid moths. We measured herbivore damage in plots where both plant species co-occur (10 insecticide sprayed and 10 control plots). Within each plot, we randomly selected four individuals of each species, and on each individual, we randomly selected 10 leaves to estimate damage. Damage on each leaf was estimated as percent leaf area removed (at intervals of 0, 1–5, 6–25, 26–50, 51–75, 76–100 %) and averaged across leaves for each individual. Plot was the unit of analysis therefore damage estimates were averaged across individuals per plot. We used two separate generalized linear models to examine how damage to *R. trivialis* and *S. altissima* responded to the herbivore treatment (insecticide-sprayed versus control) and initial planting densities of *S. carolinense*, and their interactions. Because herbivory can vary with location, we also included “site” into our model and examined all possible three-way and two-way interactions between site, *S. carolinense* density and insecticide treatment. Three-way interactions were not significant and therefore dropped from the final model. Mean damage of *R. trivialis* was 6.4 % where mean damage of *S. altissima* was 7.5 %

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