

Groundcover community assembly in high-diversity pine savannas: seed arrival and fire-generated environmental filtering

KYLE E. HARMS,^{1,†} PAUL R. GAGNON,^{2,3} HEATHER A. PASSMORE,²
JONATHAN A. MYERS,⁴ AND WILLIAM J. PLATT¹

¹*Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA*

²*Department of Biological Sciences, Murray State University, Murray, Kentucky 42071 USA*

³*Watershed Studies Institute, Murray State University, Murray, Kentucky 42071 USA*

⁴*Department of Biology, Washington University in St. Louis, St. Louis, Missouri 63130 USA*

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Abstract. Environmental filtering—abiotic and biotic constraints on the demographic performance of individual organisms—is a widespread mechanism of selection in communities. A given individual is “filtered out” (i.e., selectively removed) when environmental conditions or disturbances like fires preclude its survival and reproduction. Although interactions between these filters and dispersal from the regional species pool are thought to determine much about species composition locally, there have been relatively few studies of dispersal × filtering interactions in species-rich communities and fewer still where fire is also a primary selective agent. We experimentally manipulated dispersal and filtering by fire (pre-fire fuel loads and post-fire ash) in species-rich groundcover communities of the longleaf pine ecosystem. We tested four predictions: (1) That species richness would increase with biologically realistic dispersal (seed addition); (2) that the immediate effect of increased fuels in burned communities would be to decrease species richness, whereas the longer-term effects of increased fuels would be to open recruitment opportunities in the groundcover, increase species richness, and increase individual performance (growth) of immigrating species; (3) that adding ash would increase species richness; and (4) that increased dispersal would generate larger increases in species richness in plots with increased fuels compared to plots with decreased fuels. We found that dispersal interacted with complex fire-generated filtering during and after fires. Dispersal increased species richness more in burned communities with increased and decreased fuels compared to burned controls. Moreover, individuals of immigrating species generally grew to larger sizes in burned communities with increased fuels compared to burned controls. In contrast to dispersal and fuels, ash had no effect on species richness directly or in combination with other treatments. We conclude that filtering occurs both during fires and in the post-fire environment and that these influences interact with dispersal such that the consequences are only fully revealed when all are considered in combination. Our experiment highlights the importance of considering the dynamic interplay of dispersal and selection in the assembly of species-rich communities.

Key words: ash; community assembly; environmental filters; fire; fuels; high-diversity communities; longleaf pine savanna; seed dispersal; seed limitation; selection; species pool; species richness.

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† **E-mail:** kharms@lsu.edu

INTRODUCTION

All ecological communities assemble through the same set of four processes: speciation, dispersal, selection, and ecological drift (Vellend 2010). The common narrative of community ecology (Roughgarden 2009) is that species composition develops in a focal community through the combined influences of these processes on net gains or losses of individuals and species in that site. Species originate in situ through speciation or arrive via dispersal from the regional species pool; then, selection and ecological drift cause subsequent losses of individuals or species. This community-assembly framework has been used to study local and regional influences on communities (e.g., Ricklefs 1987), modern coexistence theory in community ecology (e.g., HilleRisLambers et al. 2012), and evolutionary dynamics of community assembly (e.g., Mittelbach and Schemske 2015). A frequently used metaphor for the process of selection depicts species selectively passing through an environmental “filter” (e.g., Keddy 1992) or “sieve” (e.g., van der Valk 1981).

Environmental filters are abiotic and biotic constraints on the demographic performance of individual organisms. If an environmental condition precludes recruitment, survival, or reproduction, the individual is filtered out (selectively excluded or removed). Abiotic filtering occurs as individual organisms interact with the abiotic environment (i.e., filters that define the boundaries of a species’ fundamental niche; Hutchinson 1957), whereas biotic filtering results from species interactions (Myers and Harms 2009b). Kraft et al. (2015) recently suggested that the “environmental filtering” concept should be restricted to abiotic filtering. However, since a species’ environment includes both abiotic and biotic components—whose consequences are difficult to separate empirically—a more inclusive definition can sometimes be helpful, particularly for complex environmental filters like fire that simultaneously influence both abiotic and biotic conditions. In any case, because of the complexity of environmental filters, their influences on community assembly are not fully understood (Kraft et al. 2015).

Fire is a broadly important, multi-faceted, and dynamic filtering mechanism in many ecosystems (Burkle et al. 2015, Myers et al. 2015). Fire may filter species in two general ways. First, fire may

exclude species or homogenize community composition when disturbance-tolerant species dominate post-fire patches (Pausas and Verdú 2008). Fire is a transient filter in a given site; when fires are more severe, there is higher likelihood of mortality (Gagnon et al. 2012, 2015) and there is decreased species richness (Myers and Harms 2011, Burkle et al. 2015). Second, fire may increase species richness by opening space for recruitment from the regional species pool (Myers and Harms 2011). In this case, the post-fire environment might present a transient recruitment opportunity after fire opens space suitable for germination and establishment (i.e., “safe sites”; Harper 1977) by temporarily reducing the depressant effects on smaller individuals of litter and larger neighbors (MacDougall and Turkington 2006, Ratajczak et al. 2012, Kirkman et al. 2016).

The influence of environmental filtering in community assembly may vary depending on rates of dispersal (Leibold et al. 2004). In particular, the degree of filtering may depend in large part on the rate of dispersal from the species pool (i.e., immigration). One way to test this prediction is to manipulate seed arrival from the species pool in combination with environmental filters such as competitors or predators, disturbance, and resource availability (Myers and Harms 2009b). For example, Gross et al. (2005) manipulated nutrients and disturbance and found that non-resident species in their low-productivity grasslands were primarily successful when seeded into disturbed plots. Similarly, Foster and Dickson (2004) found that seed addition increased species richness more in grassland plots in which resource availability was increased. Eshelinen and Virtanen (2005) and Myers and Harms (2009a) found that seed addition increased species richness more in the presence of herbivores (grazers) or in the absence of a dominant plant species (shrubs), respectively. These examples illustrate how dispersal and selective filters can interact to influence community assembly. Even so, there have been relatively few studies of the dispersal × filtering interaction in species-rich communities (Zobel et al. 2000, Myers and Harms 2009a, Iacona et al. 2010) and fewer still where fire is manipulated as a primary selective agent (Suding and Gross 2006, Myers and Harms 2011).

In our study, we experimentally tested the roles of dispersal, environmental filtering via fire, and

dispersal \times fire interactions in groundcover plant communities of the hyper-diverse longleaf pine (*Pinus palustris*) ecosystem (Walker and Peet 1983, Noss et al. 2014). Groundcover at our study site includes exceptionally species-rich, small-scale plant diversity (mean ~ 30 species \times m⁻²; our study), a characteristic of this ecosystem type (Walker and Peet 1983, Varner and Kush 2004, Mitchell et al. 2006). We hypothesized that environmental filtering happens both during fires (e.g., heat damages and kills individuals) and in the post-fire environment (e.g., reduced competition and interference owing to reduced biomass, presence of ash). We further hypothesized that these influences interact with dispersal such that the consequences of dispersal and filtering are only fully revealed when considered in combination. We tested four specific predictions: (1) Because many species are rare in high-diversity groundcover (Kirkman et al. 2001, Clark et al. 2008), we predicted that plot-level species richness would be seed dispersal-limited. (2) Because small-scale fuel loads influence fire characteristics (Williamson and Black 1981, Hiers et al. 2009, Mitchell et al. 2009, Gagnon et al. 2015) and post-fire conditions (Thaxton and Platt 2006, Myers and Harms 2011), we predicted that fire acts as a complex environmental filter (echoing Kirkman et al. 2016). We predicted that the immediate effect of adding fuels would be to decrease species richness, but that over time, open conditions would enable recruitment of more species into post-fire habitats, thereby increasing species richness. (3) Since post-fire ash can increase nutrient availability in a brief fertilization pulse as ash mineralizes (Boring et al. 2004, Carter and Foster 2004), we predicted that the effect could stimulate recruitment. We predicted that adding ash would increase species richness, at least in the short term, whereas reducing ash would decrease species richness. Over the longer term, fertilization could increase productivity, but decrease diversity, that is, the “paradox of enrichment” (Rosenzweig 1971, Tilman 1982). (4) We predicted that seed dispersal and fire-generated environmental filtering would interact (Myers and Harms 2011). Specifically, we predicted that seed addition to plots with increased fuels would generate larger increases in species richness compared to plots with decreased fuels. In addition, we predicted that seed addition to plots in which ash was removed would

generate smaller increases in species richness than in plots with increased ash.

We additionally tested hypotheses concerning individual-level performance and landscape-level patterning at smaller and larger scales than our treatment plots. (5) We hypothesized that individual plants present immediately after fire can capitalize on relatively resource-rich, open conditions in the groundcover during the early post-fire re-building phase as the growing season progresses. We predicted that individuals persisting in plots with increased fuels would perform better. (6) Finally, we hypothesized that landscape-level heterogeneity would influence species richness and composition somewhat independently from the smaller-scale influences examined by our manipulative experiments; we predicted both pre-treatment and persistent differences in species richness and composition at the scale of burn units. We found that changes in fire filtering interacted with dispersal to influence species richness, that filtering dynamics influenced plant performance, and that either heterogeneity in environmental conditions or unique colonization history produced striking differences in species composition among burn units.

METHODS

Study site: Camp Whispering Pines, Louisiana

We conducted our experiment in the restored longleaf pine ecosystem of Camp Whispering Pines (CWP), Tangipahoa Parish, Louisiana, United States (30°41' N, 90°29' W; mean annual temperature = 19°C; mean annual rainfall = 1626 mm; see Platt et al. 2006 for a detailed description of the study site). Camp Whispering Pines is owned and managed by the Girl Scouts Louisiana East and is typical of loess plain pine savannas at the western end of the East Gulf Coastal Plain. The dissected terrain is 25–50 m above msl. Soils are Pleistocene-aged, Tangi and Toula silt loams (<http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx>), and elsewhere reported as Tangi–Ruston–Smithdale fine sands mixed with and capped by loess (McDaniel 1990); they are at the high end of the soil fertility gradient in southeastern U.S. pine savannas. CWP savannas contain longleaf pine that regenerated naturally after logging in the early 1900s (Noel et al. 1998). The groundcover at CWP was open-range-grazed,

but never plowed. The site has a large species pool (>300 vascular plant species) and high species richness at local scales (mean = 22 species \times 0.5 m⁻², Myers and Harms 2011; ~30 species \times m⁻², this study; ~100 species \times m⁻², Platt et al. 2006), including a diverse groundcover assemblage of forbs, grasses, sedges, and shrubs. Since 1994, CWP has been managed with biennial early growing season (April–May) prescribed fires that alternate between large burn units (Platt et al. 2006, Thaxton and Platt 2006). We conducted our experiments west of Highway 1054 where the structural co-dominant species *Schizachyrium scoparium* and *Schizachyrium tenerum* together predominate in the groundcover, in contrast to the east side of the road in which Roth et al. (2008) reported dominance by *Andropogon virginicus* var. *virginicus*.

Experimental design: factorial manipulation of seed arrival and environmental filters

We used a factorial field experiment applied to groundcover plots. To manipulate dispersal, we added seeds using realistic immigration rates. To manipulate fire-generated environmental filters, we manipulated (removed or added) natural fuels (pine needles) and post-fire ash. We employed a 3 \times 2 \times 2 factorial treatment design with three treatments: pre-fire fuel load (fuel addition, fuel reduction, or fuel control); post-fire ash (ash addition or ash removal); and seed arrival (seed addition or seed control). We randomly assigned treatments to 96 square 1 \times 1 m plots in four burn units (treated as blocks; N = 24 plots/burn unit). We used separate burn units that were available for manipulative experiments to eliminate the pseudo-replication that would otherwise result from conducting the entire experiment in a single burn unit, thereby increasing the generalizability of the results. Prior to selecting our sites, casual observations among burn units suggested that species composition—especially of the infrequent species—differed, but that structurally dominant bunchgrass species, fuel loads, and other structural aspects (e.g., aboveground biomass, bunchgrass density) of the units were similar. Each burn unit is 16–30 ha and its centroid is 0.4–1.0 km distant from the others. In total, each factorial treatment combination was replicated eight times. Fuel and ash treatments were applied once to two burn units in 2006 and to the other two burn units in 2007, whereas seed additions

were applied in both 2006 and 2007. In each year, the two burn units were burned on separate days. To reduce edge effects within the plots, fuel and ash treatments were applied to square 2 \times 2 m areas, each centered on the centroid of its corresponding 1 \times 1 m plot. To achieve independence of treatment conditions among plots and to reduce confounding effects of pines, plots were positioned such that their edges were at least 5 m distant from one another and at least 2 m from the outermost canopy of pine trees.

To test the influence of fire on abiotic and biotic ecological filters, we manipulated fuel loads in plots before early growing season prescribed fires using three treatments (n = 32 total plots/treatment; 8 plots/treatment/block \times 4 burn units). First, on the morning of the fire, we increased fine fuels by adding 8 kg of dry, uncompacted longleaf pine needles spread evenly across one-third of the plots' 2 \times 2 m areas (fuel-addition treatment). This quantity of pine straw (2 kg \times m⁻²) matched the upper range of observed fuel loads at this relatively productive study site (Thaxton and Platt 2006, Gagnon et al. 2012). Second, we reduced fuel loads by clipping and removing all existing biomass above 5 cm in eight other plots in each burn unit (fuel-reduction treatment). Third, the eight remaining plots in each fire were fuel controls that burned under natural fuel loads. Following fuel treatments, but before burning, plots contained on average 3076 g \times m⁻² (fuel addition), 1076 g \times m⁻² (fuel control), and 444 g \times m⁻² (fuel reduction) of total aboveground biomass (live and dead; Gagnon et al. 2012).

To test the influence of fire through its effect on post-fire ash conditions, we manipulated ash using two treatments (N = 48 total plots/treatment; N = 12 plots/treatment/burn unit \times 4 burn units). First, on the same day as the prescribed fires, we removed ash from half of the plots using leaf blowers operating at low velocities (ash removal treatment). Second, after removing ash from the remaining half of the plots using the same method, we added a standardized quantity of ash (0.5 kg; about twice the amount found in a fuel-control plot immediately after a fire) back to those same plots (ash addition treatment). Thus, our ash manipulations allowed us to decouple the fire effects under different fuel loads from effects of post-fire ash (e.g., increased nutrient availability, microsites for seed germination).

To test the influence of dispersal limitation and the role of our aforementioned treatments as filters, we added seeds of 94 groundcover species (from the CWP species pool) to half of the plots (seed addition; $N = 48$ total plots; $N = 12$ plots/treatment/burn unit \times 4 burn units; Appendix S1: Table S1). The remaining plots were seed controls that received natural seed rain. We added field-collected seeds as seeds became available, mimicking the timing of natural seed dispersal for most species. The majority of our seed-addition species are gravity- and wind-dispersed forbs, which constitute the most species-rich functional group at the study site (Platt et al. 2006). To mimic natural, low levels of dispersal in high-diversity communities, we added a total of ~ 1750 seeds \cdot m $^{-2}$ \cdot yr $^{-1}$, at a median rate of 20 seeds \cdot species $^{-1}$ \cdot m $^{-2}$ \cdot yr $^{-1}$ ($N = 66$ total species in 2006 and 73 total species in 2007). In contrast, estimates of natural total seed fluxes at our study site average $\sim 11,600$ seeds \cdot m $^{-2}$ \cdot yr $^{-1}$ (E. I. Johnson, *unpublished data*). Thus, we estimate that our seed-addition treatment increased local seed rain by $\sim 15\%$. Seed viability averaged 59% among tested species (range = 12–98%; Appendix S1: Table S1; see Myers and Harms 2009a for germination methods).

Finally, to test for effects of fuel manipulation on the local performance of groundcover species in post-fire environments, we measured local abundance, numbers of leaves, and leaf sizes (lengths) of seven common seed-addition species 2 yr post-fire (see Appendix S1: Table S2 for species names). These data were collected as part of a concurrent experiment at the study site in which two of the same fuel treatments (fuel addition and fuel control) were applied to a separate set of plots located in two of the four burn units used in the present study (see Myers and Harms 2011 for details). All seven species were gravity- or wind-dispersed forbs that were added to plots as seeds. For each species, we measured local abundance as the total number of stems (or basal rosettes) present in 1×0.5 m seed-addition plots ($N = 12$ –30 fuel-control plots, $N = 17$ –29 fuel-addition plots—sample sizes vary since species occurred in a variable number of plots; Appendix S1: Table S2). In each plot, we measured the mean number of leaves per stem by counting all of the leaves on one to three stems of each species. We measured leaf size using the mean length of the longest leaf on the same

stems. Since the focal seed-addition species were generally absent or rare in seed-control plots (Myers and Harms 2011), this approach allowed us to explicitly examine the effects of fuel treatments on the recruitment and growth performance of a subset of species for which we were reasonably confident that most of the recruitment resulted from seed additions.

Data collection

We measured species richness and composition in each plot during three different census periods: prior to the fuel-manipulation treatments (pre-treatment census), 1 yr after and again 2 yr after prescribed fires. Two burn units (Oak Ridge and Sunny Trails) were censused in October 2005 (pre-treatment) and again in May–October 2006 (first growing season post-fire) and May–October 2007 (second growing season post-fire) following prescribed fires (in which fuels and post-fire ash were manipulated) in April 2006. The two other burn units (Sunset and Tall Winds) were censused in October 2006 (pre-treatment), May–October 2007, and May–October 2008 following prescribed fires (in which fuels and post-fire ash were manipulated) in May 2007. Each extended May–October census included both a spring and fall visit to the plots, to be able to include species whose phenologies make them difficult to observe or identify in the fall or spring, respectively.

Statistical analyses

We analyzed pre-treatment species composition using the R vegan package (Oksanen et al. 2015). First, we created matrices of community dissimilarity using the incidence-based Jaccard's index. Second, we used analysis of similarity (ANOSIM) to test for differences in community composition among burn units. Third, we used nonmetric multidimensional scaling (NMDS; isoMDS function) to generate a two-dimensional ordination showing differences in community similarity among treatments.

We analyzed total species richness, richness of seed-addition species, and local performance of seed-addition species using linear mixed-effects models (lme function in the R nlme package; Pinheiro et al. 2015). For species richness, we used repeated-measures models to account for correlation among plot measurements across years. Our model for total species richness included the

Table 1. Results from mixed-effects ANOVA testing for effects of ash manipulations, fuel manipulations, and seed addition on total species richness and richness of seed-addition species.

Variables	Pre-treatment (2005)				Post-treatment (Rept measures)		
	DF	denDF	F	P	denDF	F	P
Total species richness							
Fuel***	2	83	0.40	0.6715	83	15.79	0.0001
Ash	1	83	0.05	0.8131	83	00.00	0.9237
Seed***	1	83	0.90	0.3454	83	67.33	0.0001
Census***	1	–	–	–	91	67.22	0.0001
Fuel × Ash	2	83	0.45	0.6351	83	00.06	0.9353
Fuel × Seed*	2	83	2.00	0.1405	83	03.15	0.0476
Fuel × Census	2	–	–	–	91	02.14	0.1230
Ash × Seed	1	83	0.02	0.8872	83	00.74	0.3899
Ash × Census	1	–	–	–	91	00.35	0.5516
Seed × Census***	1	–	–	–	91	29.38	0.0001
Seed-addition species							
Fuel	2				39	1.95	0.1548
Ash	1				39	0.22	0.6432
Census***	1				44	90.01	0.0001
Fuel × Ash	2				39	0.24	0.7910
Fuel × Census	2				44	0.41	0.6670
Ash × Census	1				44	0.78	0.3825

Note: *P*-values < 0.05 indicated by one asterisk and bold, while *P*-values < 0.0001 indicated by three asterisks and bold; burn units modeled as random block effects; seed-addition species richness analyzed using data only from seed-addition subplots because seed-addition species occurred infrequently in seed-control subplots; 2005 pre-treatment data for total species richness log₁₀-transformed to normalize residuals; a heterogeneous variance model used for the repeated-measures ANOVA of total species richness.

three treatments (fuel, ash, and seed) and census as fixed effects, and burn units (blocks) as random effects. To analyze richness of seed-addition species, we only used data from the seed-addition treatment, which allowed us to explicitly examine the effects of fuel and ash manipulations on species we added as seed, most of which were otherwise rare or absent from our plots. These models included fuel treatments, ash treatments, and census as fixed effects, and burn units (blocks) as random effects. Our models for local performance (abundance, number of leaves, leaf size) of seed-addition species included fuel treatments as fixed effects and blocks as random effects (Myers and Harms 2011). When necessary, we log₁₀-transformed to normalize residuals. When response variables did not meet the assumption of homogeneous variances, we used a heterogeneous variance model (varIdent function in the R nlme package) and selected the model with the lowest Akaike Information Criterion (AIC) score. We used post hoc Tukey's tests from the R lsmeans package (Lenth 2016) to determine significance among treatment groups and their interactions. There were no significant

three-way interactions for species richness. For simplicity, we therefore only present results from models that included two-way interactions. All analyses were performed in R (R Development Core Team 2014).

RESULTS

In total, we recorded 239 plant species, 136 genera, and 54 families in our plots over the course of the experiment. An average unmanipulated (control) plot had 28.8 ± 8.4 (mean \pm SD; 27.5 median) species, 22.9 ± 7.0 (20.5 median) genera, and 10.6 ± 3.7 (10.5 median) families present in a single census. Prior to experimental treatments, species richness did not differ among treatment plots (Table 1).

Landscape-level influences on species composition

Pre-treatment species composition differed strikingly across the landscape. One burn unit (Oak Ridge) clearly differed in species composition from the other three (Fig. 1). The other three burn units overlapped more substantially in species composition.

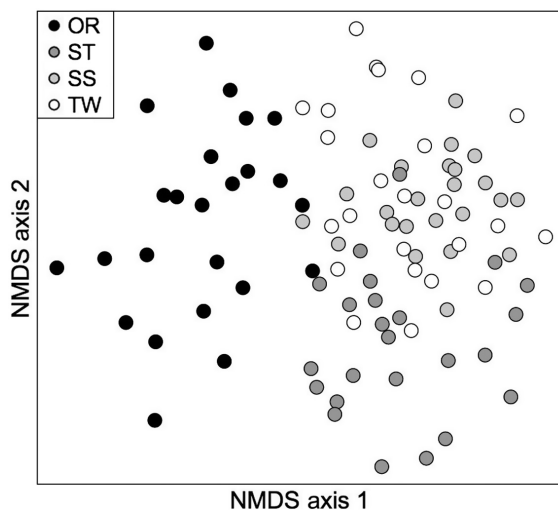


Fig. 1. Variation in pre-treatment species composition (Jaccard's dissimilarity) among sites for groundcover plant communities at Camp Whispering Pines, Louisiana, derived from nonmetric multidimensional scaling (NMDS; stress = 28.1). Circles represent replicate plots (local communities) in four different burn units ($N = 24$ plots/burn unit); communities close together in ordination space are more similar in species composition. Site abbreviations: OR, Oak Ridge; ST, Sunny Trails; SS, Sunset; TW, Tall Winds.

Community-assembly mechanisms and their interactive influences on local species richness

Seed additions and fuel manipulations affected species richness individually and in concert. Biologically realistic rates of seed addition increased species richness ($F_{1,83} = 67.33$, $P < 0.001$; Table 1). Fuel manipulations affected species richness in our plots ($F_{2,83} = 15.79$, $P < 0.001$), but not among those species we added as seeds ($F_{2,39} = 1.95$, $P < 0.159$). The influence of seed additions varied with fuel treatments (post-treatment repeated-measures Fuel \times Seed interaction; $F_{2,83} = 3.15$, $P < 0.05$; Fig. 2; Table 1). Seed addition increased species richness in both fuel-addition and fuel-reduction plots more than in fuel-control plots (Fuel \times Seed interaction plot; Appendix S1: Fig. S1).

The influence of seed addition increased over time. This was true among species naturally in the plots (post-treatment repeated-measures Seed \times Census interaction; $F_{1,91} = 29.38$, $P < 0.001$; Fig. 2; Table 1) and also for those we added as seeds (effect of census on richness of seed-addition

species: $F_{1,44} = 90.01$, $P < 0.001$). Species richness increased much more from the first post-fire growing season to the following growing season in the seed-addition plots than it did in the seed-control plots (Seed \times Census interaction plot; Appendix S1: Fig. S2).

By contrast, manipulating quantities of ash immediately after burning had no measurable effect on species richness ($F_{1,83} = 0.00$, $P < 0.924$; Table 1). Neither did ash manipulations produce interactions with fuel manipulations to influence species richness, nor with seed additions (for Ash \times Fuel interaction, $F_{2,83} = 0.06$, $P < 0.935$; for Ash \times Seed interaction, $F_{1,83} = 0.74$, $P < 0.390$). There was also no effect of ash manipulations over time ($F_{1,91} = 0.35$, $P < 0.552$), and there was no effect of ash manipulations on the richness of those species added as seeds ($F_{1,39} = 0.22$, $P < 0.643$).

Filters influence individual-level performance

Individual plants that appeared (by recruitment or resprouting) in the comparatively open post-fire groundcover of fuel-addition plots recruited and grew more than those in the relatively crowded, densely covered fuel-control plots (Fig. 3; Appendix S1: Table S2). For all seven of these seed-addition species and each of the three response variables (abundance, number of leaves, and leaf size), the mean values were larger in fuel-addition plots relative to fuel-control plots (Fig. 3). Individual-level plant performance was significantly greater in fuel-addition plots for more than half of the species as measured by the three response variables: Abundance was higher for four species; leaf number per stem was greater for five species; and leaves were larger for five species ($P < 0.05$; Appendix S1: Table S2).

DISCUSSION

Local-scale species richness is dispersal-limited in high-diversity communities

Our study clearly demonstrated dispersal-limited, plot-level species diversity. Realistic rates of seed dispersal (immigration) increased species richness in almost all cases comparing seed-addition to seed-control plots. Whereas very high levels of seed addition can be useful for testing population-level dispersal limitation (Tilman 1997), these contrast with the realistic levels we used here to serve as proxy tests for increasing

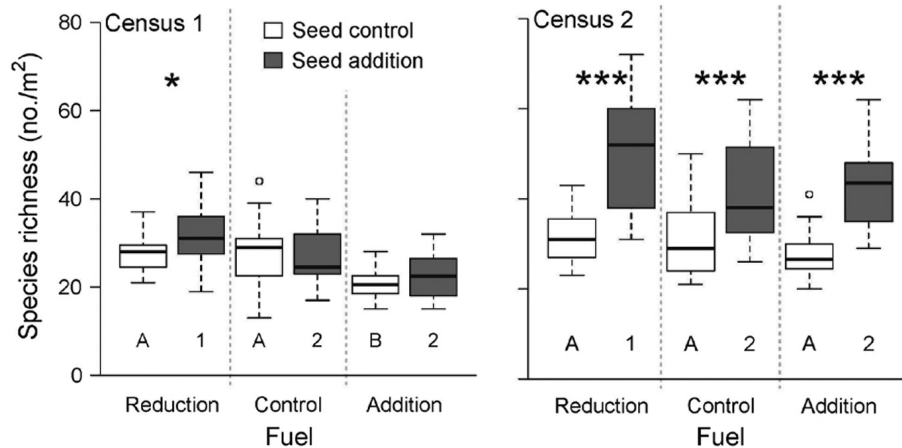


Fig. 2. Species richness in the fuel-manipulation and seed-addition treatments 1 yr (Census 1) and 2 yr (Census 2) post-fire. Boxes represent the median and 25th/75th percentiles; whiskers extend to 1.5 times the interquartile range. Asterisks above boxplots indicate significant difference between seed control vs. seed addition within a given census and fuel treatment, where one asterisk indicates $P < 0.05$ and three asterisks indicate $P < 0.0001$. Letters (A or B) below boxplots indicate significant difference ($P < 0.01$) within census among fuel treatments in seed controls, whereas numbers (1 or 2) indicate significant difference ($P < 0.01$) within census among fuel treatments in seed-addition treatments. Statistical results are provided in Table 1.

the size of the regional species pool. We achieved our proxy for an increased species pool size by adding novel species to plots that were nevertheless present in similar habitat outside the plots, as if adult individuals of those species were dispersing seeds from immediately outside the plots. Our results support the idea of a positive causal link between regional species richness and local species richness (Zobel 1997).

Our results are consistent with growing evidence that many communities are unsaturated with species and therefore open to invasion from the regional species pool (Myers and Harms 2009b, Cornell and Harrison 2014). Although dispersal limitation of community richness has been shown in a variety of plant communities (reviewed in Myers and Harms 2009b), few seed-addition experiments have been done in the highest-diversity plant communities where saturation may be most likely (Elton 1958, Tilman 1997). Our results indicate that high-diversity pine savannas are open-membership, dispersal-limited communities (a.k.a. unsaturated; Cornell 1999). As an extreme example, one plot started with 31 species, was treated with fuel reduction and seed addition, but during the course of the experiment had 81 total species present at least once during

the three census years, and contained 57 species during the final census. The results from this and other seed-addition experiments (Myers and Harms 2009a, 2011) are supported by two related findings in the longleaf pine ecosystem. First, groundcover species with low dispersal potential (e.g., gravity- and ant-dispersed species) are often absent from communities that have undergone recent restoration, even when source populations are present in intact communities nearby (Kirkman et al. 2004a). Second, large communities connected by experimental corridors have higher species richness than isolated communities (Damschen et al. 2006). Collectively, these studies support the idea that dispersal limitation is a key driver of community assembly in high-diversity pine savannas and in species-rich plant communities generally (Hurtt and Pacala 1995, Hubbell et al. 1999).

Species richness increased more in seed-addition plots relative to control plots. This is most likely an effect over time of adding seeds and having more of them germinate (or grow large enough to be detected) by the later census. Unmanipulated groundcover probably responds similarly to pulses of seeds associated with environmental fluctuations (e.g., fire, weather, soil

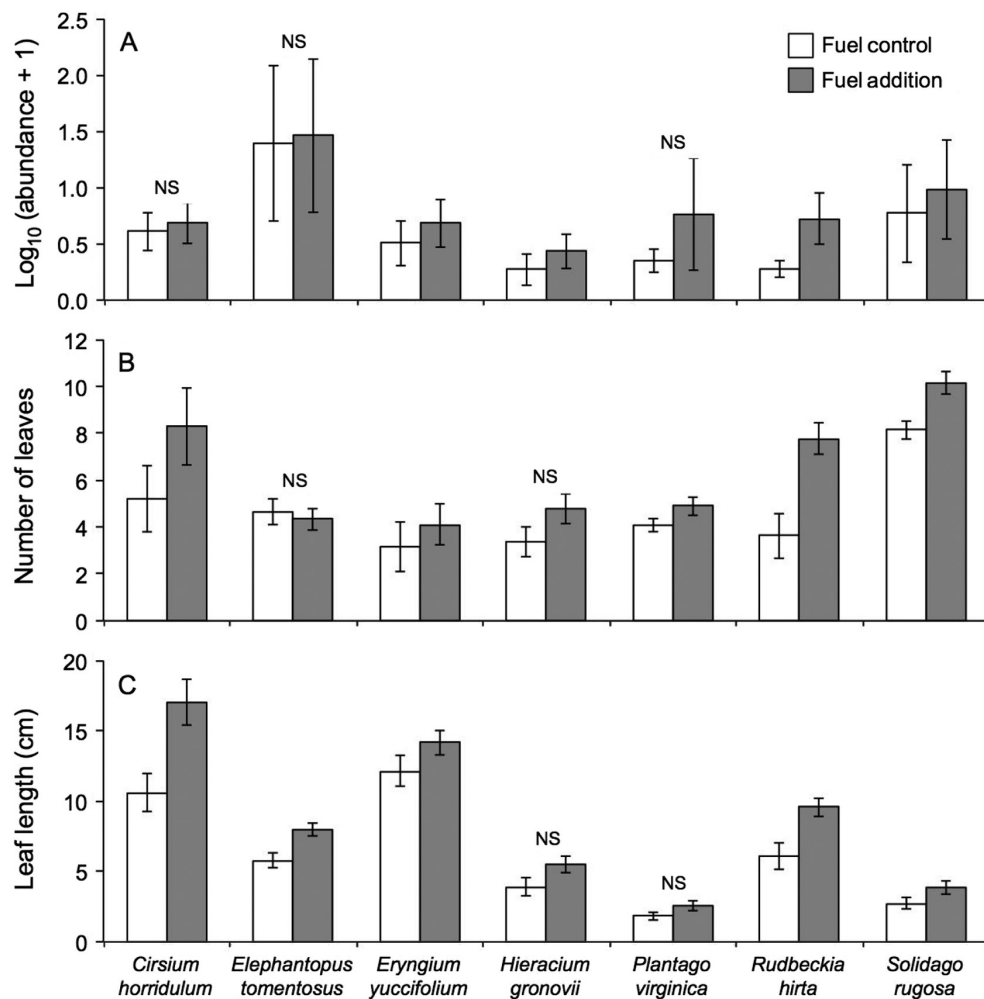


Fig. 3. Abundance and growth performance of seven common seed-addition species in fuel-control and fuel-addition plots 2 yr post-fire. (A) Local abundance (number of stems) in 0.5-m² plots, (B) number of leaves per individual stem, and (C) leaf size (length) of the three largest leaves per individual stem. Bars represent means \pm 1 standard error. NS = $P > 0.05$ based on t tests for differences within species; sample sizes and P -values are listed in Appendix S1: Table S2. These data were collected as part of a separate, but concurrent experiment at the study site (see Myers and Harms 2011 for details).

moisture, generalist herbivore outbreaks) that influence community-wide seed production, dispersal, and recruitment. Such episodic recruitment has been noted in other pine savanna communities (Iacona et al. 2010, Kirkman et al. 2016) and is likely to be a common feature of them.

Complex, fire-generated filters interact with dispersal to assemble groundcover communities

Although we expected dispersal and fire-generated filtering to interact in shaping small-scale groundcover species richness in our

high-diversity site, the nature of their interaction was surprising. We did not predict that seed addition would increase species richness similarly in fuel-addition and fuel-reduction plots compared to a more modest increase in fuel-control plots. This result illustrates the complex nature of fire-generated filtering.

Fire-generated filters operate differently during and after fires. Fuel-addition plots incur more immediate losses of species during fires, possibly owing to increased aboveground combustion and belowground heating. Fire-logger measurements

collected as part of a complementary study in a subset of the same experimental plots as those used in the current study demonstrated significantly higher maximum fire temperatures and total heat release in fuel-addition relative to fuel-control plots, as well as a substantial reduction in post-fire live vegetation cover in fuel-addition relative to fuel-control plots (Gagnon et al. 2015). Because most perennial species in our plots were capable of resprouting, soil heating sufficient to kill their regenerative belowground organs is probably the most likely cause of species losses in these fuel-addition plots (Gagnon et al. 2015). Soil heating can also decrease species richness by causing seed mortality in the soil seed bank, particularly of small-stature grasses and forbs (Myers and Harms 2011, Gagnon et al. 2015). As a consequence, fuel addition may also produce more open space for colonization. Such elevated fuel levels would occur naturally wherever downed branches and pine cones rest on the ground. These coarse, woody fuels burn longer, and thus with increased soil heating, than fine fuels like pine needles and bunchgrass culms (Thaxton and Platt 2006, Loudermilk et al. 2014).

In contrast, fuel-reduction plots may lose fewer species during the fire itself and may provide a less stressful physical environment in terms of moisture availability, temperature, or cover for avoidance of herbivores and granivores. We clipped fuel-reduction plots and removed the cut fuels; these plots then burned in a fine-scale mosaic, with small patches of low-growing vegetation remaining after fires. By comparison, fuel-control plots and fuel-addition plots both burned thoroughly to ash. Net facilitation is a possible explanation for the fuel-reduction treatment having the highest species richness. Facilitation is increasingly recognized in plant community ecology as a contributing influence toward community assembly (Bertness and Callaway 1994). It may be that ameliorating influences by vegetation during relatively cool fires or residual vegetation that remains after fires benefit individual plants. Wallett (2015) recently produced experimental evidence for diffuse facilitation in pine savanna groundcover benefitting dominant bunchgrass (wiregrass) tussocks. In contrast, even though Iacona et al. (2012) found that wiregrass tussocks cast shade that could potentially facilitate recruitment, they found no evidence that this occurs

based on microsite characteristics beneath and away from spreading tussocks and recruitment performance of seeds sown under artificial shade to mimic wiregrass tussocks. In our fuel-reduction plots, all established bunchgrass tussocks survived without measurable damage (Gagnon et al. 2012). Highest species richness in these same plots suggests that despite the extraordinary floristic diversity of these longleaf pine communities, there remained uncolonized space and resources between existing bunchgrass tussocks, including bare mineral soil for species whose seeds require it for germination.

Ash did not affect species richness as either a main effect, nor via interactions with other treatments. This is in spite of our careful incorporation of ash as a main effect fully integrated into our experimental design. This lack of ash-related filtering contrasts sharply with the clear effects of our other fire-related treatments. Studies in some other fire-adapted ecosystems have similarly found either no effect or a negative effect of ash on plant germination (Enright et al. 1997, Izhaki et al. 2000). Immediately following burning, ash in fire-dependent communities like the longleaf pine ecosystem raises pH near the soil surface and increases available phosphorus, potassium, calcium, and magnesium (Christensen 1977, Enright et al. 1997, Boring et al. 2004). This effect is short-lived in the longleaf pine ecosystem and can disappear within six months (Christensen 1977). Such a fertilization effect may simply be too ephemeral for us to have observed given our sampling frequency. A fertilization effect may also be more likely in sites with lower fertility or productivity, such as on sandier soils in the wiregrass-dominated portion of the range of longleaf pine savannas. Alternatively, if nitrogen or another nutrient limits plant growth at our study site, then we would expect no fertilization effect regardless of any pulse of exchangeable cations (Christensen 1977).

Complex, fire-generated filters create fine-scale heterogeneity

Complex filtering should foster heterogeneity. Each different environmental filter (e.g., fire, soil moisture stress, light availability) excludes a potentially unique subset of species, such that the idiosyncratic set of species that arrives via dispersal to a site from the regional species pool

is filtered differently, contributing to heterogeneity in species composition and species richness among sites, experiments, years, etc. Consider a plot with a sparse fuel load compared to one with a heavy fuel load. During a fire, fuel combustion within the sparse-fuel plot might be incomplete compared to the heavy-fuel plot. Similarly, relatively little soil heating would occur in the sparse-fuel plot relative to the heavy-fuel plot. Individuals of species incapable of surviving the fuel consumption and soil heating of the latter plot could persist in the former plot, depending of course on which species arrive in the first place. Such fine-scale differences in filtering should create fine-scale spatial heterogeneity and should contribute toward temporal heterogeneity among years or seasons.

Kirkman et al. (2016) have found similar complexity in groundcover community assembly of pine savanna groundcover dominated by wiregrass. Soil moisture is an additional temporally and spatially heterogeneous filter that potentially interacts with dispersal in these pine savannas (Iacona et al. 2010, Myers and Harms 2011).

Complex, fire-generated filters influence individual-level plant performance

Individual plants either survive to reproduce or fail to pass through the various filters that confront them. Individuals that survive a fire or that disperse into a post-fire site can take advantage of the relatively more open groundcover conditions with increased space and other resources relative to unburned sites (Brewer et al. 1996). In our experiments, recruitment (Myers and Harms 2011; this study) and growth performance (this study) increased in plots with the largest fuel loads. In the same site, Myers and Harms (2011, e.g., Appendix D) and Gagnon et al. (2012, 2015—using a subset of the same experimental plots as the current study) showed that higher fuel loads correspond to more open space in the groundcover. In addition, post-fire litter and ash samples collected from a separate but concurrent fuel-addition experiment at the same study site but using different plots indicated that seeds potentially present in the pine needle litter used as fuel-addition fuels were killed during the fire and that most of the litter in all plots was consumed by fire, yet more litter consumption occurred in fuel-addition plots relative to fuel-control plots

(Myers and Harms 2011). For subordinate taxa, this could represent a recruitment opportunity following aboveground consumption of the physically dominant bunchgrasses or woody species. To determine whether the enhanced recruitment and growth performance we observed also translate into enhanced reproductive output would require further experimentation. Even so, it may be that the majority of reproductive output, especially for many small-statured species, comes from those individuals that are temporarily released after a fire from competition and hindrance by litter. For one of the dominant bunchgrasses themselves (*S. scoparium*), Gagnon et al. (2012) found increased flowering in fuel-addition plots after prescribed fires at the same study site. The phenomenon of increased reproductive output by groundcover species when biomass in an individual's immediate vicinity is removed may also be context dependent since recent work in a different longleaf savanna site revealed habitat-specific facilitation of wiregrass by heterospecific neighboring plants in dry, relatively sparsely vegetated sandhill sites but competition in more densely vegetated seepage slopes (Wallett 2015).

We and others previously found limited evidence for competitive influences on smaller-stature species by the structurally dominant bunchgrasses at our study site (Roth et al. 2008, Myers and Harms 2009a). Roth et al. (2008) removed *A. virginicus* with herbicide and found virtually no changes in plant cover, species richness, or species composition after two fire-free years. They interpreted these results to mean that competition by the structurally dominant grass plays a minor role in community assembly at the site. Similarly, Myers and Harms (2009a) removed *S. tenerum* tussocks with herbicide and also reduced their potential for asymmetric competition for light by tying up their aboveground biomass into sheaves, yet found no influence on plot-level species richness. Furthermore, the pattern that species richness was not correlated with the percentage of total standing crop biomass contributed by wiregrass led Kirkman et al. (2001) to conclude that the competitive influence of wiregrass is negligible. The competitive influence of bunchgrass tussocks may most consequentially affect performance of neighboring plants such that coarser-level assessment than individual performance (e.g., plot-level diversity

or cover) fails to detect those influences, or such that species compositional changes occur without concomitant changes in species richness itself.

Landscape-level heterogeneity also influences groundcover species composition

Patterns consistent with large-scale influences on community assembly were also evident in our study. Our experiment focused on the very small scale of 1-m² plots with manipulations that were similarly focused. Even so, one burn unit clearly differed from the others in species composition. Differences like this could have arisen via a variety of mechanisms operating at different spatial scales, but especially those larger than our study plots. Variation in landscape-level environmental conditions could differentially filter species from a common regional species pool. Such differential filtering at the landscape scale is commonly observed in pine savannas. For example, unique species sets are found along natural gradients over which soil moisture, soil texture, or nutrient availability varies (e.g., Kirkman et al. 2001, 2004b, Carr et al. 2009). Alternatively or in combination, compositional divergence among burn units could result from chance events, including idiosyncratic colonization or extinction histories. Episodic availability of recruitment opportunities (Iacona et al. 2010) could also produce differences among sites. Burn units represent different fire histories, environmental features, colonization and extinction histories, etc. Accordingly, large-scale deterministic (e.g., filtering) and stochastic (e.g., chance historical colonization or extinction events) processes clearly influence local community composition in addition to the complex local interactions we observed between local dispersal and fire-generated, fine-scale filtering.

CONCLUSIONS

In conclusion, fires can produce heterogeneous environmental filtering at multiple spatial and temporal scales. At local scales, species are eliminated by severe fires. Then in these same locations, space and resources are newly available for colonization following severe fires. By contrast, where fire is less severe, environmental filtering is less dynamic during and after fires; fewer if

any species are eliminated by weaker fires, and less new space is available for colonization afterward. Our study also demonstrates that even extremely diverse plant communities may be unsaturated in that they retain colonization opportunities for new species. As such, the overall effect may be that even when environmental filtering is relatively stable, species richness can increase if dispersal brings new species to a local community.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1716/full>

APPENDIX

Table S1. Ninety-four species added in the seed-addition treatments in 2006 and 2007, showing their life forms, dispersal types based on seed morphology, number of seeds added per 1-m² plot in each year, and percent seed germination on petri dishes under controlled growth chamber conditions (not all species were tested for germination).

Species	Family	Life form ¹	Dispersal type	No. seeds added 2006	No. seeds added 2007	Germ (%)
<i>Ageratina aromatica</i>	Asteraceae	PF	wind	25	25	94
<i>Agrostis hyemalis</i>	Poaceae	PC ₃	wind	–	20	
<i>Agrostis perennans</i>	Poaceae	PC ₃	wind	65	–	
<i>Aletris lutea</i>	Liliaceae	PF		–	20	
<i>Allium bivalve</i>	Liliaceae	PF		20	–	
<i>Andropogon gerardii</i>	Poaceae	PC ₄	wind	25	20	
<i>Anthaenantia villosa</i>	Poaceae	PC ₄	gravity	20	–	
<i>Arnoglossum plantagineum</i>	Asteraceae	PF	wind	–	30	
<i>Asclepias connivens</i>	Asclepiadaceae	PF	wind	–	20	
<i>Baptisia bracteata</i> var. <i>leucopheae</i>	Fabaceae	PL	gravity	5	4	
<i>Bidens aristosa</i>	Asteraceae	BF	animal	–	25	
<i>Brickellia eupatorioides</i>	Asteraceae	PF	wind	–	20	
<i>Carex debilis</i>	Cyperaceae	PS	gravity	–	20	
<i>Carex glaucescens</i>	Cyperaceae	PS	gravity	20	20	84
<i>Carex tenax</i>	Cyperaceae	PS	gravity	20	20	94

<i>Carphephorus odoratissimus</i>	Asteraceae	PF	wind	–	20	
<i>Centrosema virginianum</i>	Fabaceae	PL	gravity	–	10	
<i>Ceanothus americanus</i>	Rhamnaceae	W	explosive	3	–	
<i>Chamaecrista nictitans</i>	Fabaceae	PL	gravity	–	20	
<i>Chaptalia tomentosa</i>	Asteraceae	PF	wind	5	20	
<i>Chasmanthium laxum</i>	Poaceae	PC ₄		15	30	
<i>Chromolaena ivifolia</i>	Asteraceae	PF	wind	20	20	68
<i>Chrysopsis mariana</i>	Asteraceae	PF	wind	–	20	26
<i>Cirsium horridulum</i>	Asteraceae	BF	wind	20	20	88
<i>Cirsium nuttallii</i>	Asteraceae	BF	wind	6	–	
<i>Conoclinium coelestinum</i>	Asteraceae	PF	wind	–	25	96
<i>Conyza canadensis</i>	Asteraceae	AF	wind	20	75	
<i>Coreopsis tripteris</i>	Asteraceae	PF		–	20	
<i>Crotalaria purshii</i>	Fabaceae	PL	gravity	20	20	12
<i>Ctenium aromaticum</i>	Poaceae	PC ₄	gravity	–	20	
<i>Desmodium lineatum</i>	Fabaceae	PL		22	–	
<i>Dichanthelium laxifolium</i>	Poaceae	PC ₃	gravity	20	100	
<i>Dichanthelium scoparium</i>	Poaceae	PC ₃	gravity	20	50	
<i>Diodia teres</i>	Rubiaceae	AF	gravity	20	20	
<i>Elymus virginicus</i>	Poaceae	PC ₃	gravity	–	20	
<i>Eragrostis spectabilis</i>	Poaceae	PC ₄	gravity	20	–	
<i>Eryngium integrifolium</i>	Apiaceae	PF	gravity	20	–	
<i>Eryngium yuccifolium</i>	Apiaceae	PF	gravity	–	20	28
<i>Eupatorium capillifolium</i>	Asteraceae	PF	wind	100	25	

<i>Eupatorium perfoliatum</i>	Asteraceae	PF	wind	–	20	
<i>Eupatorium rotundifolium</i>	Asteraceae	PF	wind	30	20	40
<i>Eurybia paludosa</i>	Asteraceae	PF	wind	25	20	26
<i>Euthamia leptcephala</i>	Asteraceae	PF	wind	30	–	
<i>Galium orizabense</i>	Rubiaceae	PF		20	–	
<i>Gamochaeta americana</i>	Asteraceae	PF	gravity	20	20	
<i>Helenium amarum</i>	Asteraceae	PF	gravity	20	25	
<i>Helenium flexuosum</i>	Asteraceae	PF	gravity	20	20	86
<i>Helianthemum carolinianum</i>	Cistaceae	PF		–	20	
<i>Helianthus hirsutus</i>	Asteraceae	PF	gravity	20	20	68
<i>Hibiscus aculeatus</i>	Malvaceae	PF	gravity	20	20	
<i>Hieracium gronovii</i>	Asteraceae	PF	wind	20	–	–
<i>Hypericum crux-andreae</i>	Clusiaceae	W	gravity	45	20	46
<i>Hypericum drummondii</i>	Clusiaceae	PF	gravity	35	–	
<i>Hypericum gentianoides</i>	Clusiaceae	PF	gravity	35	25	
<i>Hypericum hypericoides</i>	Clusiaceae	PF	gravity	–	20	
<i>Hypericum setosum</i>	Clusiaceae	PF	gravity	–	30	88
<i>Hyptis alata</i>	Lamiaceae	PF	gravity	75	25	54
<i>Juncus marginatus</i>	Juncaceae	PC ₃	gravity	4	–	
<i>Lactuca graminifolia</i>	Asteraceae	PF	wind	10	20	
<i>Liatris pycnostachya</i>	Asteraceae	PF	wind	–	20	28
<i>Liatris squarrosa</i>	Asteraceae	PF	wind	20	20	66
<i>Ludwigia hirtella</i>	Onagraceae	PF	gravity	75	20	82
<i>Mimosa microphylla</i>	Fabaceae	PF	gravity	20	10	

<i>Mitracarpus hirtus</i>	Rubiaceae	AF	gravity	–	25	
<i>Orbexilum pedunculatum</i>	Fabaceae	PL	gravity	20	–	
<i>Paspalum floridanum</i>	Poaceae	PC ₄	gravity	30	20	
<i>Paspalum plicatulum</i>	Poaceae	PC ₄	gravity	20	80	
<i>Paspalum setaceum</i>	Poaceae	PC ₄	gravity	20	20	
<i>Phlox divaricata</i>	Polemoniaceae	PF	gravity	5	12	
<i>Pinus palustris</i>	Pinaceae	W	wind	20	–	
<i>Plantago virginica</i>	Plantaginaceae	AF	gravity	20	10	98
<i>Polygala cruciata</i>	Polygalaceae	PF	ant, explosive	–	20	
<i>Pycnanthemum albescens</i>	Lamiaceae	PF	gravity	–	25	16
<i>Pyrrhopappus carolinianus</i>	Asteraceae	AF	wind	20	–	
<i>Rhexia mariana</i>	Melastomataceae	PF	gravity	240	25	64
<i>Rhynchosia reniformis</i>	Fabaceae	PL	gravity	20	20	
<i>Rudbeckia hirta</i>	Asteraceae	PF	gravity	20	20	30
<i>Saccharum giganteum</i>	Poaceae	PC ₄	gravity	25	20	
<i>Salvia lyrata</i>	Lamiaceae	PF	gravity	20	20	62
<i>Scutellaria integrifolia</i>	Lamiaceae	PF	gravity	20	20	
<i>Setaria geniculata</i>	Poaceae	PC ₄	gravity	20	20	
<i>Sisyrinchium rostulatum</i>	Iridaceae	PF	gravity	20	20	
<i>Solanum carolinense</i>	Solanaceae	PF	animal	20	20	
<i>Solidago rugosa</i>	Asteraceae	PF	wind	–	30	36
<i>Sorghastrum nutans</i>	Poaceae	PC ₄	gravity	–	10	
<i>Stylodon carneus</i>	Verbenaceae	PF	gravity	6	–	

<i>Symphyotrichum patens</i>	Asteraceae	PF	wind	20	20	
<i>Tephrosia onobrycoides</i>	Fabaceae	PL	gravity	8	–	
<i>Tragia smallii</i>	Euphorbiaceae	PF	gravity	20	20	
<i>Trichostema dichotomum</i>	Lamiaceae	AF	gravity	20	–	
<i>Tridens ambiguus</i>	Poaceae	PC ₄	gravity	–	30	
<i>Tridens chapmanii</i>	Poaceae	PC ₄	gravity	30	–	
<i>Vernonia gigantea</i>	Asteraceae	PF	wind	–	20	
<i>Viola primulifolia</i>	Violaceae	PF	gravity	20	–	

Table S2. Mixed-effects ANOVAs testing for effects of fuel treatments on abundance and individual growth performance of 7 common seed-addition species. Summary statistics (means and standard errors) are shown in Fig. 3. P-values <0.05 are highlighted in bold. These data were collected as part of a separate, but concurrent experiment at the study site (see Myers and Harms [2011] for details).

Species	No. of plots		Abundance	No. of leaves	Leaf size
	Control	Fuel addition	P-value	P-value	P-value
<i>Cirsium horridulum</i>	25	28	0.1728	0.0018	0.0002
<i>Elephantopus tomentosus</i>	30	29	0.1981	0.2795	0.0011
<i>Eryngium yuccifolium</i>	20	26	0.0178	0.0002	0.0401
<i>Hieracium gronovii</i>	12	19	0.0222	0.1087	0.1481
<i>Plantago virginica</i>	16	17	0.1387	0.0241	0.0604
<i>Rudbeckia hirta</i>	16	24	0.0001	0.0006	0.0113
<i>Solidago rugosa</i>	22	29	0.0079	0.0057	0.0092

Fig. S1. Two-way interactions between fuel treatments (FuelTrt) and seed-addition treatments (SeedsTrt). Species richness is the response variable on the Y-axis, and seed additions and controls are on the X-axis.

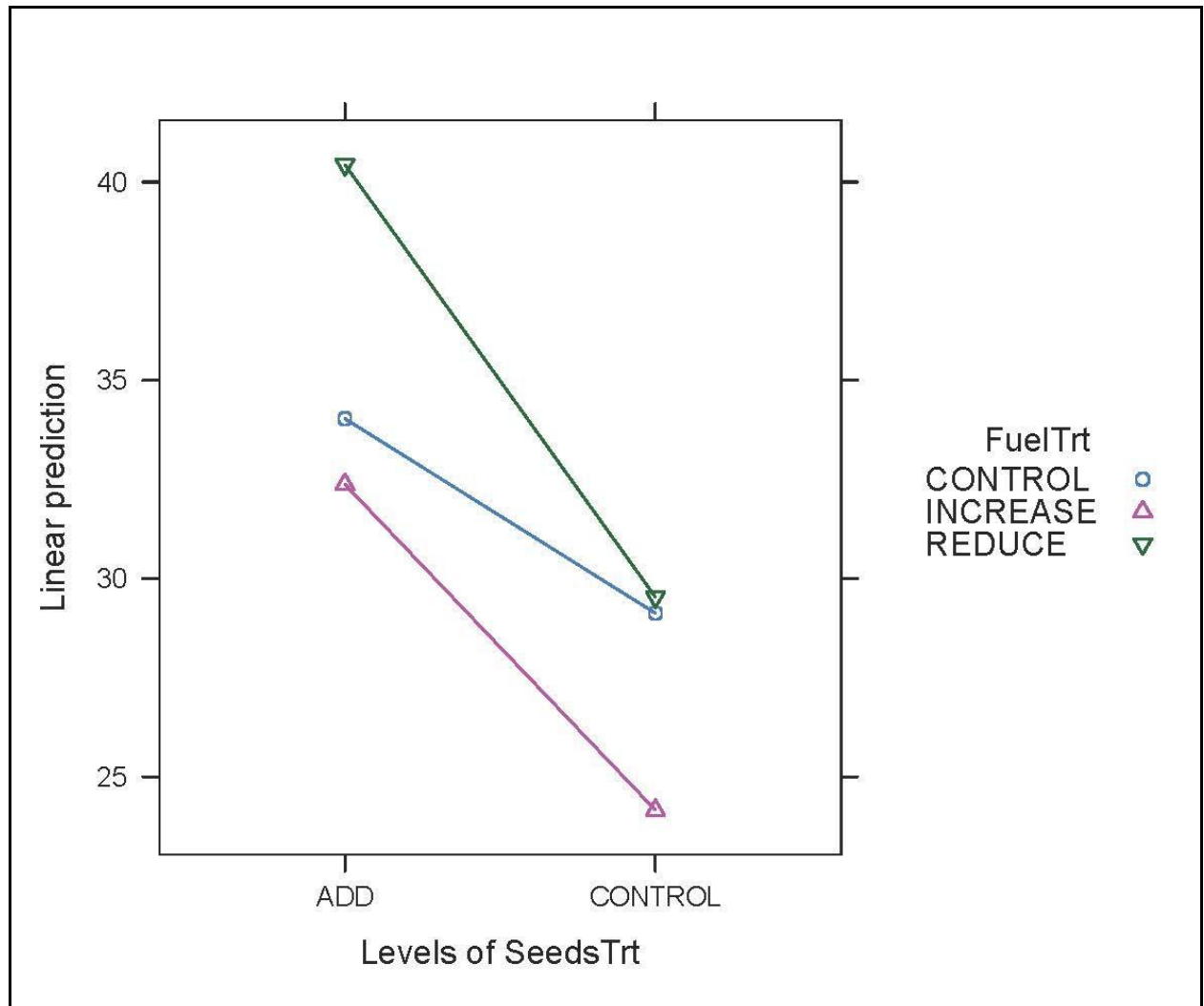


Fig. S2. Two-way interactions between census (CENS) and seed addition treatments (SeedsTrt). Species richness is the response variable on the Y-axis. Censuses 1 (A) and two (B) are on the X-axis.

