Responses of Prairie Vegetation to Fire, Herbicide, and Invasive Species Legacy

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Abstract

We evaluate prairie plant community variation in a matrix of restoration treatments in the south Puget Lowland, WA. Native and exotic plant community diversity and composition were measured across areas that differed in burning history and grass-specific herbicide application, having received one to several treatments since 2002. All plots were also variable in historical proximity to a key invasive exotic species (*Cytisus scoparius* - Scotch broom), a nitrogen-fixing shrub. Three trends were readily apparent from our data: 1) total plant species richness was higher following a prescribed fire. This trend was associated with increases in both native and exotic plants; 2) areas treated with a grass-specific herbicide generally had lower exotic and higher native cover; and 3) using a combination of GIS modeling and community analysis, we found that historical proximity to *C. scoparius* across all treatment areas was associated with suppressed native species richness. In fact, the magnitude of the effect of historical proximity to *C. scoparius* was as large as the differences among fire treatment areas. These data suggest that restoration treatments such as fire and herbicide application affect species richness and diversity in prairies, but the changes were neither rapid nor large. Further, exotic species legacies may interact with treatment effects to variably alter restoration outcomes.

Introduction

Many restoration efforts in prairie ecosystems have the broad goal of maintaining or enhancing native biodiversity and reducing exotic plants (Corbin et al. 2004). Common techniques used in the restoration of prairies in the Pacific Northwest include reintroduction of fire, herbicide application, mowing, tillage, grazing and manual removal of exotics (Sinclair et al. 2006). These methods are often used in combination across varying temporal and spatial scales (Stanley et al. 2008, 2011). In addition to direct responses to restoration treatments, plant communities may also be affected by legacies of previous vegetation, especially if prior vegetation has significantly altered the soil environment (Corbin et al. 2004, Haubensak et al. 2004, Haubensak and Parker 2004). Measuring variation in plant community diversity and composition across restoration landscapes is an important step in understanding how management actions may affect the biodiversity of plant communities.

Historically, fire has been a major ecological process in many prairie ecosystems, including the prairies of the south Puget Lowlands (Washington State, USA). Fire-reintroduction has also recently become a major tool for the restoration of prairie landscapes in this region (Hamman et al. 2011). The historically dominant species in south Puget Lowland prairies (del Moral and Deardorff 1976, Dunwiddie et al. 2006) are adapted to a regime of high-frequency, low-intensity, and high-extent fires (Agee 1996, Storm and Shebitz 2006, Hamman et al. 2011). Over the last several millennia, fires are thought to have been intentionally set at a 2-3 year fire return interval by indigenous peoples to encourage food, fiber, and medicinal plants (Storm and Shebitz 2006). Euro-American settlement of the region occurred in the mid-1800s, at which time fires ceased to be deliberately set, and were actively suppressed (Storm and Shebitz 2006). The total remnant native prairie in the region today occupies approximately 3% of its historical range (Noss 1995, Crawford and Hall 1997). Current fire reintroduction takes place in an altered landscape often dominated by exotic species. While fire can be a useful and important tool for restoring pyrogenic landscapes (Agee 1996, Pendergrass et al. 1999), the effects of fire on Pacific Northwest prairie community composition and diversity are not well-understood. Disturbances like fire (when functioning as a moderate

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disturbance) can have the immediate effect of increasing overall plant diversity by opening up niche space and reducing single-species dominance (Petraitis et al. 1989). However, fire may also encourage exotic shrubs and grasses (Agee 1996, Collins et al. 1998, Lesica and Martin 2003).

Controlling invasive exotic plants is a key element of restoration in prairies of the Pacific Northwest (Wilson and Clark 2001, Stanley et al. 2011), where exotics may threaten native biodiversity (Randall 1996, Wilson and Clark 2001, Barnes 2004). In many U.S. ecosystems, the application of selective herbicides has become the primary approach to reducing the spread of invasive exotics (Fuhlendorf et al. 2001). In prairies, this can be partially accomplished by application of graminoid-specific herbicides (graminicides; Tunnell et al. 2006). However, the long-term effects of herbicide application and invasive species control on plant communities are not well-documented (Browne et al. 2009). In Pacific Northwest prairies, graminicides are particularly important (see Dunwiddie and Delvin 2006) since invasive grasses represent some of the most dominant exotic species in the prairies, and represent a threat to native graminoid and herbaceous diversity (Dunwiddie et al. 2006).

Plant community change resulting from invasion of exotic species may be especially striking when exotics share mutualistic associations with N-fixing bacteria (D'Antonio and Meyerson 2002, Yelenik et al. 2007). In Pacific Northwest prairies, one such species is *Cytisus scoparius* (L.) Link (Scotch broom), and this species can increase N in the soil environment with potential effects on native plant communities (Haubensak et al. 2004, Haubensak and Parker 2004, Shaben and Meyers 2010). Further, increasing N-availability may be a key mechanism that encourages exotic species in native grasslands (Huenneke et al. 1990, Vinton and Burke 1995, Maron and Connors 1996). Inversely, recent experimental work has found declines in exotic species through reductions in relative N-availability, resulting from soil carbon additions (Blumenthal et al. 2003, Averett et al. 2004, Blumenthal 2009, but see Haubensak et al. 2004). Even if exotics are removed, legacies of their dominance in restored grasslands could have persistent effects on the plant community (Corbin and D'Antonio 2004). For example, Haubensak and Parker (2004) found that *C. scoparius* modified soil N and had inhibitory effects on the germination of some species (but see Haubensak et al. 2004). Shaben and Meyers (2010) also found some evidence suggesting *C. scoparius* soil modification affects plant community composition. In fact, legacy effects from N-fixing species could be widespread (D'Antonio and Meyerson 2002).

We examined differences among fire treatments, herbicide treatments, and potential legacy effects of *C. scoparius* on prairie plant communities in Washington. Our site was invaded by *C. scoparius* in the late 20th century, but starting in the 1990s, manual and chemical removal of *C. scoparius* has significantly reduced its abundance on the landscape. The peak invasion is readily apparent in aerial photos prior to the mid 1990s (Figure 1). Our study took place after much of the *C. scoparius* had been removed, ten years following the reintroduction of fire by land managers, and after initiation of herbicide treatments for targeted removal of key exotic grasses at the site (P. Dunwiddie, University of Washington, personal communication). We compared native and exotic plant communities, community structure, composition, and diversity: 1) pre- and post-fire, 2) among two burn treatment areas versus a control area, 3) among two graminicide treatments compared to an untreated control area, and 4) we examined all plots with respect to historical presence of *C. scoparius*. Since restoration activities have generally been effective at reducing woody plants and maintaining herbaceous species, we hypothesized that we would find differences in community composition and diversity among all treatments for both native and exotic species. Accordingly, we had three primary predictions: 1) fire treatment areas would differ from the control area in species composition, and would have higher species diversity, 2) graminicide treatments would differ in composition from controls, and would favor native species over exotic grasses, and 3) plots historically dominated by *C. scoparius* would be associated with high diversity and cover of exotic species, and reduced native species diversity and cover.

Study Area

Our study was conducted on the Black River-Mima Prairie Glacial Heritage Preserve (GHP; 46.8658° Latitude, -123.0411 ° Longitude; Figure 1). The 459 ha study area is jointly owned by the Washington Department of Fish and Wildlife and Thurston County, and is managed by The Nature Conservancy. The prairie is dominated by diverse grasses and forbs including native *Festuca idahoensis* ssp. *roemeri* (Pavlick) Alexeev and *Camassia quamash* (Pursh) Greene, with encroaching stands of mixed conifer forest dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Dunwiddie et al. 2006). The site receives an average annual rainfall of 146 cm and has an average annual temperature of 10.7

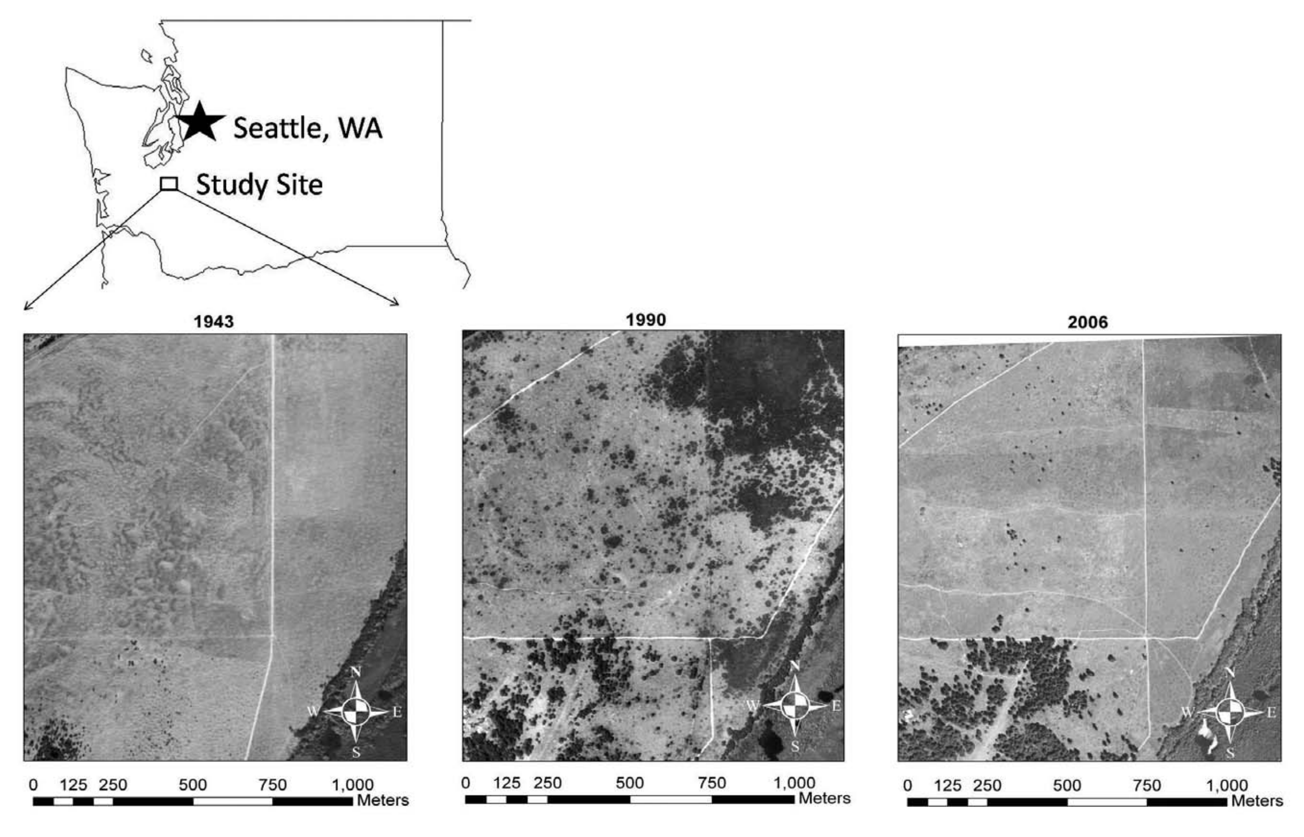

Figure 1. Glacial Heritage Preserve maps showing 1943, 1990, and 2006 orthophotography. In the 1990 orthophoto, the gray speckled clumps are predominantly the invasive exotic *Cytisus scoparius,* darker gray areas are predominantly encroaching *Pseudotsuga menziezii* and native *Quercus garryana,* and black areas represent water bodies. Note also in 1943 and 2006 photos these clumps are largely absent representing restoration of prairie physiognomy by 2006.

TABLE 1. Recent treatment history (2002-2008) and key (planted or removed) species % cover for study plot locations. Abbreviations are as follows: Su = summer, Sp = spring, and F = fall, followed by the two-digit abbreviation for the year of each treatment. The abbreviations 4-year and 1-year refer to the graminicide treatment areas. CYSC = *Cytisus scoparius*, FERO = *Festuca idahoensis ssp. roemeri*. Values in the last columns are average percent cover ± Standard Deviation (SD) for Spring 2008 measurements. † Manual out-planting of FERO.

Data set	Sample date	Fire	CYSC Removal	Herbicide	Graminicide	Planting†	%CYSC	%FERO
Pre-burn	Su06	F06	F02, F03	None	None	F05	4.35% ± 6.17	4.73% ± 9.44
Post-burn	Su07		F04, F07				1.75% ± 4.06	3.58% ± 5.89
2002 burn	Sp/Su08	F02	None	F05, F07	None	F03, F04	0.70% ± 1.07	9.75% ± 9.65
2003/6 burn	Sp/Su08	F03, F06	F02, F04, F07, F08	None	None	F05	0.68% ± 0.83	4.90% ± 9.30
4-Year	Sp/Su08	None	F08	F02, F04	Sp03, Sp06, Sp07	None	0.46% ± 1.47	14.12% ± 8.33
1-Year	Sp08	None	F03, F08	F04	Sp07	None	3.42% ± 5.75	7.51% ± 10.32
CONTROL	Sp/Su08	None	F05	F07	None	None	4.08% ± 9.05	8.13% ± 11.82

°C (Western Regional Climate Center 2010). Restoration treatments in our sample locations are described in Table 1. Current restoration efforts have focused on fire reintroduction, restoration of grassland physiognomy, and the reduction of both exotic graminoids and remaining *C. scoparius* still present on the landscape despite widespread removal efforts. In Table 1, herbicide and graminicide treatments are presented alongside 2008 percent cover estimates for *C. scoparius*. Herbicide involved spraying scattered *C. scoparius* directly with Garlon (triclopyr), a broadleaf herbicide that does not affect grasses. Graminicide involved spraying with Poast (Sethoxydim), a grass-specific herbicide that does not affect broadleaf plants or *F. idahoensis* ssp. *roemeri*. This is typically used to control the invasive grasses: *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Anthoxanthum odoratum* L., *Festuca rubra* L., and *Agrostis capillaris* L. Spot and broadcast spraying of this graminicide had been carried out for four consecutive years prior to our study in selected areas.

Methods

Designing and implementing a fully factorial, replicated experiment is often impossible in small nature preserves that are being actively and aggressively managed. Yet managers are keenly interested in understanding the effects of their management actions. To overcome this challenge, we took advantage of the complex matrix of management activities across the GHP prairie to sample the restored landscape in areas that had been differentially treated with fire and herbicide. The advantage of this approach is that the plant community can be evaluated at a spatial scale commensurate with actual restoration treatments and realistic treatment intensities. Disadvantages of this approach include: 1) samples are necessarily pseudoreplicated (Hurlbert 1984) since treatments are applied to affect as much of the landscape as possible, and they are not replicated in an experimental fashion; and 2) choosing sample locations in which treatments are isolated was difficult and potentially problematic. As such, we chose sites with similar landscape conditions (elevation, topography, proximity to water, physiognomy, aspect and location), and to minimize combinations of treatments. All sample sites were located in edaphically similar, undulating "Mima Mound" prairie developed on thick glacial till (del Moral and Deardorf 1976).

We used multiple datasets to separately answer questions related to prescribed burning treatments, graminicide applications, and legacy effects of *C. scoparius*. Details of each dataset are presented below. Nomenclature follows USDA Plants Database (USDA 2011). We estimated percent cover for each species (45 species; Appendix 1) within square 1-m^2 vegetation plots using a modified six-class Braun-Blanquet scale (<2%, 2-5%, 6- 25%, 26-50%, 51-75%, 76-100%). Data were analyzed using the midpoint of each cover class and arcsine square-root transformed prior to parametric analysis when data deviated from normality. Non-transformed cover data are presented in figures for clarity of interpretation.

Pre- and Post-Burn Measurements

We measured 20 plots in July 2006 before a prescribed fire in October 2006, and again on the same date in July 2007. The 20 plots were selected within an approximately 1 ha area of even topography and uniform vegetation using a random number generator. Each plot was located using Garmin eTrex GPS units (Garmin Ltd., Olathe, KS), and corners were flagged for relocation and resampling the following year.

Burn Treatments Comparison

In May 2008, 20 plots per treatment were measured across three burn treatments. The treatments included a 2002 burn, a two-burn treatment with burns in 2003 and 2006 (hereafter 2003/6), and an unburned control with no record of prescribed or accidental fire. Sampling locations were selected using GIS from a matrix of previous land management activities including fire and herbicide application, minimizing areas with multiple confounding treatment types (i.e., fire and herbicide). Plots were randomly selected using polygons of treatment areas in ArcGIS (v. 9.1, ESRI Inc., Redlands, CA) as constraining features for random computer-generated points. A Trimble GeoXM handheld GPS (Trimble Navigation LTD, Sunnyvale, CA, USA) equipped with ArcPad (ESRI Inc., Redlands, CA USA) and TerraSync (Trimble Navigation LTD, Sunnyvale, CA) was used to precisely locate each point on the landscape. These points were again collected in the field using point-averaging of 100 points per plot for accurate positioning in following years.

Graminicide Treatments Comparison

In May 2008, we estimated percent cover in 20 graminicide-treated plots. Control data for these comparisons came from the unburned control plots noted above. We used graminicide treatment areas where target invasive exotic grasses were spot-sprayed with the graminicide Sethoxydim over more than four years (2003-2007; see Study Area description above; Table 1). We also sampled 20 plots located in an area sprayed for only one year prior to our study with the same graminicide. The graminicide treatment areas were adjacent to the control areas. Plots were selected, located and recorded as above, except for the 1-year treatment where GIS data were used to locate approximate plot locations, but GPS data for actual plot locations were not recorded.

Legacy of Mature *C. scoparius* on Prairie Vegetation

Patches of mature *C. scoparius* are clearly discernable in 1990 aerial photos. However, active management for *C. scoparius* from 1991-2006 significantly reduced its presence on the landscape. To examine the possible legacy effects on soils and plant communities that have persisted after the *C. scoparius* was removed, we chose to reanalyze our plot data based on historical proximity to 1990 *C. scoparius* patches. For 80 plots measured in 2008 (Table 1; control, 2002 burn, 2003/6 burn, four-year graminicide), we overlaid plot locations on 1990 aerial orthophotography. These plots were chosen based on availability of GPS data with sub-meter precision. We created circular, 1-m buffers in GIS surrounding each plot, and then categorized each plot as either "*C. scoparius* present" or "*C. scoparius* absent" in reference to visible historical presence of *C. scoparius* within the buffer. We then compared differences in diversity and community composition between the two categories of plots. While these data overlay all the different treatment areas, we analyzed the data across treatment areas, but without explicitly accounting for them; this could be a potential source of error.

Statistical Analysis

In order to determine diversity differences among all treatments, we calculated standard diversity measures: species richness (S) and Shannon's H′ Diversity Index using PC-ORD (Version 4.34 MjM Software, Gleneden Beach, OR). We chose Shannon's H′ because of its accepted use with ecological data and because it places emphasis on rare species (DeJong 1975). Where assumptions of normality and equal variance were met, data for richness, Shannon's H′, and percent cover were analyzed using Student's t-tests for comparison of two groups, or one-way ANOVA for comparisons of multiple groups, followed by Tukey's Honestly Significant Difference (HSD) tests for pair-wise comparison of groups. When data did not meet these assumptions, nonparametric methods were used to assess differences among groups. In these cases Mann-Whitney tests were used for two-group comparisons, and Kruskal-Wallis tests were used for comparisons of more than two groups. Univariate analyses were conducted using JMP 8.0 (JMP statistics, SAS, Inc., Cary, NC), and multivariate and Indicator Species Analyses were conducted using PC-ORD. Non-parametric analyses are indicated in the results presented in Table 2. In all analyses, $P < 0.05$ was used to denote significance. We describe results as "marginally significant" where $P > 0.05$ and < 0.1; actual P-values are reported for all values greater than 0.005.

We used Multi-Response Permutation Procedures (MRPP) in PC-ORD to assess community composition differences among species matrices for all treatments. Briefly, MRPP uses a randomization procedure to compare community matrices in a way that is coarsely analogous to ANOVA for community matrix data. The analysis gives a probability value and a measure of strength (A) for separation among treatments. In general, MRPP A values of greater than 0.10 are considered strong patterns (McCune and Grace 2002). To graphically represent community similarity we used Non-metric Multidimensional Scaling (NMS) ordination with a Sørensen (Bray-Curtis) distance measure based on the appropriateness of this measure with empirical, heterogeneous, ecological community data (Faith et al. 1987). Community similarity is a measure of how similar communities are to each other based on the composition, abundance, and richness of species within those communities. The main matrix consisted of percent cover per species per plot; the second matrix included burn treatments, graminicide treatments, or legacy effects. We ran each ordination with 1000 runs of actual data in two dimensions with 500 maximum iterations. This ordination method resulted in the least stressful representation of the data for all ordinations (determined by examining scree plots; McCune and Grace 2002). We also used PC-ORD to conduct Indicator Species Analysis (Dufrene and Legendre 1997) for all treatments. Indicator Species Analysis takes into account both the relative frequency of species occurring under certain treatments and their fidelity to specific treatments (Dufrene and Legendre 1997). The resulting analysis gives an estimation of species fidelity to a given treatment. Indicator Species Analysis was conducted using a Monte Carlo test of significance of observed maximum with 1000 iterations.

Finally, because *C. scoparius* was targeted for removal before and during the study, and may have strong effects on community differences, we present percent cover of this species in 2008. Despite previous removal of mature plants, the species is still present on the landscape in all treatments. Similarly, because *F. idahoensis* ssp. *roemeri* was intentionally outplanted in some of our study sites (Table 1), we present 2008 data on percent cover of this species in all treatments as background information for the interpretation of community patterns.

TABLE 2. Summary of statistical results, *P*-values for comparisons of species richness (S) and Shannon's H′ diversity among groups, along with A and *P*-values for MRPP analyses. The superscript "n" indicates non-parametric analyses. The superscript "w" indicates a non-parametric Wilcoxon rank test for pair-wise comparisons. The abbreviation "n/s" refers to tests where the full model was non-significant.

		Species Richness (S)			Shannon's H′			MRPP	
Year	Comparison	All	Exotic	Native	All	Exotic	Native	A	*P*-value
2006-07	**Pre/Post Burn**	0.040	0.121	0.053	0.087	0.085	0.190	*0.045*	*<0.005*^{n}
Fire Treatments									
Full Model		*0.023*^{n}	*0.008*^{n}	0.046^{n}	0.152	0.062	0.344		
	control vs. 2002	*0.021*^{nw}	*0.245*^{nw}	0.186^{t}	n/s	0.103	0.313	*0.061*	*<0.005*^{n}
	control vs. 2003/6	*0.005*^{nw}	*0.018*^{nw}	0.043^{t}	n/s	0.098	0.676	*0.053*	*<0.005*^{n}
	2002 vs. 2003/6	*0.472*^{nw}	*0.465*^{nw}	0.769^{t}	n/s	1.000	0.808	*0.027*	*0.006*^{n}
Herbicide									
Full Model		0.023	0.161	0.503	0.039	0.467	0.015		
	4-year vs. 1-year	0.938	n/s	n/s	0.179	n/s	0.032	*0.029*	*0.005*^{n}
	4-year vs. control	0.068	n/s	n/s	0.035	n/s	0.032	*0.153*	*<0.005*^{n}
	control vs. 1-year	0.027	n/s	n/s	0.665	n/s	1.000	*0.047*	*<0.005*^{n}

Results

Pre- and Post-Burn Measurements

We hypothesized that prescribed burning would result in higher overall plant diversity, as well as higher diversity of exotics. For both overall species richness and Shannon's H′, values for exotic, native, and all species combined were higher after the 2006 prescribed burn (Figure 2A, 2B). Among these measures, only the increase in exotic species richness and native Shannon's H′ were not statistically significant (Figure 2A, 2B, Table 2). Both total percent cover and percent cover of native species were lower following the burn (Figure 2C), and these patterns were marginally significant ($P = 0.084$ and 0.072, for total percent cover and native percent cover, respectively). Values for exotic percent cover pre- and post-burn were not statistically different ($P = 0.980$). Holistic plant community composition was significantly different between pre- and post-burn treatments ($A = 0.045$, $P < 0.005$; Figure 3). This difference is mildly visible by separation of groups from the top-right to the bottom-left in the NMS ordination in Figure 3, but the low A-value (< 0.1) demonstrates that this difference was not very strong (McCune and Grace 2002). We found no differences in community composition using MRPP when data were analyzed separately for native and exotic species ($P > 0.05$; data not shown). Using Indicator Species Analysis, two exotic grasses indicated for pre-burn conditions; three native species and one exotic species indicated for post-burn conditions (Table 3). Specifically, the exotic species *Anthoxanthum odoratum* and *Holcus lanatus* L. indicated for the pre-burn conditions, and the native species *Camassia quamash* (Pursh) Greene, *Microseris laciniata* (Hook.) Sch. Bip., *Luzula multiflora* (Ehrh.) Lej., and the exotic species *Aira praecox* L. indicated for post-burn conditions. There was little difference in the average percent cover of the two heavily manipulated species *C. scoparius* and *F. idahoensis* ssp. *roemeri* (see Table 1) between the pre- and post-burn treatments.

Burn Treatment Comparison

We hypothesized that burned areas would have higher plant diversity, and specifically higher diversity and abundance of exotics, compared to control plots. In general accordance with our prediction, species richness for native and exotic species differed significantly across treatments in spring 2008 (Figure 2D). When all species where analyzed together, species richness was highest in the twice burned site (burned in 2003 and 2006) and an older burn (2002) compared to the unburned control (Figure 2D, Table 3), but Shannon's H′ was not different (Figure 2E). The 2003/6 burn area was also significantly higher in species richness compared to the control area when native and exotic species were analyzed separately (Table 2, Figure 2D). In agreement with our hypothesis, the 2002 burn treatment was generally intermediate between the other two treatments. Exotic species in the 2003/6 burn area were also higher in Shannon's H′ compared to the control area, but this pattern was only marginally significant (Table 2, Figure 2E).

Significant differences in overall plant community profiles measured with MRPP analyses were apparent across all burn treatments (Figure 4; Table 2). Interest-

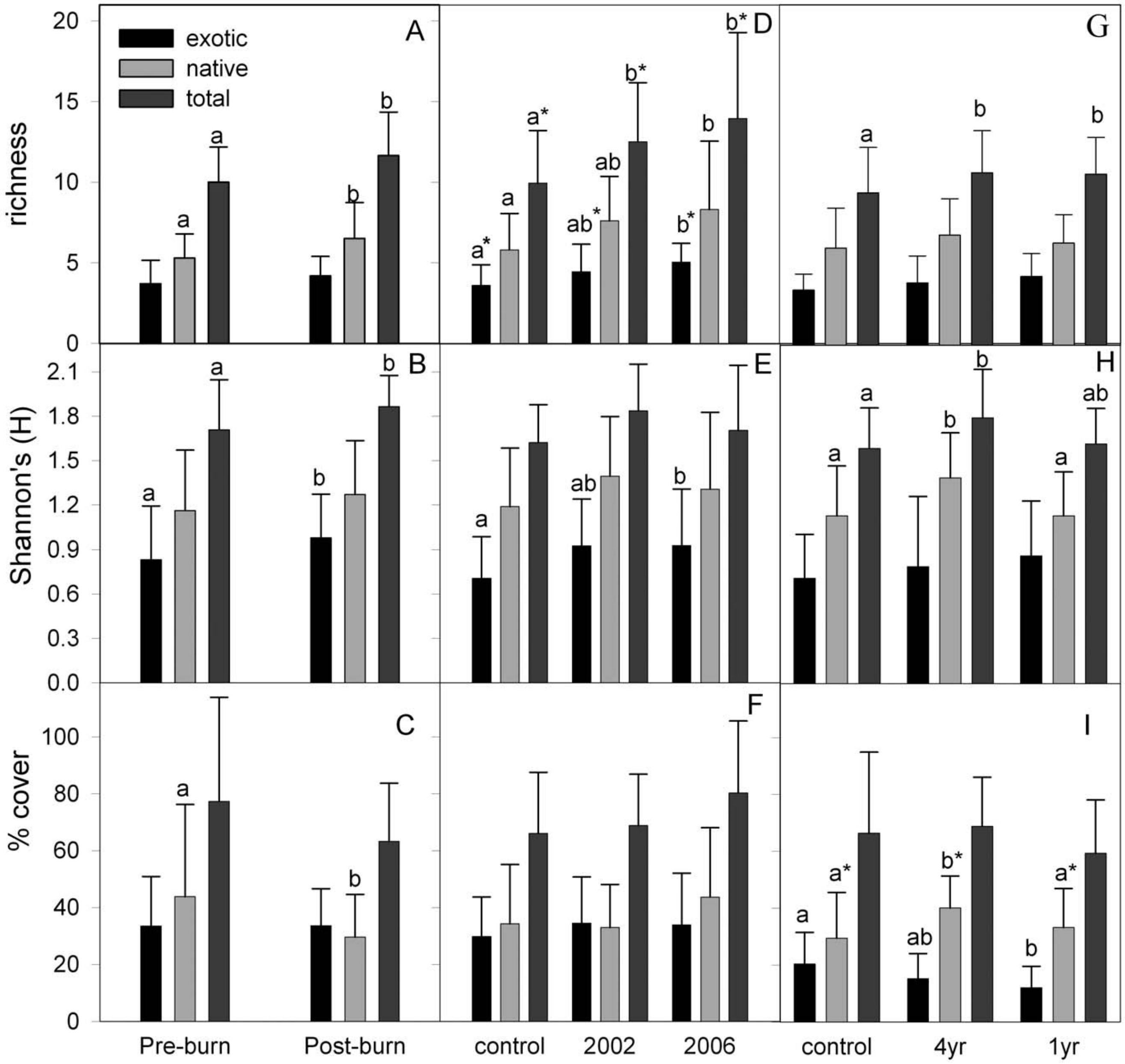

Figure 2. Prairie plant species richness, Shannon's H′, and percent cover for pre- and post-burn comparisons, 2002 and 2003/6 burn treatments, and herbicide treatments, versus a control. Differences in letters denote significance at *P* <0.10 and asterisks (*) indicate nonparametric statistics. Bars represent means ± 1 standard deviation (SD).

ingly, while the 2002 burn treatment was geographically closer to the control plots, it was closer to the 2003/6 burn treatment area in NMS ordination space (Figure 4). Additionally, no treatment had tighter community clustering in ordination space than any other (Figure 4), suggesting communities were similarly variable.

Indicator Species Analysis showed that exotic species were the primary indicators for burned treatments (Table 3), but the 2002 and 2003/6 treatment areas did not share indicator species. Cover of *C. scoparius* was generally greater in the control plots (Table 1), but it was not a significant indicator species, as Indicator Species Analysis is driven by fidelity of a species to plots and not by species cover. Thus, while *C. scoparius* may have been more abundant on average in some treatments, its presence was not an indicator of high fidelity to those treatments. The native grass *F. idahoensis* ssp. *roemeri* was among the significant indicator species for the 2003/6 burn treatment area (Table 3). Interestingly, the control area had higher percent cover of this species without any outplanting (Table 1), and it is widely recognized that this species declines for a few years after most burns. These data may indicate that despite trends in % cover, *F. idahoensis* ssp. *roemeri* had a high fidelity to plots in the burned area as a result of either outplanting or recovery of plants following fire.

Graminicide Treatments Comparison

Overall species richness was significantly greater in the one-year graminicide treatment compared to the control, and marginally significantly different between the four-year treatment and the control. However, when native and exotic species were analyzed separately, there were no significant differences among treatments in species richness (Figure 2G, Table 2). Shannon's H′ was higher in the four-year treatment compared to the control for all species combined and for native species alone (Figure 2H). Comparisons using MRPP analyses also demonstrated significantly different plant community compositions among treatments where all treatments were significantly different (Table 3). The strongest differences were between the four-year and control area. We also found significantly lower exotic graminoid

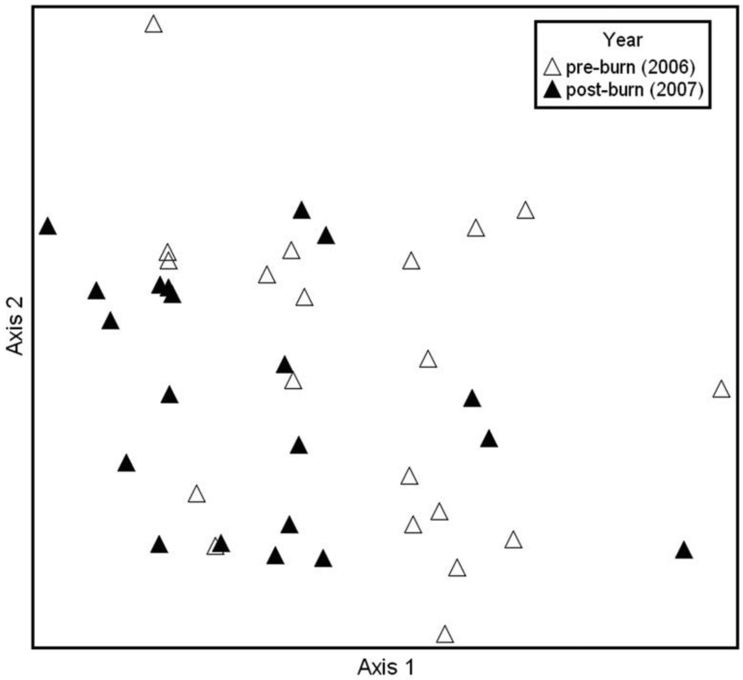

Figure 3. Non-metric multidimensional scaling (NMS) ordination of plant communities for pre- and post-burn treatments. Each point in the ordination represents an individual plot. Symbols represent different treatments: pre-burn (2006; open triangle), and post-burn (2007; closed triangles). A multi-response permutation procedure (MRPP) demonstrated significant (P <0.005) differences in community composition between treatments.

TABLE 3. Indicator Species Analysis for fire and graminicide treatment areas. Values are shown for significant indicator species only.

Indicator Species	Treatment	*P*-value	Native/Exotic
Pre/post-burn 2006/2007			
Anthoxanthum odoratum	*pre-burn*	< 0.005	E
Holcus lanatus	*pre-burn*	0.025	E
Camassia quamash	*post-burn*	< 0.005	N
Microseris laciniata	*post-burn*	0.05	N
Luzula multiflora	*post-burn*	0.024	N
Aira praecox	*post-burn*	< 0.005	E
2008 Fire (F) and Graminicide (G) Treatments			
Hypochaeris radicata	(F) 2002	0.024	E
Hypericum perforatum	(F) 2003/6	0.009	E
Rumex acetosella	(F) 2003/6	0.054	E
Festuca idahoensis			
ssp. roemeri	(F) 2003/6, (H) 4-year	0.007, 0.036	N
Cytisus scoparius	(G) Control	<0.005	E
Vicia americana	(G) Control	0.042	E
Danthonia californica	(G) 4-year	<0.005	N
Lomatium utriculatum	(G) 4-year	<0.005	N
Galium aparine	(G) 1-year	0.009	E
Teesdalia nudicaulis	(G) 1-year	0.009	E
Plantago lanceolata	(G) 1-year	0.011	N

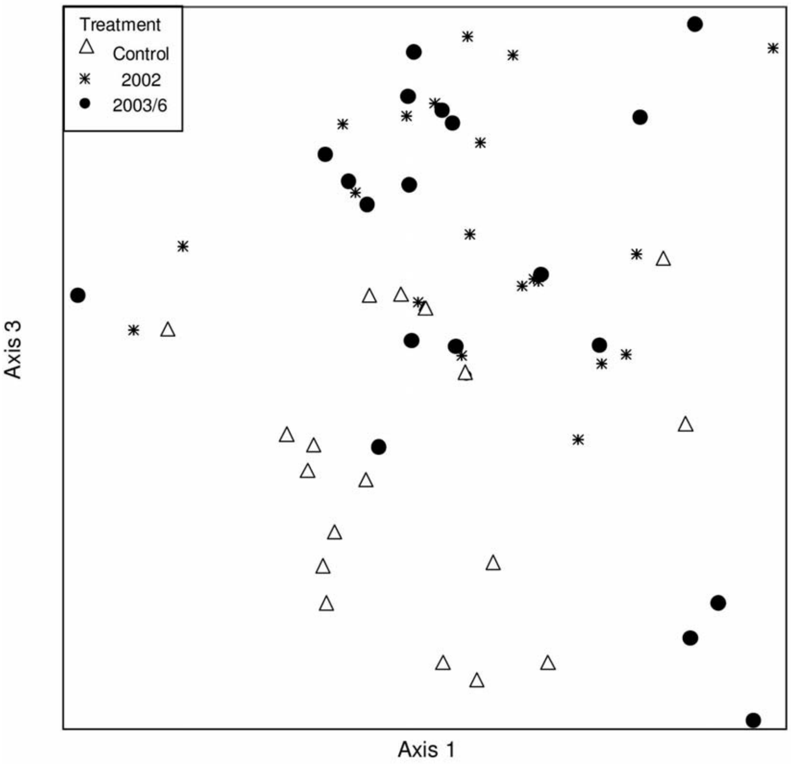

Figure 4. Plant community ordination for the burn treatments in 2002 and 2006 versus control plots. Each point in the ordination represents an individual plot. Symbols represent different treatments: control plots (open triangles), 2002 burn treatment (star) and 2006 burn treatment (solid circle). Multi-response permutation procedures (MRPP) demonstrated significant (P =0.006 to < 0.005) differences in community structure among all treatments. In the ordination, the shift in communities in response to fire is suggested by a shift in points from the lower left (control treatments – open triangles) to the upper right corner of the ordination plot (fire treatments – solid circles and asterisks).

cover in the treatment areas compared to the control (Figure 5).

Indicator Species Analysis results for the graminicide treatments generally showed native indicator species in the most intensively treated area (four-year), and exotic indicator species in the control area (Table 3). The exotic species *C. scoparius* and *Vicia americana* Muhl. ex Willd. were significant indicators for the control. Our analysis also suggested *Agrostis capillaris* was an indicator species for the control, but because this species was difficult to distinguish from *A. pallens* Trin. in the field, we were less confident of this result. The native species *Danthonia californica* Bol., *F. idahoensis* ssp. *roemeri*, and *Lomatium utriculatum* (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose indicated for the four-year graminicide treatment area. Two exotic and one native species, *Galium aparine* L., *Teesdalia nudicaulis* (L.) W.T. Aiton L., and *Plantago lanceolata* L., were significant indicator species for the one-year treatment area.

Legacy of *C. scoparius* on Prairie Vegetation

We hypothesized that, in areas historically occupied by *C. scoparius*, exotic species diversity would be higher and native species would be suppressed. In agreement with this prediction, native species richness was significantly lower in areas historically associated with *C. scoparius* compared to areas that were not associated with *C. scoparius* (t_{78} = -3.10, P = 0.004; Figure 6). However, exotic species were not different between areas (t_{78} = -0.166, P = 0.565). Shannon's H′ was marginally lower for native species where *C. scoparius* was present (t_{78} = -1.59, P = 0.069), but again exotic species were not different (t_{78} = 0.20, P = 0.423). There was no significant difference in percent cover of native (t_{78} = 0.134, P = 0.448) or exotic (t_{78} = -0.75, P = 0.766) plants between areas (Figure 6). Community analysis also demonstrated no community profile differences among the areas for native (A = 0.002, P = 0.273) or exotic plants (A = 0.002, P = 0.273). However, Indicator Species Analysis for historical presence/

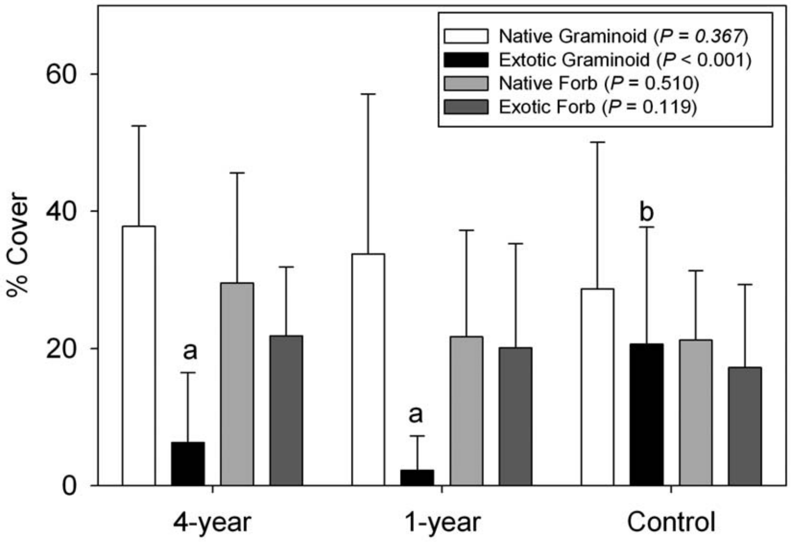

Figure 5. Native and exotic graminoid and herbaceous percent cover for herbicide treatments versus a control. Letters denote significant differences (P values are in the legend) within vegetation types across treatments using nonparametric statistical analyses. Error bars represent ± 1 standard deviation (SD) around a mean.

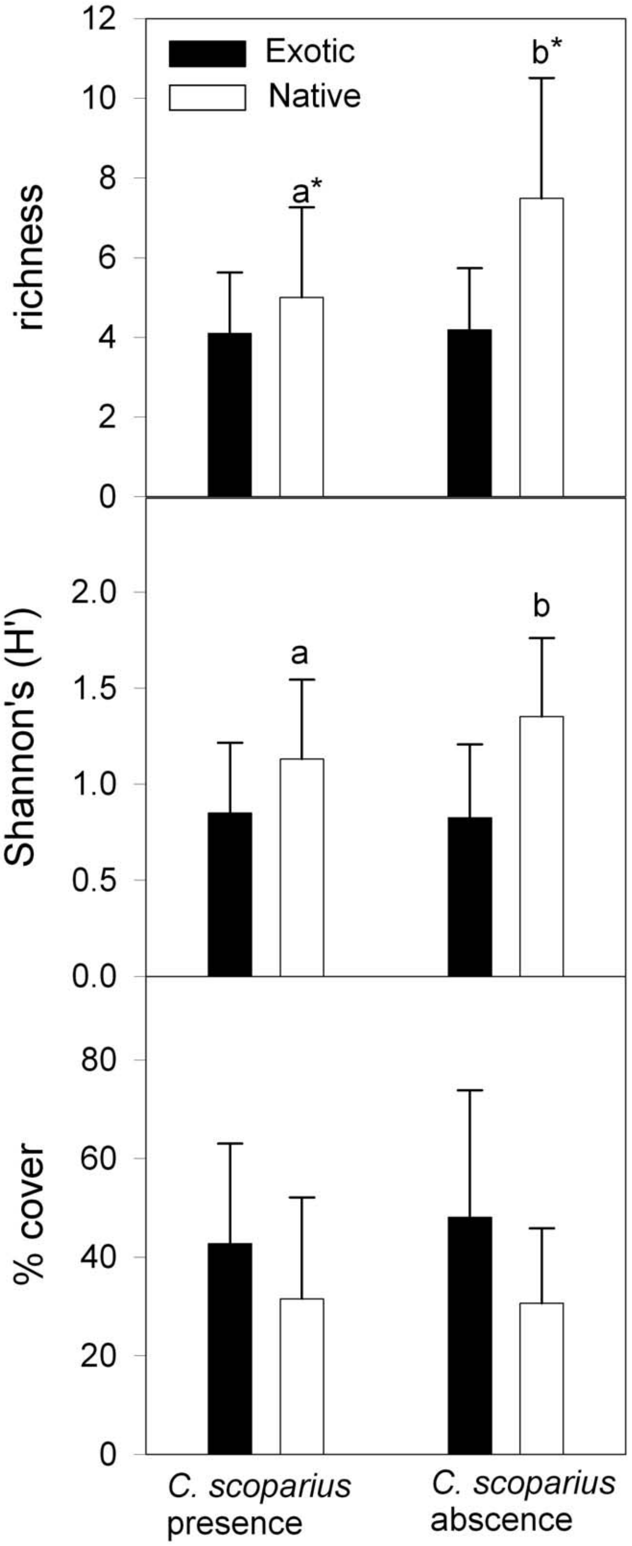

Figure 6. Prairie plant species richness, Shannon's H′, and percent cover for native and exotic plants in relation to the historical presence or absence of *Cytisus scoparius*. Differences in letters denote significant differences and asterisks (*) indicate nonparametric statistics. Error bars represent ± 1 standard deviation (SD) around a mean.

absence of *C. scoparius* showed that the invasive exotic grass, *Holcus lanatus* was significantly associated with historical presence of *C. scoparius* ($P < 0.001$). While not a significant indicator species, at the time of measurement, *C. scoparius* showed 3.1% ± 6 SD cover in areas where mature plants were historically present, and only 1.7% ± 6 SD cover in areas where *C. scoparius* had been historically absent. By comparison, the conspicuous *F. idahoensis* ssp. *roemeri* showed only 0.6% ± 1.6 SD cover in historical *C. scoparius* plots, and 7.9% ± 11.7 SD cover where *C. scoparius* was not historically present.

Discussion

We initially predicted fire treatments would favor high diversity and our results partially supported this prediction. We found a small but significant increase in species richness (1-2 species) in burned treatments. Since plots averaged approximately 12 species m^{-2}, this represented an approximately 12% difference in species richness. We also found significantly different plant community profiles in burn treatments compared to control and pre-burn measurements. Ordination of community profiles indicated more community similarity among burn treatments than either burn treatment compared to control. Disturbance caused by fire can result in colonization by new species (Grace et al. 2001, Lesica and Martin 2003, Corbin et al. 2004, Barnes 2004), and our findings are consistent with several other studies on vascular plant diversity following disturbance (Hobbs and Huenneke 1992, Safford and Harrison 2004, Barnes et al. 2004, Rooney and Leach 2010).

So, if fire could have resulted in a shift in community profile and diversity, which species were responsible for the shift? Patterns we observed were driven by differences in both exotic and native species, but our Indicator Species Analysis suggested that the exotic species *H. radicata, H. perforatum, and R. acetosella* could indicate for burn treatments. Interestingly, this is a different suite of species than the indicator species suggested for the pre- and post-burn measurements in 2006/7, where native species were the primary indicators for the burn treatment. In fact, comparison of indicator species among datasets suggests no species consistently indicated for burn treatments across different prescribed fire treatments. Even if different burned treatment areas exhibit similar increases in species diversity, the increase may result from shifts in different species dependent on site history and dispersal. Apparent differences in community response to burning could also reflect sampling time following prescribed fires. Our measurements occurred less than one year after a burn (pre-after burn comparison), more than two years after a series of two burns in the 2003/6 burn treatment, and six years following a burn in the 2002 burn treatment. These data highlight the potential importance of tracking changes in community composition over multiple years following disturbance. Post-burn communities may reside in different locations along a succession sere.

Although native communities could be adapted to frequent burning, the presence of exotic species in the sites can significantly alter the competitive balance among species, and result in variable responses to prescribed burns. As has been found in more controlled experimental studies in Pacific Northwest prairies (e.g., Stanley et al. 2011), additional measures that reduce relative exotic competition, such as herbicide or direct seeding of native species, may result in more successful restoration of the native plant community. In our study system, significantly less exotic grass cover was present in the four-year graminicide treatments, which suggests that repeated treatments are successfully reducing the abundance of invasive grasses. This finding was consistent with prior work on herbicide efficacy in western Washington prairie restoration (Dunwiddie and Delvin 2006) and our initial predictions. Further, our data show higher native cover and higher Shannon's H′ diversity, and strongly different community profiles (as indicated by $A > 0.1$) in the four-year treatment area compared to control treatments, suggesting that native species have increased in response to repeated herbicide treatments. This is important since simply eradicating exotics will not be sufficient to restore prairies if native species do not also expand. Stanley et al. (2011) demonstrated that native species are often seed-limited, and without seed addition, herbicide and burning treatments largely resulted in increases in non-targeted exotic species. Our data suggest that consistent targeting of invasive species could result in increases to native species as long as the native species populations are high enough and the treatments last long enough (> four years).

Our data also suggest that historical proximity to *C. scoparius* affected the outcomes of different treatments through suppression of native plant richness. This finding was broadly in agreement with our initial predictions and literature suggesting *C. scoparius* has legacy effects on soils that reduce germination and success of some native species (Haubensak et al. 2004, Haubensak and Parker 2004, Shaben and Meyers 2010). We found marginally significant differences in native richness and diversity, among historical presence/absence groups for *C. scoparius*, even though we found no differences in native or exotic species percent cover. Based on Indicator Species Analysis, at least one exotic graminoid (e.g., *H. lanatus*) could be responding positively to fire treatments and a *C. scoparius* legacy in combination. Because our study layered investigation of *C. scoparius* effects on top of a pre-existing management mosaic, we may not have as much statistical power as a study designed to experimentally measure *C. scoparius* legacy. However, the fact that we observed significant differences with our approach suggests promise for future studies. The differences we observed suggest that legacy effects of *C. scoparius* may be affecting the success of different restoration practices. The magnitude of the difference in native richness between presence/absence plots for *C. scoparius* legacy was equal to the magnitude of our observed differences in native richness across the burn treatments (see Figures 2D, 6). Thus, the effect of exotic species legacy on plant communities, even >10 years after exotic species removal, could be as large as the differences resulting from fire treatments.

Isolating the influences of geographic location on the landscape, management histories, exotic species legacies and specific treatments may seem intractable in actively managed sites. Our results should be interpreted in light of our study design, with particular attention to pseudoreplication issues. However, variation among treatment areas in such management matrices set the bounds for how restoration management can affect community change. Our most heavily treated sites compared to our least treated sites should demonstrate the range of possibilities for restoration efficacy. Perhaps most surprising in the current dataset is the mildness of differences among areas that have had very different management histories. We found an average difference in species richness of only about 1-2 species, a difference in Shannon's H′ of only about 0.2, and a difference in total percent cover of less than 10%. Such findings demonstrate that either 1) the restoration management treatments we evaluated were only capable of effecting subtle change over a decade, or 2) the changes induced by management may not be fully realized without a plant-succession perspective. Subtle shifts in community profile may be indicative of larger shifts in community sere that will only be observable through long-term measurements. This point is especially salient in light of potential species legacy effects. Replicated experimental studies in the region (e.g., Tveten and Fonda 1999; Dunwiddie and Delvin 2006; Stanley et al. 2008, 2011) already suggest that restoration will be most successful when dually considering species dispersal and removal over long time-frames. Our study suggests that the bounds of variation resulting from management approaches primarily concerned with exotic species removal can be relatively small. However, shifts in community profile are measurable across managed landscapes, and such shifts could indicate longer-term change.

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Appendix 1. Species list for all burned, herbicide, control, and *C. scoparius* treatments.

Scientific Name	Common Name	Native/Exotic
Achillea millefolium L.	common yarrow	N
Aira praecox L.	yellow hairgrass	E
Agrostis capillaris L.	colonial bentgrass	E
Agrostis gigantea Roth	redtop	N
Agrostis pallens Trin.	seashore bentgrass	N
Antennaria dimorpha (Nutt.) Torr. & A. Gray	low pussytoes	N
Antennaria neglecta Greene	field pussytoes	N
Anthoxanthum odoratum L.	sweet vernalgrass	E
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	tall oatgrass	E
Camassia quamash (Pursh) Greene	small camas	N
Campanula rotundifolia L.	bluebell bellflower	N
Carex inops L.H. Bailey ssp. *inops*	long-stolon sedge	N
Cirsium sp. Mill.	Thistle	E
Cytisus scoparius (L.) Link	Scotch broom	E
Danthonia californica Bol.	California oatgrass	N
Delphinium menziesii DC.	Menzies' larkspur	N
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *fasciculatum* (Torr.) Freckmann	western panicgrass	N
Erigeron speciosus (Lindl.) DC.	aspen fleabane	N
Eriophyllum lanatum (Pursh) Forbes var. *leucophyllum* (DC.) W.R. Carter	woolly sunflower	N
Festuca idahoensis Elmer ssp. roemeri (Pavlick) S. Aiken	Roemer's fescue	N
Festuca rubra L.	red fescue	N
Fragaria vesca L.	woodland strawberry	N
Galium aparine L.	Stickywilly	N
Hieracium pilosella L.	mouse-ear hawkweed	E
Holcus lanatus L.	velvet grass	E
Hypericum perforatum L.	St. John's wort	E
Hypochaeris radicata L.	hairy cat's ear	E
Leucanthemum vulgare Lam.	oxeye daisy	E
Lomatium utriculatum (Nutt. ex Torr. & A. Gray) J.M. Coult. & Rose	common lomatium	N
Lotus micranthus Benth.	desert deervetch	N
Lupinus sp. L.	lupine	N
Luzula multiflora (Ehrh.) Lej.	common woodrush	N
Microseris laciniata (Hook.) Sch. Bip.	cutleaf silverpuff	N
Plantago lanceolata L.	narrowleaf plantain	E
Plantago major L.	common plantain	N
Potentilla gracilis Douglas ex Hook.	slender cinquefoil	N
Prunella vulgaris L.	common selfheal	N
Pteridium aquilinum (L.) Kuhn	brackenfern	N
Ranunculus occidentalis Nutt.	western buttercup	N
Rumex acetosella L.	sheep sorrel	E
Taraxacum officinale F.H. Wigg.	common dandelion	E
Teesdalia nudicaulis (L.) W.T. Aiton	barestem teesdalia	E
Vicia americana Muhl. ex Willd.	American vetch	N
Viola adunca Sm.	hookedspur violet	N
Zigadenus venenosus S. Watson var. *venenosus*	death camas	N

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