LONG-TERM EFFECTS OF PRAIRIE RESTORATION:

Community structure and native plant population dynamics 6 years after experimental management

by

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Abstract

Restoring degraded habitats with the goal of achieving long-term ecological complexity and stability is an essential component in combatting global declines in biodiversity. The main objectives of prairie restoration are to reduce the abundance of exotic species while enhancing native species richness and abundance, but it is often difficult to extend monitoring to evaluate these as long-term goals. Understanding how initial outcomes persist or change over time is essential for evaluating treatment efficacy. Additionally, observing how specific native populations persist and spread following restoration treatments can inform future decisions regarding seeding practices and management timelines.

To assess the degree to which initial treatment effects continue after project completion, I revisited remnant patches of Pacific Northwest Garry oak savanna/prairie habitat 6 years after experimental restoration treatments were applied. I evaluated the composition and structure of the plant community at each site to determine if, and how, the effects of disturbance treatments and supplemental native seeding changed in the years following experimental management. I tracked the persistence of seeded species and measured spread of their populations as a metric to evaluate longer-term success, suitability of native species for restoration, and the ability of the habitat to support native plant populations.

I found that plots that received supplemental seeding continued to exhibit higher native species richness than those left unseeded, and that both seeding and disturbance treatments could positively influence the long-term pattern of native species abundance. The initially-observed effects of disturbance treatments on reducing exotic grass abundance diminished after 6 years, but nevertheless these treatments significantly influenced the population trajectories of 4 out of 8 seeded species. There was spatial advance of most seeded species' populations, as evidenced by occurrences in previously unoccupied plots. A case study of the seeded species, *Plectritis congesta*, allowed for estimation of the average rate of spread per generation and quantification of the long-term spatial influence of seeding efforts. The results from my extended monitoring confirm that seed limitation of native species and difficulties maintaining the reduction of exotic grasses continue to be major barriers to success in restoration of invaded prairies.

Preface

This thesis is original, unpublished work by the author, Charlotte C. Trowbridge. Supervision and guidance for this research was provided by Dr. Jennifer L. Williams (UBC Geography). Experimental design configuration and data sets from 2005 and 2009 were products of collaboration between Amanda Stanley (Wilburforce, Seattle, WA), Tom Kaye (Institute for Applied Ecology, Corvallis, OR), and Peter Dunwiddie (University of Washington, Seattle, WA). All 2014 data were collected and independently analyzed by the author.

Portions of this work were presented at the Northwest Scientific Association Conference (Pasco, Washington, April 2015) and the Ecological Society of America Conference (Baltimore, Maryland, August 2015).

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Lastly, I am incredibly grateful for my supportive and enthusiastic family who has always encouraged me to search for answers, challenge myself, and pursue a career that is meaningful. Particular thanks go to my father, John, who endured weeks of field work and provided advice to help me push through challenging phases.

Introduction

Habitat degradation, fragmentation, and invasion by exotic species are some of the leading causes of the worldwide decline in biodiversity (Bullock et al. 2011; Brudvig 2011; Pimental et al. 2000), and restoring degraded ecosystems is one of the crucial strategies used to slow this loss. Active and adaptive management is necessary to reverse the negative impacts of these threats and to encourage the development of self-sustaining ecosystems. Barriers to success arise due to ongoing urban and agricultural development (Mcdonald et al. 2008; Suding 2011), continuous encroachment by non-native species (Fuchs 2001; Didham et al. 2007; Richardson et al. 2007), and the possibility that a changing climate will affect the distributions and interactions of species (Chen et al. 2011; Nathan et al. 2011). Due to restricted resources, monitoring of restoration projects is rarely extended long term, but determining the legacy effects of treatments can provide land managers with valuable information (Wortley et al. 2013; Bash & Ryan 2002; Herrick et al. 2006). Periodic monitoring of communities can elucidate delayed responses, confirm the persistence of initial trends, and allow for the evaluation of reproducing and expanding populations of target native species.

Restoration projects in remnant grassland and prairie ecosystems focus on two main goals: reducing the presence of exotic species (primarily pasture grasses) and maintaining or enhancing the diversity and abundance of characteristic native species (Corbin et al. 2004; Rook et al. 2011). Restoration strategies, including mechanical, chemical, and biological reduction of non-native species, have resulted in varying levels of success and it has been demonstrated that coordination of multiple strategies is key (Corbin et al. 2004; Sinclair et al. 2006; Thorpe &

Stanley 2011). It is unlikely that any one strategy will eliminate the need for further management, but there is currently very little information about the temporal scale of removal-treatment effects or about the rate of resurgence of unwanted species. Further, several studies have shown that addition of native seed is critical to enhancing native diversity given the challenges of limited seed banks and decreased dispersal opportunities typical within degraded and fragmented landscapes (Brudvig 2011; Kiehl et al; 2010, Stanley et al; 2011a). Measuring species establishment is an effective way to assess immediate results from supplemental seeding and, when temporal and spatial monitoring scales can be extended, adding measurements of population persistence and spread can provide a comprehensive evaluation of the success of a species used for restoration purposes. By using direct measures of target species' population dynamics it may be possible to evaluate if, and how, desired species will persist in the long term (Miller & Hobbs 2007). This integration of population ecology and restoration ecology can further develop our understanding of the ecological responses observed after restoration efforts (Montalvo et al. 1997). Bolstering, or re-establishing native plant species is a critical component of restoring habitat for at-risk species. However, given the lack of studies tracking the persistence of species seeded during restoration, it is hard to know whether efforts are creating self-sustaining habitat or if the plant populations will need to be actively managed. This knowledge gap can prove problematic in situations where the end-goal of restoration includes creating habitat that will sustain populations of threatened or endangered species.

Progress toward the goal of enhancing native populations is commonly quantified using measurements of species diversity and vegetation structure, but processes such as reproduction and spatial advance of populations are also worthy proxies (Ruiz-Jaen & Aide 2005; Weinstein et al. 2014). By understanding spread patterns of populations, through observation of demographic and dispersal patterns we can recognize when, and more importantly why, plant populations are expanding, contracting, or shifting, allowing for predictions about future species distributions and community structure (Nathan et al. 2011; Hampe 2011; McConkey et al. 2012). In the context of restoration ecology, tracking the spatial advance of populations can aid in evaluating a site's ability to develop structural complexity and self-sustaining populations. Objectives of restoration are often framed on a landscape scale, necessitating that species used for restoration have the ability to establish and spread to improve habitat quality beyond the initial point of colonization (Neubert & Caswell 2000; Kindscher & Tieszen 1998; Fuchs 2001). Arguably, the spread of a species is representative of several fitness indicators, and could therefore provide evidence of suitability and productivity of a species within a habitat, but it is rarely measured in the context of restoration. Given the large range of factors that can affect the stages of establishment, persistence, and spread of a species' population, monitoring programs can benefit from employing measurements of all three stages and conducting intermittent evaluations of population statuses.

The purpose of my research was to investigate the lasting effects of multiple restoration treatments on plant community diversity and structure, as well as to investigate population spread in the context of restoration. I resurveyed community composition and evaluated plant population status at six remnant prairie sites in the Pacific Northwest that received experimental treatments and supplemental native seeding between 2005 and 2008. The principal objectives of the original study included determining which treatment combinations were successful in reducing cover of non-native grasses, and whether native species diversity increased in direct response to treatments, or if supplemental seeding was necessary. Original findings showed that several treatments were effective at decreasing abundance of non-natives and that, regardless of treatment, supplemental seeding was required for increasing native species richness (Stanley et al. 2010). In order to assess longer-term success, I wanted to know whether the desirable trends had persisted, which allows for a retrospective cost/benefit analysis of management options. I revisited sites in 2014, five years after original monitoring ceased, to address four main objectives:

(1) evaluate the lasting effects of supplemental seeding on native plant richness and abundance;

(2) evaluate the lasting effects of disturbance treatments on the cover of exotic grasses;

(3) determine the suitability of seeded species based on persistence across sites and disturbance treatments; and

(4) examine how the spatial advance of seeded species has contributed to diversity beyond initial points of colonization.

Methods

Study system

The Garry oak (*Quercus garryana*) ecosystem, alternately referred to as oak savannah, of northwestern North America is one of the most endangered ecosystems in both the United States and Canada (Noss et al. 1995; Fuchs 2001). The current extent of the Garry oak ecosystem is estimated to cover merely 1-5% of its original range (Fuchs 2001; Floberg et al. 2004; Vesely & Tucker 2004). Biodiversity of native plants in Garry oak meadows is decreasing due to continued habitat loss, invasion by non-native species, and conversion of prairies to woodlands as a result of fire suppression (MacDougall et al. 2004; Hamman et al. 2011). Given the fragmented arrangement of remnant Garry oak habitat, populations of native plant species face increased risks related to small patch size and patch isolation, such as dispersal limitation, edge effects (McCune & Vellend 2015) and increased competition (MacDougall & Turkington 2004, 2006). Restoration and preservation efforts in this ecosystem have increased in recent decades as more plant and animal species reach protected status. Recent conservation and restoration efforts have included targeted reduction of exotic plants (Wilson & Clark 2001; Dennehy et al. 2011), reintroducing extirpated species (Clements 2013; Slater & Altman 2011), and mimicking historical disturbance regimes (Rook et al. 2011; Hamman et al. 2011).

Between 2005 and 2009, a region-wide experiment was undertaken by the Institute for Applied Ecology (Corvallis, Oregon), in collaboration with The Nature Conservancy (US), to identify restoration methods that effectively reduce cover of non-native plant species and increase the abundance of native species in the Garry oak habitat. Drawing upon the findings of previous restoration studies (Tveten 1997; Smith & Knapp 1999; Wilson & Clark 2001), as well as recommendations from land managers involved in the project, researchers decided upon 4 experimental treatment combinations (and a control) to be applied over the course of 4 years (see Appendix A for descriptions of treatment combinations and timing of applications). Ten sites of remnant prairie and oak savannah habitat within natural areas and preserves were selected, ranging from southern British Columbia to Oregon's Willamette Valley. The sites are positioned along a 500-km latitudinal gradient and vary in nutrient and moisture availability and degree of non-native invasion. Despite the variation in climatic and abiotic conditions, there are commonalities in the composition of plant species (Stanley et al. 2011b), and all sites exhibited remnant populations of native species within high cover of exotic species.

These ten sites were later characterized using a site stress index (Richardson et al. 2012; Reagan 2014) to describe differences in abiotic characteristics. To calculate abiotic stress, Richardson et al. (2012) conducted a principal components analysis using site latitudes and measurements of 8 abiotic stressors: soil moisture percentage, extractable soil carbon and nitrogen, concentrations of nitrate and ammonium, surface cover by litter or bare soil, and biomass of soil microbes. Higher values of each of these environmental stressors translated to higher environmental stress, with the exception of percent cover of bare soil (Reagan 2014). Decreasing site stress was generally associated with increasing latitude, as the sites in Oregon experienced higher abiotic stress than sites in Washington. Although the single site in British Columbia was located at the highest latitude, it was assigned an intermediate stress rating due to a drier soil moisture regime caused by its geographic position within a rain shadow.

The experiment used a randomized complete block design in which sites (blocks) were divided into 20 5 × 5m treatment plots. The four disturbance treatments, consisting of combinations of burning, mowing, grass-specific herbicide (sethoxydim), and broad-spectrum herbicide (glyphosate), plus a control, were replicated four times at each site. Within each plot, a split-plot design was used to test the efficacy of post-treatment native seeding. Eight native species characteristic of the Garry oak ecosystem were chosen for supplemental seeding in 2006 and 2007: *Achillea millefolium* (Asteraceae), *Balsamorhiza deltoidea* (Asteraceae), *Danthonia californica* (Poaceae), *Eriophyllum lanatum* (Asteraceae), *Festuca roemeri* (Poaceae), *Lomatium* spp. (Apiaceae; each site receiving one of two congeners, *L. nudicaule* or *L. utriculatum*), *Plectritis congesta* (Valerianaceae), and *Ranunculus occidentalis* (Ranunculaceae) (see Appendix B for detailed species information). Vegetation sampling occurred annually in the spring from 2005 to 2009. A 1-m^2 quadrat was placed in the center of each plot quadrant and species' percent cover was determined by visual estimation.

Community composition sampling

In 2014, I chose six of the ten sites (Figure 1) for follow-up monitoring to look at the lasting effects of treatments and supplemental seeding on plant community composition. Sites were chosen based on accessibility and the ability to relocate original plot markers. Resurveying took place between late April and early June to coincide with the sampling window from the original experiment. Community composition was sampled in two 1-m^2 quadrats within each 5 × 5m treatment plot: one with no supplemental seed and one seeded in two consecutive years. All species present within the sampling quadrat were identified and assigned a cover value, rounded to the nearest 1%. Total cover for each plot, including both substrate and vegetation, was equal to or greater than 100% depending on the degree of vegetation layering.

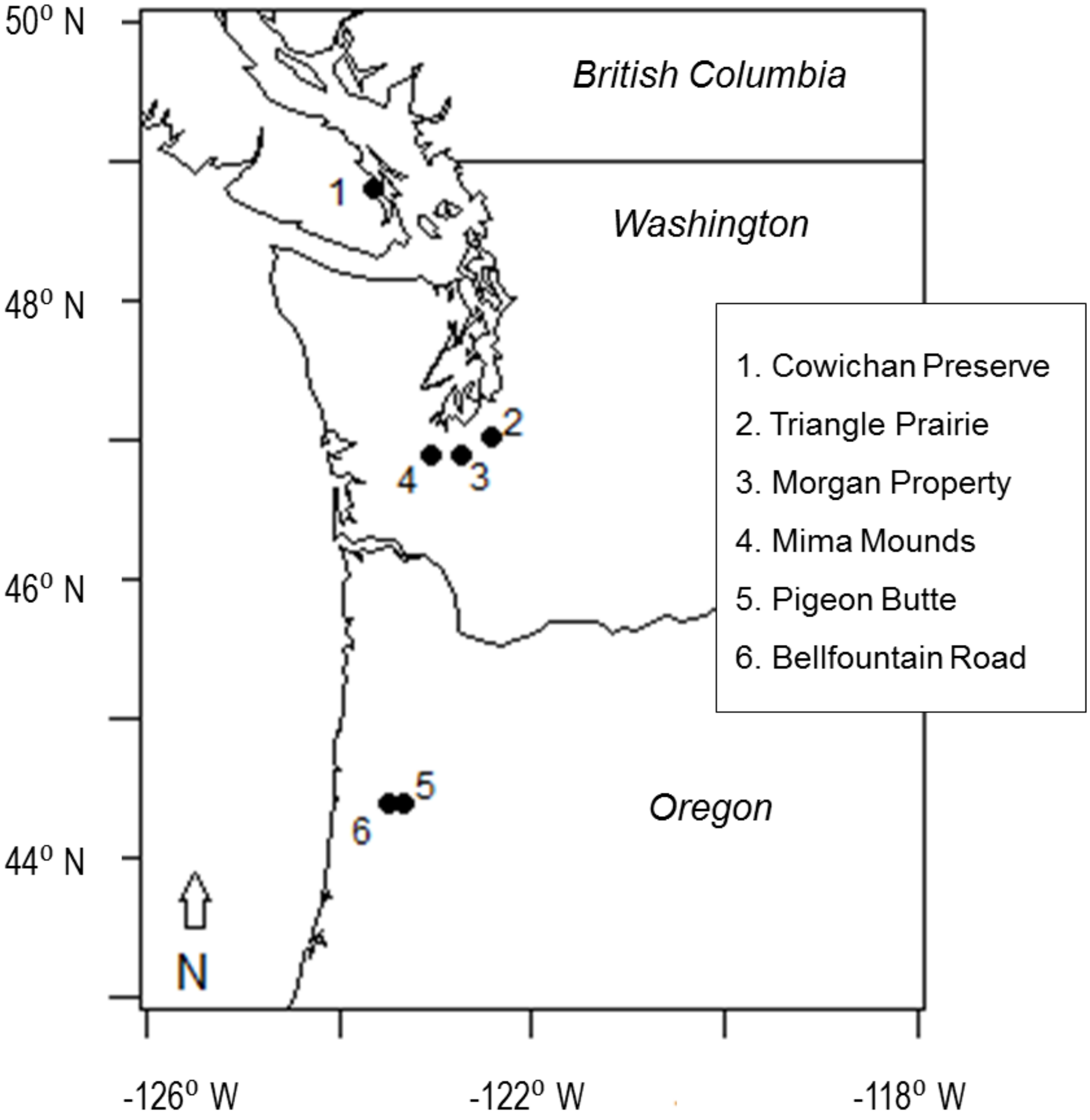

Figure 1. Locations of the six study sites along a 500 km latitudinal gradient.

Monitoring persistence and spread of *Plectritis congesta*

Evaluating spatial advance is useful for understanding the health, dynamics, and site-suitability of a plant population. While measuring the establishment of the seeded native species was possible during the initial monitoring period, the limited duration of the experiment precluded an examination of spatial distribution patterns and population spread. I monitored these populations 8 years after the first application of seeding, allowing sufficient time for increased dispersal and spread. I documented the spread of the 8 native seeded species into previously unoccupied plots and conducted an in-depth evaluation of *P. congesta* (sea blush) populations. *Plectritis congesta*, the sole annual forb seeded, presented a suitable case study for examining the influence that seeding had on native diversity beyond plot boundaries. The benefit of using an annual species to study spread patterns is that it allows inferences about the average movement of the population per generation. Sea blush was historically prevalent in Garry oak remnants, but it is thought that, like other native annuals, populations have suffered significantly from fire suppression (Dunwiddie et al. 2014). *Plectritis congesta* is often used in restoration projects, primarily because of its value as a nectar source for numerous insect species, including several listed lepidopteran species (Young-Mathews 2012), but there are few data reflecting whether the species successfully persists following establishment.

At the initiation of the original experiment, *P. congesta* was not found within the boundaries, nor within the general vicinity, of any of the experimental blocks, meaning all individuals found in 2014 could reasonably be considered a result of seeding. At sites where *P. congesta* was found, I conducted a complete census of all reproductive individuals to evaluate the persistence of the species. To quantify the spatial extent of the population, I documented the perimeters of all plant patches and mapped them in relation to treatment plots. Polygons were created to calculate the area currently occupied by individuals and measurements of distance between the furthest individuals and plot boundaries were recorded. The population at the Cowichan Preserve was revisited for a second year of monitoring in 2015 after a site-wide burn was conducted in the fall of 2014.

Statistical analysis

Data were analyzed using linear ANCOVA, followed by Tukey's Honestly Significant Difference (HSD) tests for pairwise comparisons of factor levels. Site, treatment, and seeding with interactions were treated as fixed effects and pre-treatment cover and count data (from 2005) was included as a covariate to account for initial variance between plots and sites. The most appropriate model for each response variable was determined using a backward-elimination stepwise regression process. The full model included all fixed effects and interactions and terms were subsequently dropped from the model using a deletion criteria of $p>0.05$. For any analyses comparing seeded and non-seeded subplots, quadrat was included as a random effect in the model to account for the split-plot design. Measurements of foliar cover were converted into proportions and transformed using the arcsine-square root. All response variables were analyzed with linear mixed-effects models. If a site × treatment or site × seeding interaction was significant, analysis was carried out for individual sites. The responses of native seeded species to treatments were analyzed using data from only the seeded plots in order to separate the effect of treatment from the effect of seeding, therefore fitted models did not require the inclusion of random effects. All analyses were conducted in R 3.1.2 (R Core Development Team, www.cran-r.org), using packages nlme, lme4, agricolae, and multcomp.

Results

Native species richness and abundance

The number of native species present varied widely across sites and, consistent with original findings, disturbance treatments had no noticeable effect on the number of native species found within plots (best models did not include treatment) (Appendix C). Seeding, however, continued to have a significant positive effect on native species richness, with seeded plots containing an average of 1.92 native species more than unseeded plots (Figure 2a, ($F_{(1,118)} = 76.71$, $P < 0.001$)), down from an average difference of 3.02 species in 2009. Not surprisingly, site was also a significant predictor of native richness ($F_{(5,114)} = 19.96$, $P < 0.001$). The highest native diversity was found at Triangle Prairie, and the lowest was found at the Morgan Property, both sites in Washington, separated by approximately 26 km.

Although the addition of native seed effectively increased the richness and abundance (defined as percent cover) of native species, it was not the sole treatment method that led to an increase in abundance. The model for predicting native species abundance included a significant interaction between treatment and seeding (Figure 2b, ($F_{(4,114)} = 3.57$, $P = 0.008$)). All plots receiving supplemental seed had statistically similar average cover of native species, regardless of which disturbance treatment was applied (overall mean = 36.9% ± 18). However, the average cover of native species in unseeded plots differed across treatments: the two disturbance treatments that included grass-specific herbicide yielded native species abundance values that were slightly greater than those found in all seeded plots (mean= 41.28% ± 20.29) while plots that did not receive supplemental seeding nor a treatment of grass-specific herbicide had lower native abundance (mean= 30.69% ± 17.53). Once again, site was a powerful predictor of native abundance ($F_{(5.110)} = 42.40$, $P < 0.001$), with Triangle Prairie having nearly twice the cover of native species as other sites.

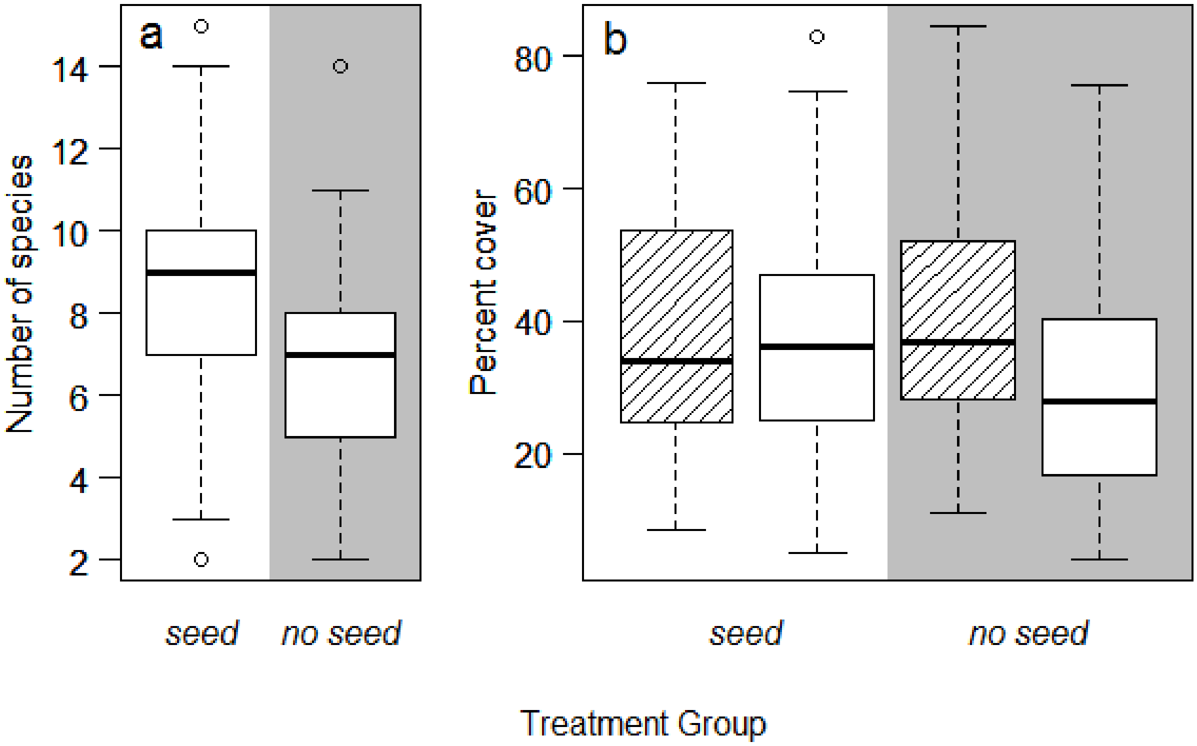

Figure 2. (a) Native species richness and (b) native species abundance (measured by percent cover) in 2014 in plots that were seeded or not in 2006/2007. In panel (b), treatments are broken down further into those with grass-specific herbicide (striped) and those without (white). Median values are represented by the central horizontal line, and upper and lower quartiles are indicated by the corresponding ends of the box. The range of the data are indicated by the whiskers

Exotic grass abundance

In addition to increasing diversity of native species, the reduction of exotic grass species is another critical component of grassland restoration. The experimental disturbance treatments were designed to remove exotic grasses without causing major detriment to the native species present. In 2014, the best model for predicting the cover of exotic grasses (Appendix C) included a significant interaction between site and disturbance treatment ($F_{(20,90)} = 2.15$, $P = 0.008$), therefore further analysis was conducted at the site level to elucidate treatment effects. Average cover of exotic grasses had increased from the low levels documented in 2009, but the rate of rebound varied across the range. Sites in Washington, which experience lower abiotic stress (Richardson et al. 2012) returned to, or exceeded, 2005 pre-treatment levels while sites in Oregon and British Columbia, which have intermediate or high abiotic stress, remained below pre-treatment abundance measurements (Figure 3). Treatment was a significant indicator of non-native species cover at only one site, Triangle Prairie ($F_{(4,14)} = 9.22$, $P < 0.001$), and marginally significant at one site, Mima Mounds ($F_{(4,14)} = 2.62$, $P = 0.08$), but the responses to specific treatments varied between the two. At Triangle Prairie there was a continuing beneficial response to the two treatments that utilized grass-specific herbicide while at Mima Mounds disturbance treatments were actually inferior to the control in the long-term. No persistent response to disturbance treatments occurred at the remaining sites. For all sites, seeding was not a significant predictor of exotic grass abundance, so cover values for seeded and unseeded areas in each plot were averaged and the random effect of the split-plot was dropped from the models.

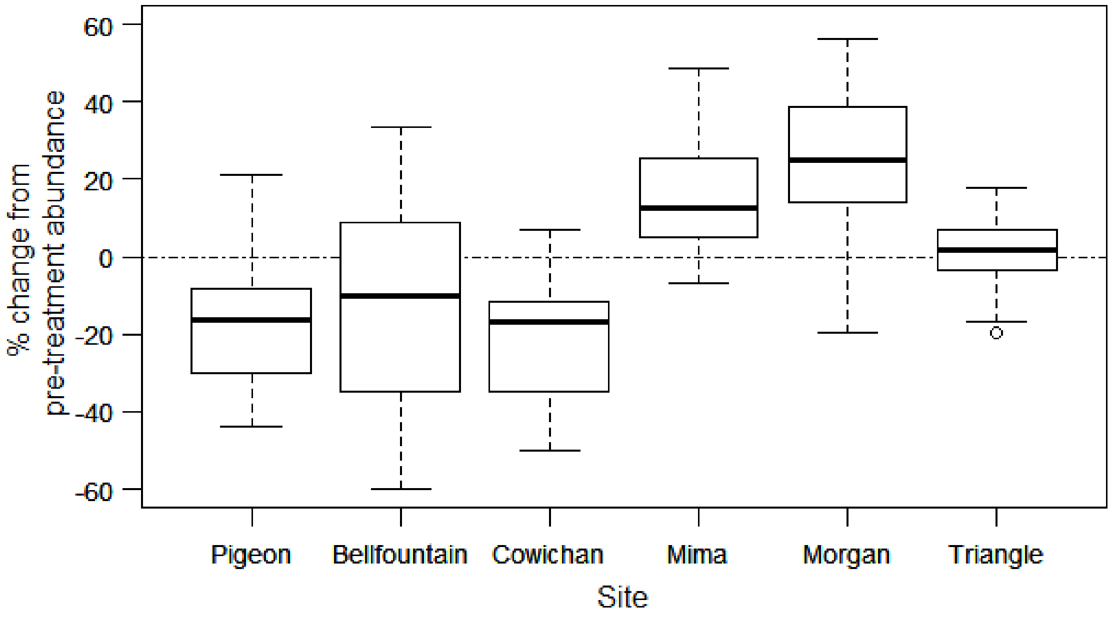

Figure 3. Change in percent cover of exotic grasses from 2005 pre-treatment levels (represented by the dotted line at zero). Sites are arranged in order of decreasing abiotic stress, as defined in Richardson et al. (2012).

Seeded native species trends

Absolute cover values for nearly all seeded species were substantially higher in 2014 than those observed at the end of previous monitoring in 2009 (Table 1). After five additional years of growth and recruitment, the absolute cover of most species had more than doubled, with the exception of *Lomatium utriculatum*, which decreased in abundance, and *P. congesta,* whose total cover remained unchanged (due to increased success at a single site and declines at all other sites).

Table 1. Changes in absolute cover of all seeded species between 2009 and 2014. Note: mean temperature and total precipitation throughout the region in 2014 were greater than in 2009 (differences averaged approximately +1.5° C and +20cm, respectively). See Appendix D for complete climate trends.

Species	**Absolute cover (m^2)**		**% change**
	2009	2014	
Achillea millefolium	0.941	2.355	+ 150
Balsamorhiza deltoidea	0.036	0.22	+ 511
Danthonia californica	0.351	0.869	+ 147
Eriophyllum lanatum	1.705	5.075	+ 198
Festuca roemeri	4.103	15.585	+ 280
Lomatium nudicaule	0.27	2.02	+ 648
Lomatium utriculatum	1.35	0.843	- 38
Plectritis congesta	0.607	0.617	+ 2
Ranunculus occidentalis	1.44	3.329	+ 131

While cover of each native species varied significantly across sites ($P \leq 0.001$ for all species for which an appropriate model was fit), for four of the eight species, treatment (or a site × treatment interaction) was also a significant predictor of cover (Table 2). Three perennial forb species, *E. lanatum*, *A. millefolium*, and *R. occidentalis*, responded more positively to one or both of the burn treatments compared to other treatments (Figure 4a, b, c; $P < 0.05$, post-hoc Tukey tests). The positive response of *E. lanatum* in the burn plots occurred across all sites, with cover in the burn plots averaging approximately twice that of the control. In contrast, the effect of burning on the cover of *A. millefolium* and *R. occidentalis* differed across sites (the best model included a significant site × treatment interaction ($F_{(20,89)} = 1.81$, $P = 0.032$ and $F_{(20,89)} = 2.33$, $P = 0.004$, respectively). This result was due to much stronger responses to fire seen at Pigeon Butte, Mima

Mounds, and Triangle Prairie, with little to no noticeable response to treatment at the remaining three sites. The native grass species, *F. roemeri*, had greater cover in treatments that included the grass-specific herbicide, sethoxydim, (Figure 4d) to which *F. roemeri* is resistant (Sinclair et al. 2006). Performance of this species was poor at the Oregon sites, but it fared particularly well in Washington (mean absolute cover at Washington sites was 22 times greater than sites in Oregon). The other seeded grass species, *D. californica*, has increased in cover since 2009, but varied only between sites ($F_{(5,113)} = 4.34$, $P = 0.001$) and not treatments. This species was more successful at sites in Oregon than those in Washington (mean absolute cover at Oregon sites was more than 5 times greater than Washington sites). Neither treatment nor site significantly predicted the presence and cover of the remaining seeded species, *B. deltoidea*, *Lomatium* spp., and *P. congesta*, presumably due to small sample sizes, low persistence, and/or extreme site-specificity.

Table 2. Components of best-fit model for predicting cover of each seeded native species. There were no appropriate models for predicting the cover of the seeded species not included in this table.

	A. millefolium			*D. californica*			*E. lanatum*			*F. roemeri*			*R. occidentalis*		
Effect	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Site	5, 89	13.67	<0.001	5, 113	4.34	0.001	5, 109	31.58	<0.001	5, 109	27.2	<0.001	5, 89	21.73	<0.001
Treatment	4, 89	4.61	0.002				4, 109	7.53	<0.001	4, 109	4.09	0.004	4, 89	1.05	0.39
Site * Treatment	20, 89	1.81	0.032										20, 89	2.33	0.004
Pre-treatment cover	1, 89	5.27	0.024	1, 113	11.04	0.001	1, 109	3.61	0.06	1, 109	9.14	0.003	1, 89	0.15	0.7

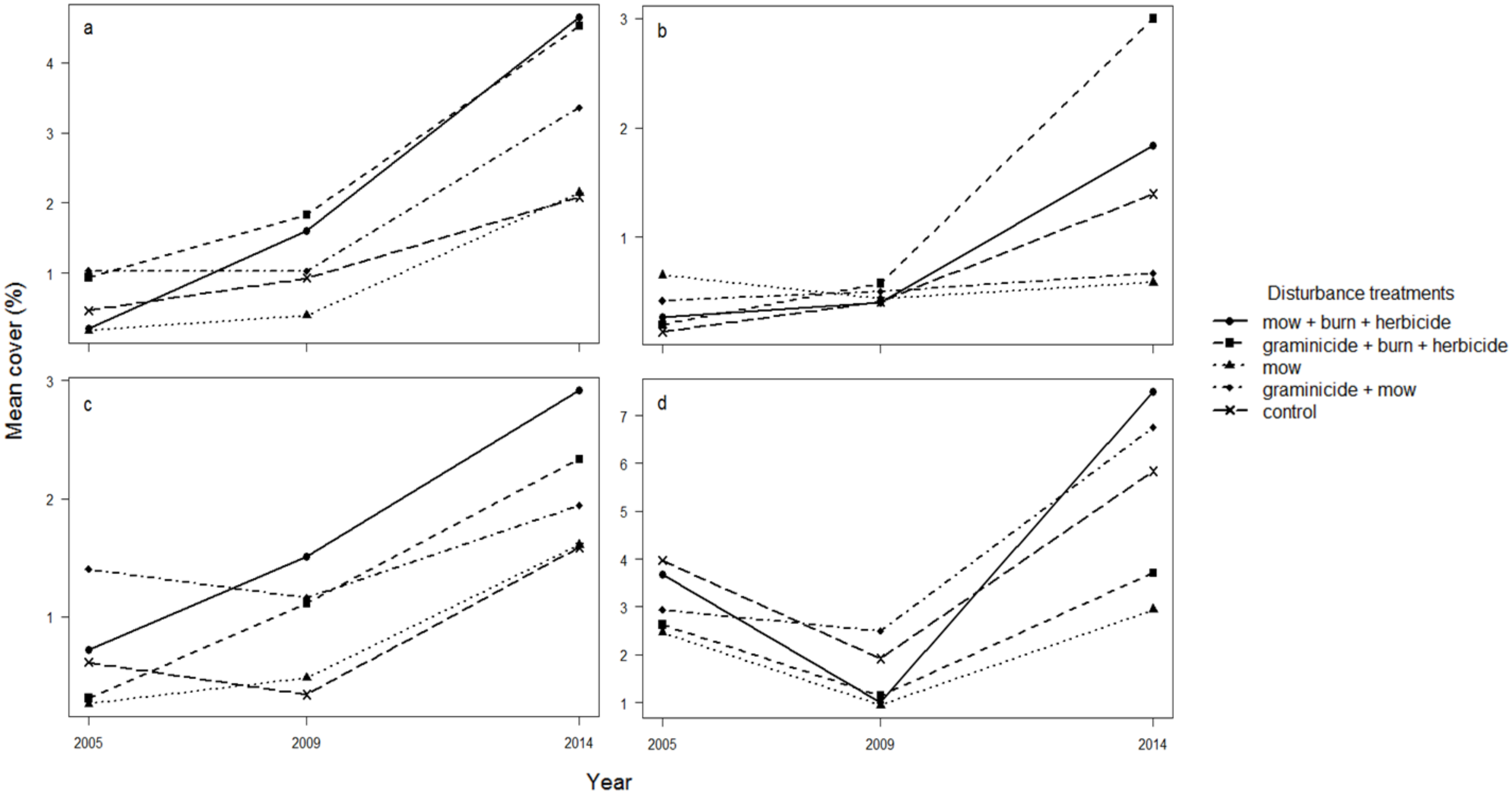

Figure 4. Percent cover of seeded native species in 2005 (before disturbance treatments were applied), in 2009 (1 year after treatments), and in 2014 (6 years after treatments) for a) *Eriophyllum lanatum*, b) *Achillea millefolium*, c) *Ranunculus occidentalis*, and d) *Festuca roemeri.* Note different y-axis scales in each panel. 'Graminicide' refers to the grass-specific herbicide, sethoxydim, while 'herbicide' refers to the broad-spectrum herbicide, glyphosate.

Although the number of plots with occurrences of the seeded species decreased slightly since 2009, there was still a marked increase in occurrences of each of the 8 species from pre-treatment conditions (Figure 5). Of all the seeded species, *F. roemeri* and *R. occidentalis* had the highest rate of occurrence, occupying 51% and 50% of monitored plots, respectively. *Festuca roemeri,* along with *A. millefolium, D. californica,* and *E. lanatum,* all increased slightly in presence since 2009, while the remaining four species experienced net declines. While most of these occurrences are of individuals or patches that were present in 2009, there is evidence of all 8 species colonizing new plots since the last round of monitoring. I found that, for six of the seeded species, at least 25 % of the currently occupied plots are a result of population spread (as determined by new occupancy in 2014).

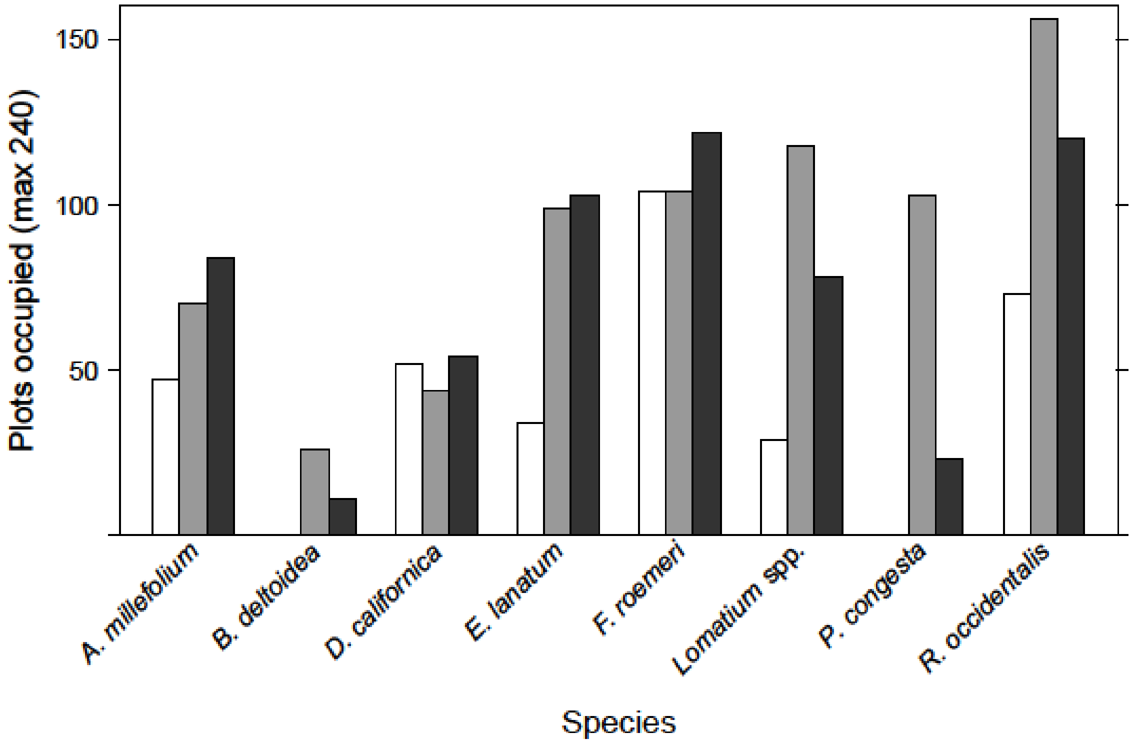

Figure 5. Number of occurrences of seeded native species within monitoring plots before treatment (2005; white), immediately after treatment (2009; grey), and five years after monitoring ceased (2014; black). The maximum number of plots each species could occupy is 240 (6 sites × 20 plots × 2 sub-plots). Congeneric *Lomatium* species are grouped together.

Population spread of *Plectritis congesta*

While most of the seeded species were present in small numbers prior to seed supplementation, *P. congesta* was absent from plots at the initiation of the project. Therefore, a more in-depth study of this species' population spread can inform about the effects of seeding on diversity beyond boundaries of seeded plots, as well as provide detailed information about its population dynamics. Although establishment of *P. congesta* was high during the initial monitoring period, Cowichan Preserve (BC) was the only site with a substantial, persistent population. A few individuals were seen at all sites except Morgan Property, but populations were too small and had insufficient evidence of movement for inclusion in a case study of spread. At the Cowichan Preserve, *P. congesta* was still present in 9 out of 20 treatment plots and spread of the population from these plots was visible. There was no relationship between population persistence and disturbance treatment (as it was not a significant predictor of whether plant patches persisted between 2009 and 2014).

In 2014, the maximum extent of spread from a plot measured 3.25 m from the boundary of the seeded area, while the average furthest distance traveled from plots was 1.19 m. The population count totaled 8,986 individuals, over a quarter (28%) of which were located outside of the seeded plots. Plants were found to spread equally into treated areas and matrix areas. The entire block of plots was burned in the fall of 2014 and monitoring was repeated in spring of 2015 to capture the population changes after a fire disturbance. In spring 2015, the total number of *P. congesta* individuals had increased 33% to 11,938 individuals (26% located outside of seeded plots). The maximum distance spread from seeded plot boundaries had increased nearly 1 m to 4.2 m and the average furthest distance traveled from plots was 1.54 m. Although it is impossible to know exactly which areas have been occupied by *P. congesta* individuals since seeding first occurred in 2006, I can estimate the area that has been exposed to seed rain based on where plants are currently situated. By mapping polygons of the current extent of the population, I calculated that the area outside of seeded plots that has been influenced by seeding treatments equals 31.87 m^2.

Discussion

Ongoing efforts to restore invaded grasslands face numerous barriers to success due to dwindling native seed banks and the high degree of exposure to exotic seed sources. Innovative techniques to decrease the abundance of exotic plant species and increase the richness and abundance of native populations are essential for overcoming these barriers. It is a challenge to understand the trajectories of ecosystems undergoing restoration given the financial and temporal constraints on monitoring. Therefore, the intention of this follow-up study was to determine how the effects of disturbance treatments and native seeding endure over the long-term and to evaluate whether short-term results were good predictors of long-term patterns. In summary, these results show that the positive effects of supplementary seeding persist even in the absence of active management, but that differences observed between exotic-removal treatments have diminished over the years. My results also demonstrate that long-term monitoring of target plant species can elucidate population dynamics that are not immediately observable, and I provide a case study of how population spread can be used as a metric to understand the spatial influence of seeding efforts.

Native species richness and abundance

This study showed that the positive effects of supplemental seeding were persistent after 8 growing seasons, albeit to a slightly lesser degree than was observed immediately after seeding occurred. Positive, lasting effects of seed addition have been seen in a few other grassland habitats (Foster & Tilman 2003; Zobel et al. 2000), but seeding has not been universally successful across all grassland types. Several studies in both arid and subhumid grasslands

(Wilsey & Polley 2003; James et al. 2011), as well as grass-seeding projects in sagebrush-steppe (Davies et al. 2012) and chaparral (Busby & Southworth 2014) have found that restoration seeding often has only ephemeral or marginal effects. Therefore, it is promising to see that seed addition at sites in the Garry oak ecosystem effectively led to continued improvement in richness of native species. In many cases where persistence of seeded populations has been reported, monitoring was carried out for fewer than 5 growing seasons (Rinella et al. 2012), but lengthening monitoring periods can highlight differences between short and long term effects of treatments (Peppin et al. 2010; Endress et al. 2012) and reveal how the rate of return on seeding changes over time.

This study confirms, once again, that seed limitation is a major barrier to successful restoration of oak savanna and grassland plant communities (Foster & Tilman 2003; Stanley et al. 2010; Richardson et al. 2012). This is unsurprising given the extensive fragmentation experienced by this ecosystem and the large seed input from nearby agricultural lands. Previous studies have suggested that the relative importance of seed limitation is likely overestimated when evaluated over short time periods due to the exclusion of factors that affect the fate of populations at later life-stages (Zobel & Kalamees 2005; Clark et al. 2007; Foster et al. 2007; Carrington 2014). The successful establishment of seeded species across all disturbance treatments provided strong evidence for high seed limitation at all of our study sites (Reagan 2014), and the persistence of most of these species after 8 years reinforces that seed availability is likely the most limiting factor, above other factors such as negative interactions (e.g. competition for resources, herbivory). If resource availability were the most limiting factor, one would expect to see a preference (in both establishment and persistence) for restoration techniques that cleared away competitors, but there was no observable effect of disturbance treatment on overall species richness (Stanley et al. 2010). Moreover, if herbivory were highly limiting, one would expect to see a strong decline in the effect of seeding over time as continued herbivore pressure was exerted on the established populations. I found that the overall positive effect of seeding was still noticeable and is unrelated to disturbance treatment; therefore I can conclude that the relative importance of seed limitation would not have been considerably overestimated based on the data available at the end of the original monitoring period.

A major question posed during the original experiment was whether disturbance treatments alone were sufficient to generate an increase in the richness and/or abundance of native species, or whether supplemental seeding was required. As discussed above, achieving increased richness did, in fact, rely on seeding due to seed limitation. An increase in abundance of native species, however, could be achieved either through native seed supplementation or by using a disturbance treatment that included grass-specific herbicide (without seed supplementation). That is, while native abundance could be increased, across all treatments, with the addition of seed, unseeded plots that received application of grass-specific herbicide could achieve comparable levels of native species cover. The native cover in the plots treated with grass-specific herbicide consisted of equal parts grasses (predominantly *F. roemeri*) and forbs. Three perennial forb species, *Camassia quamash*, *Fragaria virginiana*, and *Sanicula crassicaulis*, (none of which were seeded) responded particularly well to the removal of exotic grasses, providing evidence that exotic grasses are not only displacing natives within their own functional group, but limiting the resources required by native forbs as well. It is important to note that successful prairie restoration is reliant on both the reduction of exotic grasses and the expansion of extant native species. The results of this follow-up study show that targeting exotic grasses with grass-specific herbicide may have lasting effects on the performance of native individuals and the expansion of native populations. It also aligns with findings from similar studies in which applications of grass-specific herbicides were found to be effective exotic-removal methods that also resulted in increased native plant biomass (Flory & Clay 2009).

These findings show that, while seeding is a consistently successful option for increasing cover of native species, the targeted removal of exotic grasses can create sufficient space and resources for existing native plants to expand spatially and to support recruitment of new individuals. This result was not immediately apparent when monitoring ended in 2009, presumably due to a lag time between the removal of exotic grasses and the resulting response of the extant natives being released from competition. Stanley et al. (2010) noted that neither disturbance nor seeding treatments caused an immediate increase in native plant abundance but they correctly predicted that, as seeded species continued to grow, they would contribute to cover values. This study now shows that supplemental seeding and grass-specific herbicide treatments were equivalent determinants of increased abundance of native species over the long-term, but that their effects were not additive.

Exotic grass abundance

The effects of disturbance treatments on the reduction of non-native grasses were less pronounced in 2014, 5 years after original monitoring had ceased. Initially, treatments that included grass-specific herbicide were the most effective at reducing the abundance of exotic grasses throughout the ecoregion (Stanley et al. 2010), but in 2014 the persistence of this effect was only detectable at one site, Triangle Preserve (which was the least invaded site initially). The persistence and dominance of exotic grass species are major barriers to success in grassland restoration and results from this study highlight the extreme difficulty in combatting their influence over the long-term. Given the aggressive nature of the exotic grasses in this ecosystem, it is unsurprising that there would be some resurgence in abundance in the years following treatment applications. Interestingly, the degree of the undesirable rebound differed greatly between sites, with those in Oregon and British Columbia remaining well below pre-treatment levels and those in Washington equaling or exceeding their original levels. Examining this pattern in the context of abiotic site stressors (e.g., nutrient availability, annual precipitation) may provide some explanation. According to Richardson et al. (2012), the three sites in Washington experience lower abiotic stress than the two sites in Oregon or the single site in British Columbia. Throughout the entirety of the experiment and extended monitoring (2005-2014), precipitation levels varied inter-annually at all sites. Washington sites consistently received higher amounts of rainfall than both Oregon and British Columbia and, in the years since previous monitoring ended, the precipitation reductions experienced in comparatively dry years (2011, 2013) were not as drastic in Washington as in Oregon (Appendix D).

Numerous studies have suggested that decreased abundance of exotic species is associated with areas experiencing high abiotic stress, due to physiological constraints on growth or the lack of traits required for tolerating stressful conditions (Holway et al. 2002; Williamson & Harrison 2002; Gerhardt & Collinge 2003). Even though the abundance of exotic grasses had decreased at all sites by 2009 in response to disturbance treatments (Stanley et al. 2010), there has since been a more rapid resurgence at sites experiencing low abiotic stress (where abiotic constraints are not as strong) and higher annual precipitation. Furthermore, it is worth noting that the two sites that experienced the greatest resurgence of non-native grasses had the lowest initial native species richness (Stanley et al. 2010). There is substantial evidence that more diverse communities have greater resistance to invasion (or in this case, re-invasion) at local scales due to competitive exclusion by established groupings of native species (Tilman 1997; Levine 2000; Naeem et al. 2000). The long-term trend seen in this study elucidates the important roles that both abiotic and biotic factors play in ensuring resistance to invasion within this ecosystem.

Seeded native species trends

The long-term success of each of the 8 seeded species varied considerably. Several species experienced steady, gradual increases in abundance over time, others established well but experienced drastic population declines, while yet another rebounded after an initial set-back. The trajectories of each of these populations can provide valuable information about the suitability (or potential for self-sustainability) of species used in seeding, particularly when put in the context of site location, feasibility of restoration treatments, and specific goals of habitat enhancement. When framing restoration goals in the context of habitat enhancement, understanding the mechanisms that support the persistence and spread of desirable plant populations becomes increasingly important. In this experiment, half of the seeded species have the potential to create valuable habitat for threatened lepidopteran species (see Appendix B), but only if the plant populations can persist to provide nectar sources and larval host plants for multiple generations. Therefore, it is important to determine the optimal restoration techniques (in this case through disturbance treatments) that encourage establishment, but that also have an influence on long-term population persistence and can set the stage for spatial advance.

While forbs native to the oak savanna ecosystem typically have greater establishment success following fire (Maret & Wilson 2000; Dunwiddie et al. 2014), it is often unclear whether fire plays a role in determining the potential for a species' persistence. For example, *P. congesta* (the only annual species seeded in this experiment) had the highest establishment success overall (Stanley et al. 2010), particularly in burn treatments, but there was very low persistence after 8 growing seasons, and where persistence did occur it was unrelated to initial disturbance treatment. *Achillea millefolium*, *E. lanatum*, and *R. occidentalis* (all perennial species) also had greater establishment success in plots with a burn treatment (Stanley et al. 2010) but, in contrast with *P. congesta*, the long-term persistence and abundance of these species was also positively associated with burn treatments. These contrasting trends contribute to the recently-studied issue of loss of native annual forbs throughout the prairie system in the absence of fire (Dunwiddie 2014). If fire is indeed what promotes establishment of many forbs, the perennial species likely gain enough benefit from a single burn (after which point they can persist relatively well without disturbance), while the viability of annual forb populations remains more deeply dependent on the repeated influence of fire.

Unlike the forbs mentioned above, the native grass, *F. roemeri*, initially had a negative response to fire, as it experiences temporary setbacks after major disturbance (Dunwiddie 2002). In the long-term, the most important determinant of success for this species at all sites was the reduction of competition with exotic grasses using a grass-specific herbicide. Presumably, this difference shows that the forbs required the creation of suitable microsites to aid establishment (by using fire to clear thatch) while the grass required release from direct competition to aid growth and recruitment. The two grass species were the only seeded species that exhibited distinct geographic patterns. Although *F. roemeri* and *D. californica* are both long-lived, native bunchgrasses that are adapted to disturbance-prone environments, the abundance of *F. roemeri* in Washington (low abiotic stress) greatly exceeded its abundance elsewhere. In contrast, success of *D. californica* was almost exclusive to Oregon (high abiotic stress). This result indicates that abiotic differences throughout the range are substantial enough to promote particular native species over others.

Spatial advance of restoration species

In addition to measurements of establishment and persistence, using population spread as a metric of success is useful for evaluating longer-term suitability of restoration species and the ability of habitats to support native plant populations. Supplementing sites with native seed is often a very cost-prohibitive restoration technique so it is essential to understand how seeding efforts influence native species richness and abundance both within and beyond plot boundaries. There is a larger return on seeding investments if the species used can successfully reseed and spread beyond the initial point of application instead of remaining restricted to areas that were directly manipulated. The results of this study show that establishment rates are good metrics for understanding a species' particular microsite requirements, but are not necessarily indicative of long-term persistence and spread capabilities. In this experiment, there was evidence of movement and colonization by most of the seeded species, as individuals were observed in plots that had been vacant prior to 2014.

Plectritis congesta was the only seeded species for which I could derive exact measurements of the spatial influence of seeding, given that all individuals found at sites were a direct result of seeding efforts (it was not present in or around plots prior to the experiment). For this species, initial establishment was high (Stanley et al. 2010) and long-term persistence across sites was low, but where persistence was sufficient, spatial spread had occurred. Reasonable expectations of spread can be deduced from analysis of seed type and dispersal mechanism. Although some of *P. congesta*'s seeds have morphological structures for wind-assisted dispersal (approximately 75% have wing structures), most seeds fall within 10 cm of the parent plant, indicating that spread rates will be somewhat slow (C. Trowbridge, unpublished data). Over the course of 9 years, the boundaries of the *P. congesta* patches at the Cowichan Preserve had expanded at an average rate of 17.1 cm per generation (year), which falls in line with our minimum theoretical expectations of spread, given the short range of dispersal. It is likely that plant species with taller statures, lighter seed, or more advanced dispersal mechanisms would disperse seed further (Thomson et al. 2011), and therefore be able to expand their spatial extent more rapidly, so these physical characteristics must be considered when defining expectations and success criteria for movement of seeded restoration species. Most species seeded in this experiment are wind-dispersed or autodispersed, with only a few having specialized seed dispersal characteristics (*D. californica*,twisted awns; *R. occidentalis*, hooked achenes). Only one species, *A. millefolium* exhibits the ability to spread clonally.

Interestingly, the movement of the *P. congesta* population had occurred in all directions from the seeded areas, both into the unseeded half of treatment plots and into the untreated matrix. This suggests that the establishment of this species is not necessarily constrained by a lack of available microsites and it can successfully reseed amongst exotic grasses as long as a prolific seed source is available. It appears that the area exposed to seed rain from *P. congesta* individuals is continuing to increase with each generation. The movement observed between 2014 and 2015 provides insight into the potential for spread over just one generation, but more interestingly, highlights the degree to which fire disturbance can encourage the spatial expansion of this native forb's population. While there is some documentation of how fire can promote establishment, it is not often feasible to document how it affects the distribution of individuals in a population. As seen in this study, both the abundance and spatial extent of an established population of *P. congesta* benefited from the influence of fire.

Conclusion

Seeding native species was the most consistently effective treatment option across the entire range of sites, while the initial effects of disturbance treatments on reducing the abundance of exotic species diminished over time. It was promising to see that even at sites where the abundance of exotic grasses had rebounded to pre-treatment levels, the populations of seeded species had been able to persist amongst the invaders. These findings reinforce the major challenge posed by seed limitation in the invaded remnant patches of Garry oak habitat, but they also provide hope for success in situations where enhancing native diversity is the primary goal (as is often the case with habitat enhancement for sensitive butterfly species).

While seeding was effective on the whole, there was variation between each seeded species' population dynamics following initial establishment. Choosing fast-growing perennial species for restoration seeding appears to be an assured option given that their populations were likely to persist if they established after the initial disturbance. Seeding of annual species, however, may be a riskier choice if continual application of treatments is not feasible, due to the apparent reliance of establishment of annuals on disturbance. It is important that species used in restoration projects have the ability to expand their population boundaries, preferably without additional management, in order to mimic natural spatial patterns rather than remaining restricted to artificial seed islands. Most populations of the species used in this experiment have spread beyond the initially-seeded areas, and their varying degrees of spatial advance provide comparative information about suitability and habitat enhancement value.

Although disturbance treatments did not result in a lasting reduction of exotic grass abundance across all sites, I found that several of these treatments played a role in determining the success (in regards to abundance) of native species. The appropriateness of future applications of these disturbance treatments can be determined by evaluating the status of extant native populations at a site, or by identifying specific native species to target for enhancement. Grass-specific herbicide treatments are beneficial when aiming to enhance populations of herbicide-resistant native graminoids (such as *Festuca roemeri* or *Carex inops*), and they are equally appropriate for areas where populations of native species are well-established, but require release from competition with exotic grasses. Additionally, treatments involving fire can aid in the establishment of several forb species, but the long-term enhancement may be experienced only by species with perennial life histories.

The key to restoring degraded grassland habitats is identifying feasible and effective techniques to reduce the negative impacts of exotic species and promote self-sustaining native populations over the long-term. Collaborative research with scientists has provided land managers with valuable guidance for restoring their lands, and follow-up studies, such as this one, can help managers understand how initial monetary investments relate to long-term improvement. Monitoring the trajectories of the seeded populations, through measurements of persistence and observations of spatial advance, can inform future selection of restoration species and influence the layout of seeding plans. Additionally, understanding which restoration techniques produce ephemeral effects (such as the exotic-removal treatments in this experiment) aids in determining appropriate disturbance intervals for ongoing management. Extended monitoring of this restoration experiment has proven beneficial as it revealed the emergence of delayed responses and allowed for measurements of population persistence and spread to help evaluate long-term suitability and success of restoration species. The results of this study have practical applications for the continued efforts to restore native grasslands, as well as theoretical implications for utilizing findings from population ecology studies in the broader context of restoration ecology.

References

Bash, J.S. and Ryan, C.M. 2002. Stream restoration and enhancement projects: is anyone monitoring? *Environmental Management,* 29(6):877-885.

Brudvig, L. 2011. The restoration of biodiversity: where has research been and where does it need to go? *American Journal of Botany,* 98(3):549-558.

Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., and Rey-Benayas, J.M. 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends in Ecology and Evolution*, 26(10):541-549.

Busby, L.M. and Southworth, D. 2014. Minimal persistence of native bunchgrasses seven years after seeding following mastication and prescribed fire in Southwestern Oregon, USA. *Fire Ecology*, 10(3):63-71.

Carrington, M.E. 2014. Seed size and recruitment limitation influence seedling establishment in three tallgrass prairie species. *Plant Ecology*, 215:1163-1172.

Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B., and Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science,* 333:1024-1026.

Clark, C.J., Poulsen, J.R., Levey, D.J., and Osenberg, C.W. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *The American Naturalist*, 170(1):128-142.

Clements, D.R. 2013. Translocation of rare plant species to restore Garry oak ecosystems in western Canada: challenges and opportunities. *Botany,* 91:283-291.

Corbin, J.D., D'Antonio, C.M., and Bainbridge, S.J. 2004. Tipping the balance in the restoration of native plants: experimental approaches to changing the exotic:native ratio in California grassland. Pages 154-179 In: Gordon, M.S., Bartol, S.M (eds) *Experimental approaches to conservation biology*. University of California Press, Berkeley, CA.

Davies, G.M., Bakker, J.D., Dettweiler-Robinson, E., Dunwiddie, P.W., Hall, S.A., Downs, J., and Evans, J. 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications,* 22(5):1562-1577.

Dennehy, C., Alverson, E.R., Anderson, H.E., Clements, D.R., Gilbert, R., and Kaye, T.N. 2011. Management strategies for invasive plants in Pacific Northwest prairies, savannas, and oak woodlands. *Northwest Science,* 85(2):329-351.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., and Ewers, R.M. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution,* 22(9):489-496.

Dunwiddie, P.W. 2002. Management and restoration of grasslands on Yellow Island, San Juan Islands, Washington, USA. Pages 78-87 in: Burton, P.J. (ed), *Garry Oak Ecosystem Restoration: Progress and Prognosis. Proceedings of the Third Annual Meeting of the B.C. Chapter of the Society for Ecological Restoration, April 27-28, 2002.* Victoria, British Columbia: B.C. Chapter of the Society for Ecological Restoration.

Dunwiddie, P.W., Alverson, E.R., Martin, R.A., and Gilbert, R. 2014. Annual species in native prairies of South Puget Sound, Washington. *Northwest Science*, 88(2):94-105.

Endress, B.A., Parks, C.G., Naylor, B.J., Radosevich, S.R., and Porter, M. 2012. Grassland response to herbicides and seeding of native grasses 6 years posttreatment. *Invasive Plant Science and Management*, 5:311-316.

Floberg, J., Goering, M., Wilhere, G., MacDonald, C., Chappell, C., Rumsey, C., Ferdana, Z., Holt, A., Skidmore, P., Horsman, T., Alverson, E., Tanner, C., Bryer, M., Iachetti, P., Harcombe, A., McDonald, B., Cook, T., Summers, M., and Rolph, D. 2004. Willamette Valley-Puget Trough- Georgia Basin Ecoregional Assessment, Volume One: Report. Prepared by The Nature Conservancy with The Nature Conservancy of Canada, Washington Department of Fish and Wildlife, Washington Department of Natural Resources, Oregon State Natural Heritage Information Center and the British Columbia Conservation Data Centre.

Flory, S.L. and Clay, K. 2009. Invasive plant removal method determines native plant community responses. *Journal of Applied Ecology*, 46:434-442.

Foster, B.L., Murphy, C.A., Keller, K.R., Aschenbach, T.A., Questad, E.J., and Kindscher, K. 2007. Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment. *Restoration Ecology*, 15(4):652-661.

Foster, B.L. and Tilman, D. 2003. Seed limitation and the regulation of community structure in oak savanna grassland. *Journal of Ecology*, 91:999-1007.

Fuchs, M. 2001. Towards a recovery strategy for Garry oak and associated ecosystems in Canada: ecological assessment and literature review, technical report. Environment Canada, Canadian Wildlife Service.

Gerhardt, F. and Collinge, S.K. 2003. Exotic plant invasions of vernal pools in the central valley of California, USA. *Journal of Biogeography*, 30(7):1043-1052.

Hamman, S.T., Dunwiddie, P.W., Nuckols, J.L., and McKinley, M. 2011. Fire as a restoration tool in Pacific Northwest prairies and oak woodlands: challenges, successes, and future directions. *Northwest Science*, 85(2):317-328.

Hampe, A. 2011. Plants on the move: the role of seed dispersal and initial population establishment for climate-driven range expansions. *Acta Oecologica*, 7:666-673.

Herrick, J.E., Schuman, G.E., and Rango, A. 2006. Monitoring ecological processes for restoration projects. *Journal for Nature Conservation*, 14:161-171.

Holway, D.A., Suarez, A.V., and Case, T.J. 2002. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *Ecology*, 83(6):1610-1619.

James, J.J., Svejcar, T.J., and Rinella, M.J. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *Journal of Applied Ecology*, 48:961-969.

Kiehl, K., Kirmer, A., Donath, T., Rasran, L., and Holzel, N. 2010. Species introduction in restoration projects- evaluation of difference techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology*, 11:285-299.

Kindscher, K. and Tieszen, L.L. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. *Restoration Ecology* 6(2):181-196.

Levine, J.M. 2000. Species diversity and biological invasions: relating local processes to community pattern. *Science* 288(5467):852-854.

MacDougall, A.S., Bechwith, B.R., and Maslovat, C.Y. 2004. Defining conservation strategies with historical perspectives: a case study from a degraded oak grassland ecosystem. *Conservation Biology*, 18(2):455-465.

MacDougall, A.S. and Turkington, R. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology*, 92:422-434.

MacDougall, A.S. and Turkington, R. 2006. Dispersal, competition, and shifting patterns of diversity in a degraded oak savanna. *Ecology*, 87(7):1831-1843.

Maret, M.P. and Wilson, M.V. 2000. Fire and seedling population dynamics in western Oregon prairies. *Journal of Vegetation Science*, 11:307-314.

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., and Santamaria, L. 2012. Seed dispersal in changing landscapes. *Biological Conservation*, 146:1-13.

McCune, J.L. and Vellend, M. 2015. Using plant traits to predict the sensitivity of colonizations and extirpations to landscape context. *Oecologia*, 178(2):511-524.

Mcdonald, R.I., Kareiva, P., and Forman, R.T.T. 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141:1695-1703.

Miller, J.R. and Hobbs, R.J. 2007. Habitat restoration- do we know what we’re doing? *Restoration Ecology*, 15(3):382-390.

Montalvo, A.M., Williams, S.L., Rice, K.J., Buchmann, S.L., Cory, C., Handel, S.N., Nabhan, G.P., Primack, R., and Robichaux, R.H. 1997. Restoration biology: a population biology perspective. *Restoration Ecology*, 5(4):277-290.

Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., and Gale, S. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91(1):97-108.

Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F.M., Katul, G.G. 2011. Spread of North American wind-dispersed trees in future environments. *Ecology Letters*, 14:211-219.

Neubert, M. and Caswell, H. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, 82:1613-1628.

Noss, R.F., LaRoe, E.T, and Scott, J.M. 1995. Endangered Ecosystems of the US: A Preliminary Assessment of Loss and Degradation. Washington DC: U.S. Department of the Interior, National Biological Service.

Pakeman, R.J., Pywell, R.F., and Wells, T.C.E. 2002. Species spread and persistence: implications for experimental design and habitat re-creation. *Applied Vegetation Science*, 5(1):75-86.

Peppin, D., Fule, P.Z., Sieg, C.H., Beyers, J.L., and Hunter, M.E. 2010. Post-wildfire seeding in forests of the western United States: an evidence-based review. *Forest Ecology and Management*, 260:573-586.

Pimental, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience*, 50:53-65.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reagan, K. 2014. Restoration of native plant communities: an examination of seed limitation and microsite limitation in the Garry oak ecosystem (Doctoral dissertation). University of Washington, Seattle, WA.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., Pysek, P., and Hobbs, R.J. 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions*, 13:126-139.

Richardson, P.J., MacDougall, A.S., Stanley, A.G., Kaye, T.N., and Dunwiddie, P.W. 2012. Inversion of plant dominance-diversity relationships along a latitudinal stress gradient. *Ecology*, 93(6):1431-1438.

Rinella, M.J., Mangold, J.M., Espeland, E.K., Sheley, R.L., and Jacobs, J.S. 2012. Long-term population dynamics of seeded plants in invaded grasslands. *Ecological Applications*, 22(4):1320-1329.

Rook, E.J., Fischer, D.G., Seyferth, R.D., Kirsch, J.L., LeRoy, C.J., and Hamman, S. 2011. Responses of prairie vegetation to fire, herbicide, and invasive species legacy. *Northwest Science*, 85(2):288-302.

Ruiz-Jaen, M.C. and Aide, T.M. 2005. Restoration success: how is it being measured? *Restoration Ecology*, 13:569-577.

Sinclair, M., Alverson, E., Dunn, P., Dunwiddie, P.W., and Gray, E. 2006. Bunchgrass Prairies. Pages 29-59 In: Apostol, D., Sinclair, M. (eds) *Restoring the Pacific Northwest: The art and science of ecological restoration in Cascadia*. Island Press, Washington, DC.

Slater, G.L. and Altman, B. 2011. Avian restoration in the prairie-oak ecosystem: a reintroduction case study of western bluebirds to San Juan Island, Washington. *Northwest Science*, 85(2):223-232.

Smith, M.D. and Knapp, A.K. 1999. Exotic plant species in a C4-dominated grassland: invisibility, disturbance, and community structure. *Oecologia*, 120:605-612.

Stanley, A.G., Kaye, T.N., and Dunwiddie, P.W. 2010. Regional strategies for restoring invaded prairies, final technical report. The Institute for Applied Ecology and The Nature Conservancy, Corvallis, OR.

Stanley, A.G., Kaye, T.N., and Dunwiddie, P.W. 2011a. Multiple treatment combinations and seed addition increase abundance and diversity of native plants in Pacific Northwest prairies. *Ecological Restoration*, 29:35-44.

Stanley, A.G., Dunwiddie, P.W, and Kaye, T.N. 2011b. Restoring invaded Pacific Northwest prairies: management recommendations from a region-wide experiment. *Northwest* Science, 85(2):233-246.

Suding, K.N. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics*, 42:465-487.

Thorpe, A.S. and Stanley, A.G. 2011. Determining appropriate goals for restoration of imperiled communities and species. *Journal of Applied Ecology*, 48:275-279.

Thomson, F.J., Moles, A.T., Auld, T.D., and Kingsford R.T. 2011. Seed dispersal is more strongly correlated with plant height than with seed mass. *Journal of Ecology* 99:1299-1307.

Tilman, D. 1997. Community invisibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78(1):81-92.

Tveten, R. 1997. Fire effects on prairie vegetation. *In* P.Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy, Seattle, WA. 123-130.

Vesely, D. and Tucker, G. 2004. A landowner's guide for restoring and managing Oregon white oak habitats. USDI Bureau of Land Management, Salem District.

Weinstein, M.P., Litvin, S.Y., and Krebs, J.M. 2014. Restoration ecology: ecological fidelity, restoration metrics, and a systems perspective. *Ecological Engineering,* 65:71-87.

Williamson, J. and Harrison, S. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications,* 12(1):40-51.

Wilsey, B.J. and Polley, H.W. 2003. Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands. *Ecology,* 84(4): 920-931.

Wilson, M.V. and Clark, D.L. 2001. Controlling invasive *Arrhenatherum elatius* and promoting native prairie grasses through mowing. *Applied Vegetation Science,* 4(1):129-138.

Wortley, L., Hero, J-M., and Howes, M. 2013. Evaluating ecological restoration success: a review of the literature. *Restoration Ecology*, 21(5):537-543.

Young-Mathews, A. 2012. Plant fact sheet for shortspur seablush (*Plectritis congesta*). USDA-Natural Resources Conservation Service, Plant Materials Center, Corvallis, OR.

Zobel, M., Otsus, M., Liira, J., Moora, M., and Mols, T. 2000. Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, 81(12):3274-3282.

Zobel, M. and Kalamees, R. 2005. Diversity and dispersal- can the link be approached experimentally? *Folia Geobotanica,* 40:3-11.

Appendices

Appendix A Restoration treatment details

Disturbance treatments were designed to decrease the cover of exotic species (specifically grasses). Sethoxydim, a grass-specific herbicide, was used to directly target exotic grasses; fall burning can reduce thatch and open up microsites for seed germination; glyphosate, a broad-spectrum herbicide, was used to eliminate ruderal, exotic species that emerged immediately after burns; and mowing can prevent seed set from exotic grasses (spring) and reduce biomass that contributes to thatch accumulation (fall). A supplemental seeding treatment was applied in a split-plot design in all plots in 2006 and 2007.

Treatment Code*	2005		2006			2007			2008	
	spring	fall	spring	fall		spring	fall		spring	fall
SBG	sethoxydim		sethoxydim	burn + glyphosate	seeding	sethoxydim		seeding		burn + glyphosate
MBG	mow			burn + glyphosate						burn + glyphosate
MM	mow	mow	mow	mow		mow	mow		mow	mow
SM	sethoxydim	mow	sethoxydim	mow		sethoxydim	mow			mow
Control	*no manipulation*					*no manipulation*			*no manipulation*	

*Treatment codes used in Stanley et al. 2010, Stanley et al. 2011a, and Stanley et al. 2011b are included to facilitate cross-referencing.

Appendix B Seeded species information

Species-specific details are included for all native species used in the seeding treatment. Abbreviations in parentheses indicate whether a species is a larval host plant or a nectar source for any of three endangered lepidopteran species within the Garry oak ecosystem: FBB = Fender's blue butterfly (*Icaricia icariodides fenderi*), federally endangered (U.S.); MS = Mardon skipper (*Polites mardon*), federally endangered (U.S.); TC = Taylor's checkerspot (*Euphydryas editha taylori*), federally endangered (U.S., Canada).

Species	Common Name	Family	Duration	Ecological & cultural importance
Achillea millefolium	yarrow	Asteraceae	perennial	Butterfly nectar source (MS); soil stabilization
Balsamorhiza deltoidea	deltoid balsamroot	Asteraceae	perennial	Pollinator habitat
Danthonia californica	California oat-grass	Poaceae	perennial	Butterfly host plant (MS); improves spatial structure of bird habitat
Eriophyllum lanatum	Oregon sunshine	Asteraceae	perennial	Pollinator habitat; butterfly nectar source (FBB)
Festuca roemeri	Roemer's fescue	Poaceae	perennial	Butterfly larval host (MS); soil stabilization
Lomatium nudicaule	bare-stem desert parsley	Apiaceae	perennial	Butterfly nectar source
Lomatium utriculatum	common lomatium	Apiaceae	perennial	Butterfly nectar source (TC, MS)
Plectritis congesta	seablush	Valerianaceae	annual	Butterfly nectar source (FBB, TC, MS) and larval host (TC)
Ranunculus occidentalis	western buttercup	Ranunculaceae	perennial	Pollinator habitat; butterfly nectar source (MS)

Appendix C ANOVA table of community composition response variables

Components of the best-fit models for predicting community composition response variables are included in the table below. Dashed spaces indicate effects that were not included in the predictive models.

	Native species richness			Native species abundance			Exotic grass abundance		
Effect	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Site	5, 114	19.96	<0.001	5, 110	38.68	<0.001	5, 90	30.82	<0.001
Treatment	--	--	--	4, 110	3.52	0.01	4, 90	1.49	0.21
Seeding	1, 118	76.71	<0.001	1, 110	2.02	0.16	--	--	--
Site * Treatment	--	--	--	--	--	--	20, 90	2.15	0.008
Treatment * Seeding	--	--	--	4, 114	3.57	<0.001	--	--	--
Pre-treatment data	1, 118	24.84	<0.001	1, 114	13.07	<0.001	1, 119	1.95	0.17

Appendix D Regional climate trends

Mean annual temperature (a) and total annual precipitation (b) differed throughout the region. Data for Oregon and Washington comes from the National Oceanic & Atmospheric Administration *(*https://www.ncdc.**noaa**.gov/cdo-web/), collected at weather stations in Corvallis, OR and Olympia, WA. Data for British Columbia were made available by Environment Canada (http://climate.weather.gc.ca), collected from the Victoria International Airport. Measurements at this site are currently unavailable for 2013 and 2014.