Plant Ecol (2012) 213:637–647
DOI 10.1007/s11258-012-0028-2

Dominance of native grasses leads to community convergence in wetland restoration

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Received: 25 April 2011 / Accepted: 24 January 2012 / Published online: 5 February 2012

Abstract Wetland restoration is a pressing conservation priority, but there are few replicated field studies that provide a scientific foundation for these activities. We conducted a 3-year, replicated field experiment to examine the effectiveness of initial site preparation techniques (combinations of solarization, herbicide, tilling, and thermal weed control) in restoring native plant biodiversity to an agricultural field in a former wetland prairie in Oregon, USA. Post-treatment, plots were sown with a typical restoration mix of native graminoids and forbs. Treatments were compared to three high-quality managed reference wetlands and the adjacent agricultural field. Site preparation treatments varied in their effectiveness in suppressing extant vegetation and eliminating the residual seed bank. After 1 year, the solarization and fall herbicide application treatments were the most effective at reducing exotic cover. However, after 3 years, plant community composition converged in all treatments due to a loss of annual species and increasing dominance of native perennial bunchgrasses. Plant community composition became more similar to the reference wetlands each year, but diversity and richness diverged, apparently due to a trade-off between the cover of the dominant native bunchgrasses and diversity. Successional theory offers insights into how priority effects and competitive inhibition may influence community trajectories, and offers a useful model for restoring plant communities with high native diversity and dominance. Finding ways to mitigate the tradeoff between native plant cover and diversity by actively managing successional trajectories is an important challenge in wetland restoration that deserves further investigation.

Keywords Competition · Diversity · Priority effects · Restoration · Succession · Wetland prairie

Introduction

Wetland restoration is a relatively new field with little accumulated scientific knowledge (National Research Council 2001). Restoration design is often based on anecdotal information and case studies, rather than on rigorous experimental investigations, with some notable exceptions (reviewed by Young et al. 2005). Potentially reflecting the lack of a sound scientific

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Electronic supplementary material The online version of this article (doi:10.1007/s11258-012-0028-2) contains supplementary material, which is available to authorized users.

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foundation, restorations are not always successful in establishing a native plant community, and both natural and restored wetlands often are dominated by introduced plant species (National Research Council 2001; Kellogg and Bridgham 2002). Moreover, restored wetlands often do not attain the diversity of natural wetlands even after long periods of time (Seabloom and van der Valk 2003). For these reasons, wetland restoration provides a challenging venue for testing basic ecological principles in an important applied context.

Successional theory offers a useful framework for restoring and maintaining diverse, native communities (Temperton et al. 2004; Young et al. 2005; Walker et al. 2007). Indeed, restoration activities try to direct, and typically accelerate, secondary succession, generally beginning with suppressing extant vegetation and establishing an initial suite of desirable species. However, success depends on the effectiveness of site preparation treatments in eliminating the existing plants and seed bank of the site, as they are often dominated by invasive species (see mini-review of site preparations techniques in Online Resource 1), and the ability to re-establish native plant communities of desired species composition and diversity. Despite the clear importance of initial site preparation, few studies have compared different techniques (e.g., Wilson and Gerry 1995; Ewing 2002; Marushia and Allen 2011), with even fewer in wetlands (e.g., Adams and Galatowitsch 2006). Even the best site preparation techniques are only partially effective at eliminating unwanted plant species, and new propagules almost always continue to invade. Consequently, understanding and directing trajectories of plant community change through soil-vegetation site preparation techniques, composition of native seed mixes, and subsequent site management are essential to achieving and sustaining desirable species diversity and composition (Sheley et al. 2006).

Effective approaches to wetland restoration are urgently needed. More than 50% of the original wetland area in the contiguous U.S. has been lost, with agricultural activities responsible for 70% of wetland losses in the last half century (Dahl 2006). Wetland losses have been particularly severe in western Oregon's Willamette Valley. Since 1850, over 97% of wetland prairies in the valley have been converted to agricultural or urban land uses (Hulse et al. 2002), and these wetlands are currently listed as a critically endangered U.S. ecosystem (Noss et al. 1995). Given their imperiled status, wetland prairies are the focus of extensive restoration efforts in the Willamette Valley, and much of the potentially restorable wetland area is currently in agricultural production with relatively intact hydrology. The primary goal of wetland prairie restorations in this region generally is to maximize native plant cover and diversity and associated native fauna (Sinclair et al. 2006).

Our objective was to test the effectiveness of different site preparation techniques in restoring native plant biodiversity in a real-world restoration setting, and to link our findings with ecological theory of how communities are created and structured (i.e., successional theory, priority effects). We set up a large, replicated field experiment of ten different site preparation techniques in a prior *Lolium multiflorum* Lam. (annual ryegrass) field with relatively intact hydrology, and compared these experimental plots to three of the highest quality local remnant wetlands and to the adjacent agricultural field to address the following questions: (1) Which site preparation techniques are most effective at eliminating the extant vegetation and seed bank, and thereby support the initial establishment of a diverse native plant community? (2) Do initial differences in native plant composition and diversity persist in the face of long-term successional processes? (3) How does plant composition and diversity of the restoration treatments compare with that found in high-quality reference wetlands over time?

Methods

Study sites

Our experimental site, Coyote Prairie, was an agricultural field near Eugene, OR, USA used in the production of *Lolium multiflorum* seed for 25 years. It is representative of a typical restoration site in the region as much of the restorable land is currently in grass seed production. The field was tilled and burned annually in the fall until 2003 and fertilized twice annually in the spring with 4 g N m^{-2}, 2 g P m^{-2}, and 3.5 g K m^{-2} until 2004. The site is relatively flat with a 0.35% slope from east to west. Plots were located randomly across the 4.5 ha restoration site, as well as in an immediately adjacent 1 ha area that continued to be actively farmed. In addition, we chose three high-quality remnant wetland prairies as "reference wetlands" within 4 km of Coyote Prairie. Historically, these remnant prairies were likely regularly burned by Native Americans, and subsequently, grazed by livestock after Euro-American settlement (circa 1840) (Sinclair et al. 2006). These wetlands have not been grazed in recent decades and have never been plowed. Currently, they experience periodic management primarily to control aggressive invasive and woody species encroachment, including occasional controlled burns and mowing.

The local climate is Mediterranean with 91% of annual precipitation falling between November and May (National Oceanic and Atmospheric Administration 1979–2009). Wetland prairies in this region are inundated during the winter months and dry out through June, with peak growing season in mid-June and almost complete vegetation senescence by mid-July. *L. multiflorum* is tolerant of this hydroperiod, so the Coyote Prairie agricultural field was never drained, similar to other commercial grass seed operations in the region. Consequently, we observed a similar water-depth and degree of surface inundation in the experimental site, the adjacent farm field, and the three reference wetlands, with the exception that the reference wetlands have much greater microtopography. A recent comprehensive local hydrological study, that included our study sites, found that undrained farm fields and restored wetlands retain the hydrologic functions of reference wetlands (Marshall 2011).

All sites have similar soils (Natroy series, very-fine, smectitic, mesic Xeric Endoaquerts). In addition, we collected extensive soil nutrient, mineralization rates, and gas flux measurements (Pfeifer-Meister 2008). Soil nutrient availability in the experimental treatments quickly returned to low levels similar to the reference wetlands (e.g., mean ± SE soil inorganic nitrogen availability (μg N/g soil) in the reference, restored, and farm field during the growing season were, respectively: 5.5 ± 1.4, 1.7 ± 1.4, 9.9 ± 1.4; and total soil carbon (mg C/cm^3): 23.0 ± 1.6, 26.7 ± 1.6, 27.3 ± 1.6).

Experimental design

We conducted a 3-year study to determine the effect of site preparation techniques on eliminating exotic species and favoring native plant establishment and persistence. An unbalanced factorial design was chosen that combined and contrasted ten treatment combinations based upon input from a forum in which approximately 50 local wetland restoration practitioners identified the most relevant techniques. Treatment combinations were: (1) summer herbicide application, (2) tilling, (3) tilling & summer herbicide, (4) tilling & thermal treatment, (5) summer herbicide & thermal, (6) tilling, summer herbicide & thermal, (7) summer & fall herbicide, (8) tilling, summer & fall herbicide, (9) tilling & solarization, and (10) tilling, summer herbicide & solarization. See Online Resource 1 for a detailed description of each treatment.

The first summer herbicide application had no detectable effect on plant communities probably because it was applied after a long period of drought when plants were not actively growing. Given this, we lumped the summer herbicide application with its like counterpart (e.g., till/summer herbicide and till only were combined), thus reducing the total number of treatments from ten to seven. One treatment received only a summer herbicide application, which we subsequently refer to as 'control'.

Plots were 15 m by 15 m with 5 replicates of each treatment. There were 10 m mowed buffers between the plots and a 23 m buffer around the entire site. Prior to treatment implementation, the entire site was mowed twice and the *L. multiflorum* thatch was removed. In each reference site and the adjacent farm field, we also randomly established five 15 m by 15 m plots.

Treatment implementation

A field disk and cultipacker pulled by a tractor was used twice to break up the soil to a 20 cm depth for the tilling treatment (once north–south in June and once east–west in July 2004). Glyphomate 41 (salt formulation) was applied for the herbicide treatments in July (summer herbicide) and/or October (fall herbicide treatment) at a rate of 3.9 kg ai per ha. For the solarization treatment, clear plastic (0.15 mm, 15 m width) was placed over the plots, and edges were tucked into 20 cm deep trenches and buried for 4 months (July–October). A Sunburst infrared burner (Eugene, OR, USA) was used in August for the thermal weed control treatment (temperature output range: 650–800°C).

Sowing

A seed mix of 5 native graminoid and 10 native forb species was sown in all treatment plots with hand broadcasters in October 2004 (Table 1). Together, these species comprise 52% of the relative cover in the reference prairies. The quantities and mix of forb and graminoid species was typical of local restoration practices at the time of the study, although, a larger number of species was generally used.

Table 1 Species mix for experimental plots planted in October 2004 with associated life history (*A* annual; *P* perennial), densities planted, and average relative cover in the three reference wetlands

Species	Life history	mg seed/m^2	Seeds/m^2	Ref. Cover (%)
Graminoids				
Agrostis exarata Trin.	P	35	430	<1
Carex densa (L. H. Bailey) L. H. Bailey	P	60	70	<1
Danthonia californica Bol.	P	70	22	10
Deschampsia cespitosa (L.) P. Beauv.	P	50	165	24
Juncus tenuis Willd	P	15	660	2
Forbs				
Camassia quamash (Pursh) Greene ssp. *maxima* Gould	P	45	10	1
Epilobium densiflorum (Lindl.) Hoch & P.H. Raven	A	90	170	<1
Grindelia integrifolia DC.	P	70	20	1.5
Madia glomerata Hook.	A	60	95	3.5
Microseris laciniata (Hook.) Sch. Bip.	P	70	22	1.5
Plagiobothrys figuratus (Piper) I.M. Johnst. ex M. Peck ssp. *figuratus*	A	70	200	<1
Potentilla gracilis Douglas ex Hook. var. *gracilis*	P	25	80	2
Prunella vulgaris L. ssp. *lanceolata* (W. Bartram) Hultén	P	35	60	4
Symphyotrichum hallii (A. Gray) G.L. Nesom (syn. *Aster hallii)*	P	70	410	1.5
Wyethia angustifolia (DC.) Nutt.	P	70	5	<1

Plant sampling

Within each 225 m^2 plot, three 1 m^2 subplots were randomly located to monitor plant cover and diversity. Due to the homogenous nature of the farm, only one 1 m^2 subplot was sampled per plot. Percent cover was measured by species using the point-intercept method (Elzinga et al. 1998) with 25 pins in a 1 m^2 sampling frame. Pins were dropped vertically from the plant canopy to the soil surface and every plant touch was recorded by species, thus allowing greater than 100% cover due to multiple layering. The presence/absence was recorded for any species not hit by a pin. Plant cover was measured in mid-June for 3 years after establishment (2005–2007), but in 2005 farm field plots were not measured and in 2006 reference wetlands were not measured. Species nomenclature followed the Flora of North America (Flora of North America Editorial Committee 1993).

Statistical analyses

Data from the three 1 m^2 subplots were averaged, with the 225 m^2 plot used as the replicate unit for statistical tests (i.e., $n = 5$). Cover, species richness, and Simpson's index of diversity (1-D) were analyzed with repeated-measure ANOVAs using SPSS 11.0. Greenhouse-Geisser values are reported to correct for violations of sphericity, and appropriate transformations were used to normalize the distribution of the residuals. As data from the reference wetlands and farm field were only available for two of the three years, these treatments could not be included in the repeated-measures analyses. However, when exploring the significant interaction between treatment and year, one-way ANOVAs were run within a year and reference and farm field data were included in these analyses as appropriate. Tukey's pairwise comparisons were used to explore differences among treatments within a year. Linear least squares regression was used to examine the relationship between perennial bunchgrass cover and Simpson's diversity.

We compared plant community composition (% cover of individual species) in the experimental treatments, farm field, and reference wetlands over the 3 years using non-metric multidimensional scaling (NMS), with relative Sorensen (Kulczynski) distance and 1,000 Monte Carlo runs, to test for statistical significance. Species that were present, but not hit by a pin were assigned a cover of 0.5%. We tested for community differences among treatments with the multi-response permutation procedure (MRPP) using relative Sorensen distance. Finally, we performed an indicator species analysis using 1000 Monte Carlo runs to describe the axes in our NMS ordinations. NMS, MRPP, and indicator species analyses were performed with PC-ORD (McCune and Grace 2002).

Results

Site preparation treatments created large differences in plant communities, although these effects depended upon year (Online Resource 1, Table S1). In 2005, native plant cover was highest in the till/solarization treatment (Fig. 1a, $p < 0.001$). In 2006, native cover was lower in the control and till only treatments ($p < 0.05$) and similar in the rest of the experimental treatments. In 2007, native cover did not differ among experimental treatments, but all were significantly higher than the reference wetlands and farm field. Exotic cover was lower in the fall herbicide, till/fall herbicide and the till/solarization treatments than in all other experimental treatments in 2005 and 2006. By 2007, however, experimental treatment effects were no longer evident and the restored plots had 15-fold lower exotic cover than the reference wetlands (Fig. 1b). The farm field was an almost monotypic field of *L. multiflorum* and had the greatest exotic and total cover in all years measured.

Species richness was highest in the reference wetlands and lowest in the farm field (Fig. 2a). In 2005 and 2006, we observed some treatment differences (i.e., till/solarization < all others, $p < 0.05$), but there generally was a decrease in species richness (total, native, and exotic; Fig. 2a, b, c), such that by 2007 no differences were detected among experimental treatments. Furthermore, by 2007 all experimental treatments had lower total and native species richness than the reference wetlands. Exotic richness in the reference wetlands was twofold (2005) to sevenfold (2007) higher than in the experimental plots.

In 2005, total Simpson's diversity in the experimental treatments was similar to the reference wetlands except in the till-only treatment (Fig. 2d). However, by 2007 all treatments except the till and the till/fall herbicide had lower diversity than the reference wetlands. In 2007, the till/solarization treatment had the lowest diversity among experimental treatments. Native diversity followed a similar trend as total diversity (Fig. 2e). Treatment effects on exotic diversity were not dependent upon year (Online Resource 1, Table S1). Experimental treatments did not differ, but all had lower exotic diversity than the reference sites (Fig. 2f).

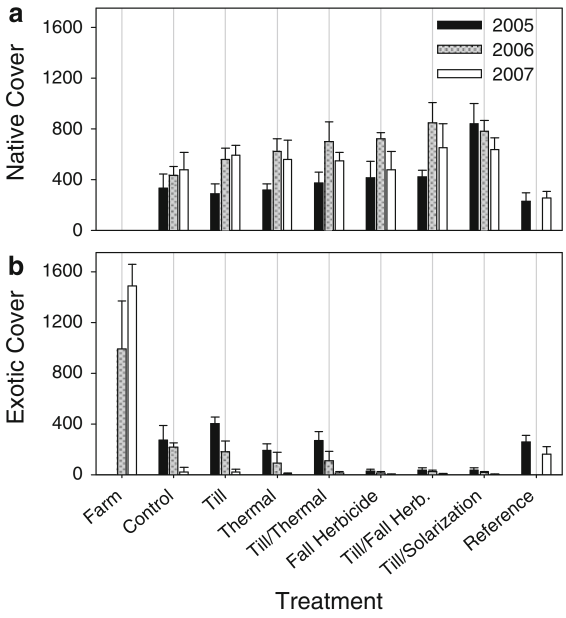

Fig. 1 Mean (**a**) native and (**b**) exotic percentage vegetation cover for the farm field, experimental treatments, and reference wetlands in 2005, 2006, and 2007. *Error bars* represent 95% confidence intervals. Treatments by year interactions are significant at $p < 0.001$

When analyzing non-seeded species only (a measure of how effective treatments were at eliminating extant vegetation and the seed bank as well as resistance to subsequent invasion), the solarization treatment initially had the fewest species (mean ± SE: 4.5 ± 1.0, $p < 0.001$) and the till treatment had the most (16.4 ± 1.0, $p < 0.021$). Over time, non-seeded species decreased in all plots from an average of 12 species in 2005 to 4 species in 2007 ($p < 0.001$), and the only treatment difference by 2007 was that the till treatment still had significantly more non-seeded species than the solarization and herbicide treatments ($p < 0.014$).

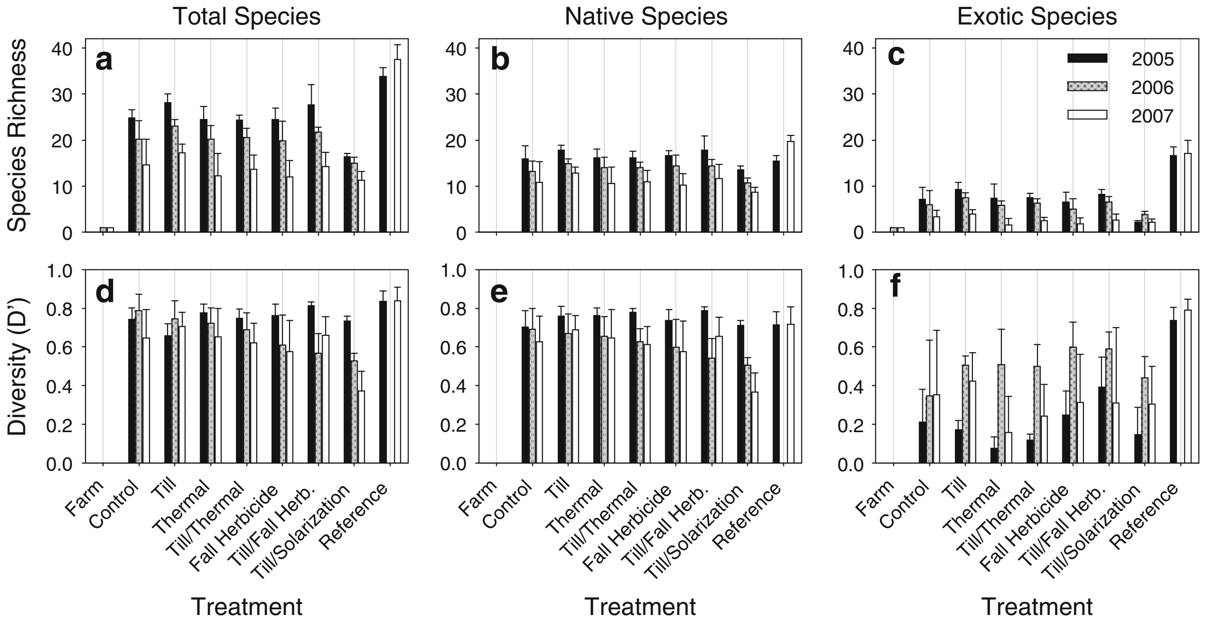

Fig. 2 Mean (**a**) overall species richness, (**b**) native species richness, (**c**) exotic species richness, (**d**) overall Simpson's diversity, (**e**) native Simpson's diversity, and (**f**) exotic Simpson's diversity per m^2 for the farm field, experimental treatments, and reference wetlands in 2005, 2006, and 2007. *Error bars* represent 95% confidence intervals. High values for Simpson's index of diversity indicate high diversity

We observed a negative association between cover of the two dominant native perennial grasses, *Agrostis exarata* and *Deschampsia cespitosa*, and diversity in 2006 ($r^2 = 0.78$, $p < 0.001$) and in 2007 ($r^2 = 0.65$, $p < 0.001$), but not in 2005 (Fig. 3). The slope of this relationship became more negative over the three years, suggesting an increasing inhibitory effect of the cover of these two native grasses on diversity over time. This trend was similar for native diversity (2005 $r^2 = 0.10$, $p < 0.024$; 2006 $r^2 = 0.65$, $p < 0.001$; 2007 $r^2 = 0.45$, $p < 0.001$), and not significant for exotic diversity.

Plant community composition in the restored plots, reference wetlands, and farm field differed significantly from each other (NMS ordination Fig. 4; MRPP: A = 0.52, $p < 0.0001$). The experimental plots were more similar to one another than to either the reference wetlands or farm field. However, the experimental treatments did become more similar to the reference wetlands over time (i.e., along axis 1, points progressed further right each year, Fig. 4) primarily due to a reduction in dominance of annuals, particularly *L. multiflorum* (Online Resource 1, Table S2). In addition, over time experimental treatments became increasingly dominated by the native perennial bunchgrasses, *A. exarata* and *D. cespitosa*. Finally, the variance in the experimental treatments was much smaller than the variance in the reference wetlands, reflecting the greater number and patchy distribution of species in the reference wetlands.

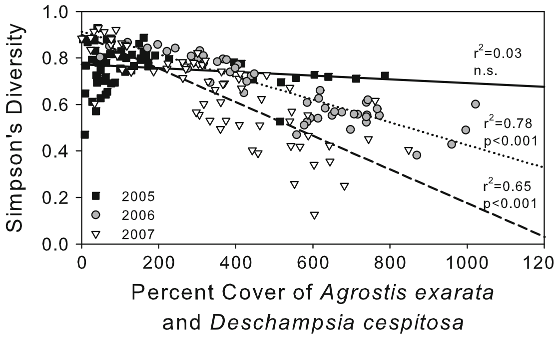

Fig. 3 Simpson's diversity as a function of percent cover of *Agrostis exarata* and *Deschampsia cespitosa* in the experimental treatments and reference wetlands. Regression lines are drawn for 2005 (*solid*), 2006 (*dotted*), and 2007 (*dashed*) and r^2 and p values are reported. Farm field is excluded from regression because those plots had a Simpson's diversity of zero. High values of Simpson's index of diversity indicate high levels of diversity

Significant differences in plant community composition also occurred among the experimental

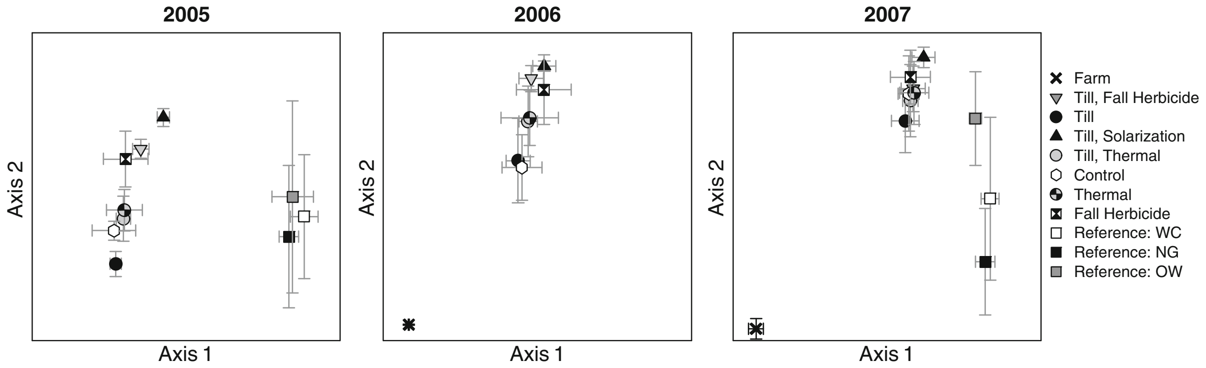

Fig. 4 Nonmetric multidimensional scaling (NMS) of plant community composition in the farm field, experimental treatments, and reference wetlands using relative Sorensen distance ($A = 0.52, p < 0.0001$). All 3 years of plant cover data were ordinated together, but are split for visual clarification (i.e., axes are equivalent for all three panels). Axis 1 explained 62% and axis 2 explained 21% of the variation in plant community composition. Although, the analysis was performed on plots, the plot mean and 95% confidence intervals for each treatment ($n = 5$) are shown for graphic representation. For plant species loadings on axis 1 and 2 see Table S2. Plant community composition was not measured in the farm field in 2005 and reference wetlands were not measured in 2006

treatments (Online Resource 1, Fig. S1; MRPP: A = 0.46, $p < 0.0001$). Treatments were initially most differentiated along axis 1, which primarily represented a gradient of annual graminoid/forbs on the left (the till, thermal, till/thermal, and control treatments) and perennial graminoids on the right (the till/solarization treatment, Online Resource 1 Table S3). Over time, the treatments converged while simultaneously changing in species composition. These changes were primarily driven by declines in a large number of annual species, and increases in perennial graminoids, particularly the seeded species *D. cespitosa*, *A. exarata*, and *Juncus tenuis*, and the exotic *Schedonorus arundinaceus* (Online Resource 1 Table S3). *L. multiflorum* also decreased dramatically in abundance over time in all experimental treatments.

Discussion

We observed large initial effects of site preparation techniques on plant communities, but treatment effects on diversity, species richness, plant cover, and composition dampened over time as plant communities became more similar. In particular, communities became increasingly dominated by seeded perennial native bunchgrasses and this was mirrored by decreasing species richness and diversity. After 3 years, plant communities in the experimental treatments remained significantly different from the three reference wetlands, although there was a trend toward convergence in species composition (Fig. 4), but not richness or diversity (Fig. 2). Below, we address our three original questions.

(Q1) Which site preparation techniques are most effective at eliminating the extant vegetation and seed bank, and thereby support initial establishment of a diverse native plant community?

To differentiate initial treatment effects from successional and competitive effects, we used only first year results to answer this question. Solarization and the fall herbicide application were the most effective treatments for initially decreasing exotic cover and reducing the seed bank. Solarization appears to have similar effects in California grasslands, where it decreased cover and seedling density of the dominant annual exotic grass, allowing native bunchgrass establishment (Moyes et al. 2005). However, the positive effect of solarization in reducing exotic cover (Fig. 1) was offset by its negative effect on native and overall species richness and diversity (Fig. 2). The plastic covering the solarization plots retained soil moisture and this favored early germination of native perennial grasses at high densities ($\sim$3 times greater than other treatments).

The fall herbicide application was also effective at decreasing exotic cover because it was applied after the seed bank (primarily *L. multiflorum*) had germinated, highlighting the importance of timing in herbicide use, as demonstrated by Kilbride and Paveglio (1999) and Adams and Galatowitsch (2006). Neither the tilling nor thermal treatments were effective at reducing exotic cover and enhancing native cover initially (Fig. 1). Tilling brings seeds to the surface, which could promote the establishment of exotic species, though repeated tilling over several years might exhaust the seed bank (Mohler 1993). Although, the thermal treatment was advertised as being able to significantly reduce the seed bank, it acted more like a surface fire and was only effective at killing small seedlings.

Even though solarization and an appropriately timed herbicide application are effective at eliminating extant vegetation, priority effects (i.e., order of colonization) must be considered when selecting a seed mix. In California grasslands, native forbs were unable to establish if bunchgrasses had previously been planted (Lulow 2004), and Collinge and Ray (2009) demonstrated the importance of priority effects for native species establishment in vernal pools. If the solarization or herbicide application were followed by seeding with lower densities of competitive perennial grasses (at least initially), these treatments have the potential to establish a diverse native community, as demonstrated by Marushia and Allen (2011).

(Q2) Do initial differences in native plant composition and diversity persist in the face of long-term successional processes?

Despite the substantial initial effects of the site preparation techniques, these differences were quickly overwhelmed as successional processes led to a convergence of community composition within the treatments (Figs. 4 & S1). The successional trajectory, we observed appeared to combine inhibitory priority effects (Drake 1991; Young et al. 2005) and subsequent competitive dominance of perennial bunchgrasses (Seabloom et al. 2003). In the solarization plots, where bunchgrasses established earlier than other species (priority effects), they became dominant in the first year. Over time, however, bunchgrasses became dominant in all treatments. Their high competitive ability appeared to be due to their dense swaths of tillers, tussocks, and thatch, which inhibited the germination and growth of other species, resulting in low cover of exotic species, fewer non-seeded species establishing, and low diversity across treatments. *L. multiflorum* has been shown to be competitively superior to native perennial grasses (Fehmi et al. 2004) particularly during establishment, including those species planted in this experiment (Pfeifer-Meister et al. 2008). However, our results here suggest that once established, native perennials outcompete this annual grass. Despite *L. multiflorum's* high initial cover in many of the treatments, it was not a dominant competitor over multiple growing seasons, and no other dominant exotic species significantly colonized the plots during the course of the experiment. In a California grassland, competitive interactions initially favored exotic annual grasses, but over time establishment of native perennial grasses reduced the productivity of exotic grasses (Corbin and D'Antonio 2004). Similarly, Seabloom et al. (2003) demonstrated that if native perennial grasses were not recruitment limited, they were able to decrease the biomass and seed production of annual exotic grasses.

This trade-off between competitive C_3 bunchgrasses and species diversity continued to be observed even after 5 years in these plots (unpublished data, Amanda Stanley). It also has been observed in both the calcareous grasslands (Fagan et al. 2008) and C_4 dominated tallgrass prairies (Baer et al. 2003; Heslinga and Grese 2010; McCain et al. 2010), and thus, appears to be a common phenomenon in grassland restoration projects. If our seed mix had included a lower density of the competitively dominant native bunchgrasses, the trajectories of our experimental plots may have been substantially different. Treatments that initially were more effective at eliminating *L. multiflorum* might have maintained a higher diversity of other seeded native plants, and in contrast, the ineffective treatments (e.g., tilling) would likely have remained dominated by *L. multiflorum* until another dominant competitor invaded. Indeed, the removal of perennial grass biomass has been shown to enhance species richness and diversity (McCain et al. 2010).

(Q3) How does plant composition and diversity of the restoration treatments compare with that found in high-quality reference wetlands over time?

Reference sites are useful for providing a baseline condition to evaluate the success of restorations. We did not expect full convergence over the 3 years of our study given the unique histories of each site and that we only seeded 15 native species in the restoration. Consequently, the reference sites contained many more native species (68 vs. 40). Despite these differences, the species composition of the experimental treatments became more similar to the reference wetlands each subsequent year due to a reduction in the cover of *L. multiflorum*, a loss of annual species, and increasing dominance of perennial grasses (Fig. 4).

Comparing diversity metrics, rather than species composition, of the experimental plots and reference wetlands is perhaps most instructive. The reference sites have both high native and exotic plant cover and diversity, and these patterns, together with their community composition, were relatively stable over 3 years (Figs. 1, 2, 4) and appear to have been over a much longer period (per. comm. Ed Alverson, The Nature Conservancy). In contrast, native richness and diversity were similar in the reference sites and experimental treatments in the first year, but subsequently declined in the experimental treatments due to increasing dominance by perennial bunchgrasses. While perennial bunchgrasses occur in large quantities in the reference wetlands (Table 1), they have not formed the dense monocultures found in our experimental plots. The reference wetlands experience occasional disturbances as part of their management (e.g., fire and mowing) and have greater microtopography (e.g., subtle swales and well developed grass hummocks), and this may help maintain their richness and diversity as shown by Bonis et al. 2005. Indeed, plant species have been shown to separate along micro-hydrological niches (Silvertown et al. 1999; Araya et al. 2010). In addition, the high diversity of established plant species in the reference sites may limit the opportunity for bunchgrasses to become as dominant as they did in the treatment plots, as suggested by inhibitory priority effects (Young et al. 2005). In support of this hypothesis, Heslinga and Grese (2010) found that tallgrass prairie plant communities with the highest and lowest cover of a dominant native grass diverged over a period of 15 years, with the former losing diversity and the latter maintaining it.

Conclusions

Certain site preparation techniques (solarization and a fall herbicide application) were effective at reducing the seed bank and extant vegetation. However, we found that using a seed mix with a prominent component of native bunchgrasses led in a few years not only to a site with high native and low exotic plant cover, but also to low diversity. The dominant competitive effects of the native bunchgrasses have continued for at least 5 years. Recent results from other grassland studies suggest that this trade-off is generalizable. The dense sowing of native bunchgrasses was typical of local restoration efforts at the time of this study, and often is done elsewhere, because of the heavy emphasis on high native and low exotic cover in mitigation wetlands (e.g., Oregon Department of State Lands 2011) and the desire to restore native bunchgrasses which frequently have been extirpated.

We suggest that effective initial site preparation must be followed with an appropriate seed mix and by careful management during the first years of rapid succession to sustain native plant diversity. Such management is not only simply an issue of controlling exotics, but also of restraining the increasing dominance of native bunchgrasses. This might be achieved in several ways. Seed mixes and planting schedules may be manipulated to increase initial diversity and reduce the dominant native competitors (e.g., perennial bunchgrasses). This reduction can be achieved by decreasing seeding density of dominants (Rowe 2010), and also by withholding them from initial seed mixes to allow other native species to establish first and then planting them 1–2 years later. Furthermore, reintroduction of micro-topographical features in highly altered sites such as agricultural fields could restore new niche spaces, and thus enhance diversity (Araya et al. 2010). Finally, selective disturbances can be used during the first years following the establishment to guide these systems closer to the diversity of reference communities (Hughes et al. 2007). Finding ways to mitigate the apparent tradeoff between high native cover and high diversity through a successional management framework that accounts for the interactions among site preparation, seeding protocols, and disturbances is a critical step toward establishing and sustaining diverse wetland communities. More generally, our results are consistent with an emerging understanding that restoration will be most successful when it is informed by both generalizable mechanisms, such as priority effects and competitive inhibition, and localized knowledge of species and environmental conditions.

Acknowledgements For assistance with site selection and use, experimental design, treatment implementation and plot maintenance, we thank the West Eugene Wetlands partnership. Key partnership staff included Eric Wold [City of Eugene (COE)], Paul Gordon (COE), Trevor Taylor (COE), Jean Jancaitis (COE), Jesse Cary Hobbs (COE), Dal Ollek (COE), Ed Alverson [The Nature Conservancy (TNC)], Greg Fitzpatrick (TNC), Jason Nuckols (TNC), and Sally Villeges (Bureau of Land Management). We also thank Lane Council of Governments, and numerous individuals who assisted with plant sampling. Funding was provided by a wetland development program grant from the U.S. Environmental Protection Agency (EPA), with matching funds provided by the COE, and an EPA STAR fellowship granted to L. P-M. Although this research was funded by the EPA, it has not been subjected to any EPA review and does not necessarily reflect the views of the Agency.

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