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Restoring wetland prairies: tradeoffs among native plant cover, community composition, and ecosystem functioning

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Abstract. Despite a U.S. goal of 'no-net-loss' of wetland structure and function, restoration performance standards are typically based on limited criteria, with soil carbon, nutrient, and microbial criteria being particularly rare. We examined plant community composition, diversity, and various soil functional variables for two different restoration techniques, topsoil-removal and solarization, in wetland prairies in Oregon, USA. We compared three site-level replicates of each treatment to three high-quality remnant wetland prairies. We found significant tradeoffs among diversity, native cover, and ecosystem functioning between restoration treatments. Wetlands with topsoil removed had similar diversity to remnants, but lower productivity, soil carbon and nitrogen, microbial biomass, and arbuscular mycorrhizal fungal infection rates. Solarization sites had the highest native cover, but diversity was approximately half that of remnant wetlands. We attribute this to both a priority effect of seeded native perennial bunchgrasses establishing early in the restoration process and competitively excluding other species, and to a lack of microtopographic variation in the restored sites. Our results suggest that restoration projects should evaluate both structural and functional processes, since they may reveal tradeoffs among important goals. Mitigation efforts should strive to understand the mechanisms causing these tradeoffs among structure and function and try to minimize these in restoration designs.

Key words: arbuscular mycorrhizal fungi; diversity; ecosystem function; mitigation; restoration; solarization; topsoil removal; wetland prairie.

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INTRODUCTION

Compensatory wetland mitigation is often required under Section 404 of the Clean Water Act (U.S. Army Corps of Engineers and U.S. Environmental Protection Agency 2008). That is, the destruction or degradation of wetlands should be mitigated by creating or restoring wetlands elsewhere. Furthermore, the United States' federal policy of 'no-net-loss' has a goal of not only maintaining or increasing wetland area, but also no loss of overall wetland function. Despite this goal, evaluations of wetland restoration success frequently take only a limited number of criteria into account (e.g., high native plant cover), and many functions are ignored

(Mitsch and Wilson 1996, National Research Council 2001, Zedler 2003, Matthews and Endress 2008). Additionally, restored or created wetlands may not have similar function or structure to those of 'natural' wetlands (National Research Council 2001, Turner et al. 2001, Aronson and Galatowitsch 2008, Rey Benayas et al. 2009). The net result of these concerns is while the conterminous U.S. experienced no change in wetland area from 2004–2009 (Dahl 2011), the nation may still be experiencing a net loss of wetland function. In this study, we examined above- and belowground responses of restored (1–7 years old) and high-quality remnant wetland prairies to understand the effects of mitigation practices on wetland function and community composition.

Over the last century, approximately 50% of wetlands have been lost in the conterminous United States (Dahl 2011), with the predominant mechanism being conversion to agriculture (Frayer et al. 1983). Similarly, wetland prairies of Oregon's Willamette Valley have been listed as a critically endangered ecosystem (Noss et al. 1995), with greater than 97% loss since c. 1850 of this once widespread ecosystem (Hulse et al. 2002). From 1980–1990, 70% of wetland losses in the Willamette Valley were attributed to agricultural activity (Bernet et al. 1999), predominately for commercial grass-seed production. Currently, grass-seed fields comprise much of the restorable wetland area within the Willamette Valley.

Our objective was to assess the effectiveness of two restoration techniques, topsoil-removal and solarization, for restoring native plant biodiversity and ecosystem function to agricultural fields that had retained wetland hydrology. These techniques were widely used in the southern Willamette Valley for wetland prairie restorations beginning in the 1990s.

Topsoil-removal has been employed as a means to eliminate existing vegetation and deplete the upper seed bank (which is typically dominated by exotic species), reduce nutrient levels in heavily fertilized fields, and bring deeply buried viable seeds of native species to the soil surface (Tallowin and Smith 2001, Holzel and Otte 2003, Pywell et al. 2007, Buisson et al. 2008). However, topsoil-removal may also have deleterious effects on ecosystem function because it can increase soil bulk density and decrease organic matter and available nutrients, leading to lower cover and productivity of desirable plant species (Woodward 1996, Patzelt et al. 2001, Tallowin and Smith 2001).

Solarization uses plastic for several months to trap heat from solar radiation in order to kill extant vegetation and the associated seed bank (Horowitz et al. 1983). This technique works best on moist soils, which more effectively conduct heat (Fitzpatrick 2004). Solarization does not involve as intensive or long-lasting a physical disturbance to the soil as does topsoil-removal, although the soil often is tilled prior to applying the plastic. Studies implementing solarization have shown increased establishment of seeded native forbs and grasses and a reduction in exotic species (Wilson et al. 2004, Moyes et al. 2005, Pfeifer-Meister et al. 2012). Other studies have also shown short-lived decreases in microbial community composition and biomass (Bendavid-Val et al. 1997, Wang et al. 2006).

In previous work on a Willamette Valley wetland prairie, we found that initial differences in plant community composition resulting from different restoration treatments quickly diminished with community composition converging across treatments over time (Pfeifer-Meister et al. 2012). In particular, we observed a tradeoff between native plant cover and diversity—areas with high native cover had low diversity and vice versa. This relationship appeared to be driven primarily by the dominant native bunchgrasses found in this ecosystem, which provided high native cover and competitively eliminated other native and exotic plant species. At the same time, impacts on belowground functions were relatively minor among the suite of site preparation techniques tested compared to reference wetlands (Pfeifer-Meister 2008). However, this former study only focused on a single site over 3 years, and we were interested in determining whether these phenomena were consistent across restored wetland prairies in this region. Moreover, the earlier study did not include topsoil-removal, which involves much greater soil disturbance and thus may lead to quite different plant community and soil dynamics.

In the current study we compared the plant communities and soil function of six restoration projects (three topsoil-removal and three solarization sites) to those of three nearby, high-quality

Table 1. Site history, soil type, and location for topsoil removal, solarization, and reference wetland prairies (n = 3).

	Treatment	Site†	Prior to restoration	Year restored	Owned and managed	Soil classification	Location
1	Topsoil removal	NG	*L. multiflorum* field	1998	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′43″ N 123°12′38″ W
2	Topsoil removal	TS	Unmanaged pasture	2001	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′54″ N 123°12′06″ W
3	Topsoil removal	NG	*L. multiflorum* field	2002	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′54″ N 123°12′38″ W
4	Solarization	NG	*L. multiflorum* field	1998	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′36″ N 123°12′44″ W
5	Solarization	NG	*L. multiflorum* field	2000	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′38″ N 123°12′44″ W
6	Solarization	CP	*L. multiflorum* field	2004	City of Eugene	Natroy silty clay loam	44°02′26″ N 123°14′43″ W
7	Reference	WC	NA	NA	The Nature Conservancy	Natroy silty clay loam	44°02′10″ N 123°10′18″ W
8	Reference	NG	NA	NA	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′38″ N 123°12′44″ W
9	Reference	OW	NA	NA	City of Eugene and BLM	Dayton silt loam, clay substratum	44°03′26″ N 123°11′29″ W

Note: NA = Not Applicable because reference sites were never cultivated.
† Site abbreviations are: NG, North Greenhill; TS, Turtle Swale; CP, Coyote Prairie; WC, Willow Creek; OW, Oxbow West.

remnant wetland prairies that served as reference sites. We hypothesized that (1) topsoil-removal would have deleterious effects on ecosystem function and soil properties (e.g., reduced soil carbon, nutrients, and microbial biomass), leading to lower productivity than reference wetland prairies, (2) solarization would result in high cover of native species with less impact on belowground processes, and (3) the restored sites, regardless of treatment, would have lower species richness and diversity than the reference wetlands due to seeded native bunchgrasses inhibiting subsequent establishment of other species (i.e., inhibitory priority effects).

Materials and Methods

Site selection and experimental design

We selected three replicate sites for each of the restoration treatments, topsoil-removal or solarization, and compared these to three of the highest quality wetland prairies available (subsequently referred to as reference wetlands, Table 1). These latter sites were never drained, plowed or otherwise converted to agriculture, and have retained comparatively high levels of historically associated native plant species. They have, however, received varying levels of biodiversity management including prescribed burning, and removal of invasive trees and shrubs. All restored sites are part of the West Eugene Wetlands mitigation bank, Oregon, USA. We were constrained by site availability, which meant that the restorations were implemented at different times (between 1–7 yr prior to sampling). For the topsoil-removal treatment, the sites were restored in 1998, 2001, and 2002, and for the solarization treatment, sites were restored in 1998, 2000, and 2004. The 2004 solarization site, Coyote Prairie, was part of an experiment we used in a previous study (Pfeifer-Meister et al. 2012). Despite its recent implementation, it was included because there were only two other nearby solarization sites available for sampling.

Prior to restoration, all sites were either in commercial grass-seed production with *Lolium multiflorum* Lam. or abandoned pastures. The topsoil-removal treatment was applied using a large excavator, and approximately 10 cm of topsoil was removed from each site. For the solarization treatment, the sites were tilled and then covered with sheets of clear plastic (15 m width, 30 m long) for a minimum of three months, with the edges of the plastic buried in trenches to minimize water evaporation. After site preparation, the six restorations were seeded with a similar mix of native graminoids and forbs (Table 2). All sites, including the three reference sites, received varying degrees of selective weeding, mowing, and burning that are typical

Table 2. Seed mixes for the six restored sites with associated life history (A = annual; P = perennial), functional group (G = graminoid, F = forb), wetland indicator status for the Pacific Northwest (Region 9, OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland, NOL = not on list), and densities planted. Seed densities reported are from the West Eugene Wetland Mitigation Bank Annual Reports 1999–2004, City of Eugene, Eugene, OR, USA.

Species	Life history	Funct. group	Wetland indicator	Seed mix (mg seed/m^2)					
				Topsoil removal			Solarization		
				1998	2001	2002	1998	2000	2004
Agrostis exarata Trin.	P	G	FACW	24.7	28.4	56.8	24.7	19.9	35.0
Allium amplectens Hook.	P	F	NOL	0.2		0.7	0.2	3.7	
Asclepias speciosa Torr.	P	F	FAC+	0.5			0.5		
Brodiaea coronaria (Salisb.) Engl.	P	F	NOL	0.2		0.2	0.2		
Camassia leichtlinii (Baker) S. Watson	P	F	FACW−	2.7		4.9	2.7	11.3	
Camassia quamash (Pursh) Greene	P	F	FACW	10.6	14.8	14.8	10.6	26.9	45.0
Carex densa (L.H. Bailey) L.H. Bailey	P	G	OBL	3.5	19.8	14.8	3.5	19.4	60.0
Carex feta L.H. Bailey	P	G	FACW		9.9			8.7	
Carex ovalis Goodenough	P	G	FACW	14.3			14.3		
Carex unilateralis Mack.	P	G	FACW	14.8	24.7	24.7	14.8	25.6	
Castilleja tenuis (A. Heller) T.I. Chuang & Heckard	A	F	FACU−	0.7	2.5	1.8	0.7	2.3	
Collomia grandiflora Douglas ex Lindl.	A	F	NOL					0.3	
Danthonia californica Bol.	P	G	FACU*	11.1	12.4	28.4	11.1	24.1	70.0
Deschampsia cespitosa (L.) P. Beauv.	P	G	FACW	49.4	49.4	61.8	49.4	13.2	50.0
Deschampsia danthonioides (Trin.) Munro	A	G	FACW−		0.8	1.7		6.6	
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark	P	G	FACW	5.9	7.4	1.2	5.9	10.3	
Dichelostemma congestum (Sm.) Kunth	P	F	NOL					1.1	
Downingia elegans (Douglas ex Lindl.) Torr.	A	F	OBL	13.8	37.1		13.8		
Downingia yina Applegate	A	F	OBL	24.5		12.4	24.5		
Epilobium brachycarpum C. Presl	A	F	UPL	2.5			2.5		
Epilobium ciliatum Raf.	P	F	FACW−					2.4	
Epilobium densiflorum (Lindl.) Hoch & P.H. Raven	A	F	FACW−	29.7	24.7	24.7	29.7	10.2	90.0
Eriophyllum lanatum (Pursh) Forbes	A/P	F	NOL	1.2	12.4	12.4	1.2	10.2	
Galium trifidum L.	A	F	FACW+	0.7	0.2		0.7		
Grindelia integrifolia DC.	P	F	FACW	10.4	4.1	12.4	10.4	13.6	70.0
Hordeum brachyantherum Nevski	P	G	FACW−		44.7	74.1		37.1	
Juncus acuminatus Michx.	P	G	OBL	12.6	17.3		12.6		
Juncus bolanderi Engelm.	P	G	OBL	2.2			2.2		
Juncus ensifolius Wikstr.	P	G	FACW	9.1	6.9	0.5	9.1		
Juncus nevadensis S. Watson	P	G	FACW		11.1			0.1	
Juncus tenuis Willd.	P	G	FACW−	6.4		9.9	6.4	24.9	15.0
Lomatium nudicaule (Pursh) J.M. Coult. & Rose	P	F	NOL		8.6			15.9	
Lotus formosissimus Greene	P	F	FACW+	1.7	0.5	1.2	1.7	0.9	
Lotus unifoliolatus (Hook.) Benth.	A	F	NOL	3.5	3.7	3.7	3.5	7.1	
Lupinus polyphyllus Lindl.	P	F	FAC+			7.4		12.7	
Lupinus rivularis Douglas ex Lindl.	P	F	FACU			12.4			
Luzula campestris (L.) DC.	P	G	NOL	1.2		0.5	1.2	0.7	
Madia glomerata Hook.	A	F	FACU+	?		4.9	?	1.7	60.0
Madia sativa Molina	A	F	NOL	7.4	3.7	7.4	7.4	1.9	
Microseris laciniata (Hook.) Sch. Bip.	P	F	NOL	18.0	24.7	24.7	18.0	50.6	70.0
Microsteris gracilis (Hook.) Greene	A	F	FACU		2.0			2.4	
Montia linearis (Douglas ex Hook.) Greene	A	F	NOL		4.7			2.0	
Orthocarpus bracteosus Benth.	A	F	NOL	2.5	2.5	1.2	2.5	1.0	
Perideridia gairdneri (Hook. & Arn.) Mathias	P	F	FAC*		0.8	0.6		1.8	
Perideridia oregana (S. Watson) Mathias	P	F	NOL	2.0		1.2	2.0	1.7	
Plagiobothrys figuratus (Piper) I.M. Johnst. ex M. Peck	A	F	FACW	7.7	14.8	15.2	7.7	9.4	70.0
Potentilla gracilis Douglas ex Hook.	P	F	FAC	21.0	17.3	16.7	21.0	11.0	25.0
Prunella vulgaris L.	P	F	FACU+	12.4	12.4	12.4	12.4	17.3	35.0
Pyrrocoma racemosa (Nutt.) Torr. & A. Gray var. racemosa	P	F	FAC+		3.3				
Ranunculus occidentalis Nutt.	P	F	FAC		24.7	19.8		10.5	
Ranunculus orthorhynchus Hook.	P	F	FACW−	24.7	24.7	24.7	24.7	10.3	
Rumex salicifolius Weinm.	P	F	FACW		7.4	7.4			
Saxifraga oregana Howell	P	F	FACW+	3.7	1.6	0.2	3.7	3.1	
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	P	G	OBL		plug				
Sidalcea cusickii Piper	P	F	NOL	4.4			4.4	2.3	
Sidalcea malviflora (DC.) A. Gray ex Benth. ssp. virgata	P	F	NI					0.2	
Sisyrinchium californicum (Ker Gawl.) Aiton	P	F	FACW+					1.2	
Sisyrinchium idahoense E.P. Bicknell	P	F	FACW	1.2	2.4	0.7	1.2	5.2	
Symphyotrichum hallii (A. Gray) G.L. Nesom	P	F	FAC	2.7		24.7	2.7	0.5	70.0

Table 2. Continued.

Species	Life history	Funct. group	Wetland indicator	Seed mix (mg seed/m^2)					
				Topsoil removal			Solarization		
				1998	2001	2002	1998	2000	2004
Triteleia hyacinthina (Lindl.) Greene	P	F	FACU	0.5		0.2	0.5	3.6	
Veronica scutellata L.	P	F	OBL	39.5	30.9		39.5		
Wyethia angustifolia (DC.) Nutt.	P	F	FACU	29.7	24.7	24.7	29.7	22.6	70.0
Zigadenus venenosus S. Watson	P	F	FACU*	0.5	0.7	0.2	0.5	2.5	
Total weight of seed mix				436.1	544.7	570.8	436.1	471.9	835.0

for the management of wetland prairies in this region. The restored sites were never drained, and all sites have hydric soils (either Natroy [Very-fine, smectitic, mesic Xeric Endoaquerts] or Dayton Series [Fine, smectitic, mesic Vertic Albaqualfs]) and similar hydrology. Elevation of sites varied between 117 and 120 m.

The climate is Mediterranean with warm, dry summers and mild, wet winters. Mean annual precipitation and temperature are 125 cm and 12°C, respectively (National Climatic Data Center 2005). Because precipitation primarily falls from October to May, these wetland prairies dry out through the summer months, and the water table is more than one meter below the soil surface from July–September (Marshall 2011). During winter months, the water table is often perched on these shrink-swell clays, with approximately 5–10 cm of standing water. The primary growing season begins in March, although some species germinate with the fall rains, with almost complete plant senescence by mid-July.

At each of the nine sites, fifteen 1 m^2 subplots were randomly located within a 900 m^2 portion of the site to measure plant cover, species richness, diversity, and aboveground productivity. Five of the subplots at each site were also randomly selected to measure soil variables described below.

Plant sampling

In July 2005, we determined percent cover of plant species in each 1 m^2 subplot with the point-intercept method (Elzinga et al. 1998). We used 1 m^2 frames with 25 equally spaced pins that were dropped vertically from the plant canopy to the soil surface. Each plant touch was recorded by species. Because multiple hits were possible for each pin, greater than 100% cover often occurred. Any species in the plot not hit by a pin was recorded as present to enable calculations of species richness and diversity. Species nomenclature followed the Flora of North America (Flora of North America Editorial Committee 1993+).

We estimated aboveground net primary productivity in July 2005 at peak standing biomass by clipping three 100 cm^2 quadrats within each 1 m^2 subplot and sorting the biomass into graminoids, forbs, woody (small shrubs and tree seedlings), and litter material. The plant material was dried at 60°C for 48 hours and weighed. The three 100 cm^2 quadrats were averaged for each subplot.

Soil sampling

On 23 April 2005, we measured in situ ecosystem CO_2 respiration, CH_4 production, and N_2O production in five 1 m^2 subplots per site. In each plot, we placed PVC chambers (10.2 cm diameter, 35 cm tall) 5 cm in the ground to create good soil contact and sealed the tops with rubber caps fitted with stainless steel compression bands. We collected 20 cm^3 gas samples from the headspace every 30 minutes for two hours after capping, and associated soil temperature at a 5 cm depth. Gas samples were stored in pre-vacuumed serum bottles sealed with rubber septa. Gas samples were analyzed on a SRI model 8610C gas chromatograph (Torrance, CA, USA) for N_2O using an ECD detector and for CO_2 and CH_4 using a FID detector with a methanizer.

After gas collection, we removed the chambers and collected soil cores from within the footprint of each chamber (5.7 cm diameter, 8.5 cm depth). Soil cores were brought back to the laboratory and stored in a dark incubator at the average soil

temperature for all sites (13.8°C). The following day, roots were removed from soil cores by hand. Soil bulk density was determined by weighing the entire core and correcting for soil moisture (determined by drying a sub-sample at 60°C for 48 hours). We measured pH using a 1:1 soil-deionized water slurry. Two days after soil collection, we extracted sub-samples of soil from each plot for PO_4^{3-} using 0.5 M $NaHCO_3$ (Kuo 1996) and NH_4^+ and $NO_2^- + NO_3^-$ using 2 M KCl (Maynard and Kalra 1993). The soil extracts were filtered through acid-washed filter paper and frozen until analysis. We used an Astoria II autoanalyzer (Astoria Pacific International, Clackamas, OR, USA) to measure available PO_4^{3-} using the ascorbic acid method (Murphy and Riley 1962), $NO_2^- + NO_3^-$ using the cadmium reduction method (Wood et al. 1967), and NH_4^+ using the phenate method (Solorzano 1969).

Microbial biomass carbon (C), nitrogen (N), and phosphorus (P) were determined for each soil core using the chloroform-fumigation extraction method (Voroney and Winter 1993, Horwath and Paul 1994). Two days after collection, a soil subsample from each plot was extracted with 0.5 M K_2SO_4 to determine initial total C and N. We used the $NaHCO_3$ extracts to determine initial P. Soil subsamples were then placed in 50-mL centrifuge tubes, fumigated with chloroform to lyse microbial cells, capped, and stored in an incubator at 13.8°C. After three days, soils from the centrifuge tubes were extracted again. All extracts were frozen until analysis. We used the persulfate digestion method (Wetzel and Likens 2000) and measured the CO_2 produced on a LiCor 7000 infrared gas analyzer (Lincoln, NE, USA) to determine total C. Total N was determined by digesting the K_2SO_4 extracts using the potassium persulfate method (Ameel et al. 1993) and measuring $NO_2^- + NO_3^-$ on the autoanalyzer as previously described. We measured PO_4^{3-} in the $NaHCO_3$ extracts using the ascorbic acid method (Murphy and Riley 1962). Microbial biomass was calculated as the difference between the final and initial extracts for C, N, and P, with no extraction efficiency correction factor.

We measured total soil C and N on two subsamples of dried (60°C for 48 hr), ground soil from each plot using a Costech Analytical Technologies 4010 elemental combustion analyzer (Valencia, CA, USA). To determine soil texture, we sieved dry soils to less than 2-mm diameter. Percent clay was calculated using the hydrometer method (Gee and Bauder 1986), percent sand was determined by weighing the material retained on a 53-μm sieve, and percent silt was calculated as the difference.

To determine arbuscular mycorrhizal fungal (AMF) colonization of grass roots, we used the fungal-specific stain, trypan blue, and measured percent colonization using the point-intercept method (Giovannetti and Mosse 1980). On 16 May 2005, we collected the plants and associated roots of the three dominant native (*Agrostis exarata* Trin., *Danthonia californica* Bol., and *Deschampsia cespitosa* (L.) P. Beauv.) and three dominant exotic grasses (*Anthoxanthum odoratum* L., *Holcus lanatus* L., and *Schedonorus arundinaceus* (Schreber) Dumort.). At each site, ten replicates of each grass species were randomly collected when possible, but not all grasses occurred at all sites. *Deschampsia cespitosa* and *H. lanatus* did occur at all sites, and overall sample sizes for native ($n = 195$) and exotic ($n = 158$) grasses were similar. Roots were collected to a depth of approximately 15 cm, washed free of soil, and fixed in 50% ethanol until staining. Prior to staining, the roots were cleared in 10% KOH overnight and bleached in alkaline H_2O_2 for 30 minutes. To improve adherence of the stain, the roots were then acidified in 1% HCl. The roots were stained overnight in acidic glycerol containing 0.05% trypan blue and then de-stained in acidic glycerol (Koske and Gemma 1989, Bauer et al. 2003). After staining, the roots were cut into 1-cm segments, dispersed evenly over a square grid, and examined under a dissecting microscope (10–100×). The presence or absence of infection (including arbuscules, vesicles, and/or hyphae) was determined at 100 grid intersections for each root system.

Statistical analyses

We used nested one-way ANOVAs to determine the effect of restoration treatment on plant and soil response variables, with the exception of AMF colonization. The 1 m^2 subplots were nested within sites, so that sites were the replicate unit ($n = 3$). In the ANOVA model, sites were treated as a random effect and treatment was a fixed effect. We used Tukey's

pairwise comparisons to explore significant treatment effects. To correct for violations of normality, square root transformations were used for exotic cover, exotic richness, total NPP, grass NPP, forb NPP, litter biomass, belowground biomass, NH_4^+ availability, PO_4^{3-} availability, NO_3^- availability, and ecosystem respiration. A natural log transformation was used for native cover, and Simpson's diversity was squared. For AMF colonization, mean percent colonization was calculated by site for the two functional groups, native grasses (3 species) and exotic grasses (3 species), and one-way ANOVAs were conducted with treatment as the fixed main effect. Linear least squares regression was used to examine the relationships of native cover and *Deschampsia cespitosa* cover to Simpson's index of diversity. ANOVAs and regressions were run using SPSS vs. 16.0 (SPSS Inc. 2007).

To explore differences in plant community composition among treatments, we used non-metric multidimensional scaling (NMS), which, unlike other ordination techniques, has no assumption of linear relationships among variables (McCune and Grace 2002). We used a Monte Carlo test (1000 randomized runs) to test for statistical significance of the ordination. We also used the non-parametric technique multi-response permutation procedure (MRPP) to test for community differences among restoration treatments and to obtain an estimate of the effect size, A (McCune and Grace 2002). For both the NMS and MRPP analyses, we used relative Sorensen distance. Only significant indicator species are reported with the associated NMS axes loadings (significance determined using a Monte Carlo test on 1000 randomized runs).

In addition to understanding how plant community composition differed among treatments, we were also interested in how composition was related to ecosystem functioning. For this, we used the direct gradient ordination technique canonical correspondence analysis (CCA). Unlike NMS, CCA only accounts for the variation in community composition that is related to the environmental matrix (McCune and Grace 2002) and has the same assumptions as multiple regression. To avoid multicollinearity, highly autocorrelated soil variables ($r > 0.6$) were not included in the environmental matrix; autocorrelated variables included percent clay and percent sand ($r = 0.7$), total soil C and total soil N ($r = 0.9$), and microbial biomass C, N, and P ($r > 0.6$). The resulting matrix included eleven variables: bulk density, pH, percent moisture, NH_4^+, NO_3^-, and PO_4^{3-} availability, ecosystem respiration, microbial biomass P, total soil C, percent clay, and total percent AMF colonization. For the plant matrix, species that only occurred in a single plot were eliminated, resulting in a total of 53 species used. To test for a significant relationship between the plant and environmental matrices, we used a Monte Carlo test with 1000 randomized runs. We report linear combinations of the environmental variables (LC scores) for axis loadings. NMS, MRPP, and CCA were all run using PC-ORD vs. 4.34 (MjM Software Design, Gleneden Beach, Oregon, USA).

Results

Plant community response

The restored and reference wetlands differed from one another for all plant responses measured (Figs. 1–3). Whether examining species richness at the plot level (per m^2) or at the site level (totaled across the 15 one m^2 plots), fewer species were found in the restored wetlands than in the reference sites ($p < 0.01$). Site richness ranged from an average of 57 in the reference wetlands to 30 in the solarization sites, with the topsoil-removal sites being intermediate at 47 species ($p < 0.001$). The solarization sites also had fewer native species (mean = 16 per site) than topsoil-removal and reference wetlands (mean = 29 per site, $p < 0.001$). At the plot level, the trend was similar for total richness and diversity (Fig. 1B, C), though native richness was no longer different among the treatments. Reference sites had double the exotic species richness of the restored sites and marginally higher exotic Simpson's diversity than the solarization treatment ($p < 0.10$).

Total plant cover in the topsoil-removal treatment was approximately half that of the reference and solarization sites (marginally significant at $p < 0.087$), and native plant cover was more than two times higher in the solarization sites than in the topsoil-removal and reference sites (marginally significant at $p < 0.074$, Fig. 1A). Exotic cover was fourfold higher in the reference sites than the restored sites ($p < 0.01$).

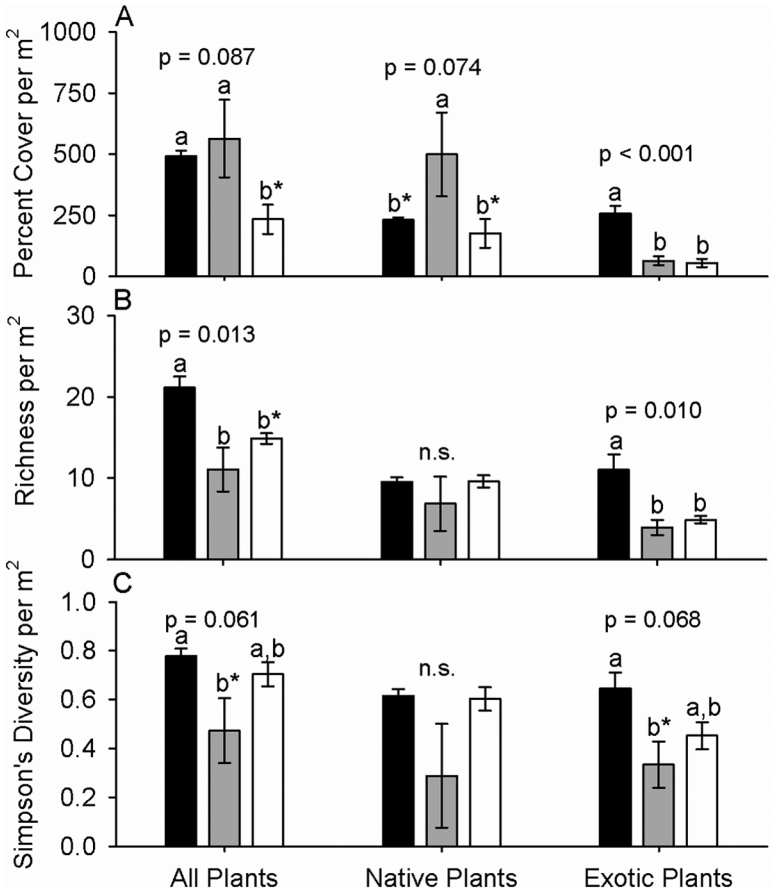

Fig. 1. Mean percent cover (A), species richness (B), and Simpson's diversity (C) for reference (black), solarization (gray), and topsoil-removal (white) wetlands by plant origin (e.g., all, native, or exotic). Error bars represent one standard error and lower case letter differences indicate significant ($p < 0.05$, $^*p < 0.10$) effects of treatment within a plant group.

Aboveground net primary productivity (ANPP) was lower in the topsoil-removal treatment than the reference sites (Fig. 2). Additionally, ANPP varied significantly among functional groups. The reference and solarization sites had more than twice the graminoid biomass of the topsoil-removal sites ($p < 0.001$), and the solarization treatment had substantially less forb biomass than the reference and topsoil-removal treatments ($p < 0.001$). Small seedlings of woody species were found only at the reference sites. Finally, the solarization treatment had more than twice the litter biomass (mean = 348 g/m^2) than the reference (mean = 166 g/m^2) and topsoil-removal (mean = 145 g/m^2) sites ($p < 0.005$).

When all treatment types are considered together, there was a significant tradeoff between native cover and Simpson's diversity, i.e., plots with high native plant cover tended to have lower overall diversity ($r^2 = 0.39$, $p < 0.001$, Fig. 4A). This negative trend also was observed within each treatment, although the slope for the reference wetlands was not as steep (data not shown). This tradeoff appeared to be primarily driven by the dominant native perennial bunchgrass, *Deschampsia cespitosa* (Fig. 4B). In general, the solarization sites had higher cover of *D. cespitosa* and lower overall diversity, and the reference sites had the highest diversity and lowest *D. cespitosa* cover. When regressing *D. cespitosa* percent cover with Simpson's diversity, we were able to explain 20% more of the variation ($r^2 = 0.59$, $p < 0.001$) than when using all native cover.

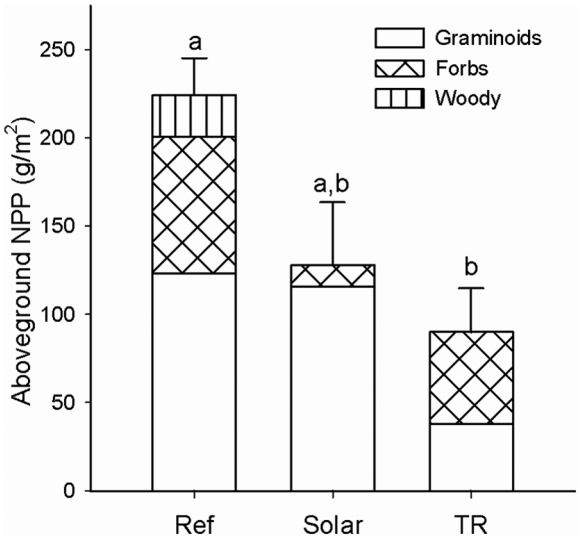

Fig. 2. Mean aboveground net primary productivity (NPP) in the reference (Ref), solarization (Solar), and topsoil-removal (TR) wetlands. NPP is further partitioned into graminoids, forbs, and woody biomass. Error bars represent one standard error of total aboveground NPP, and lower case letter differences indicate significant effects ($p < 0.05$) among treatments.

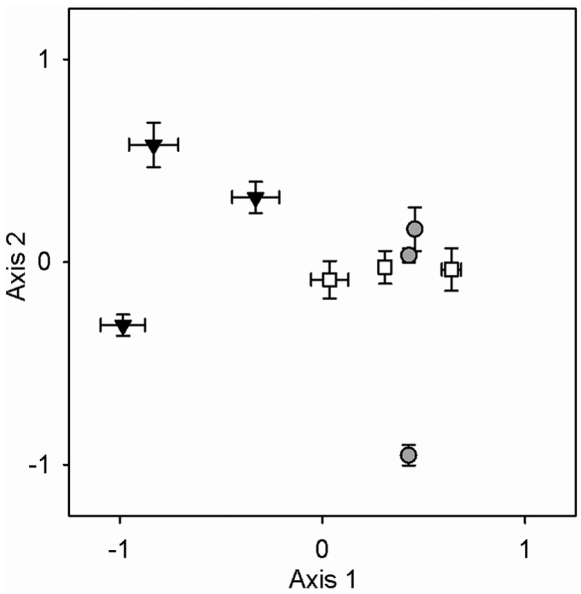

Fig. 3. Nonmetric multidimensional scaling of plant community composition in reference (black triangles), solarization (gray circles), and topsoil-removal (white squares) wetlands. Axis 1 explained 40% and axis 2 explained 25% of the variation in plant community composition (A = 0.16, $p < 0.0001$). Although the analysis was performed on plots, the plot mean and bidirectional standard error for each site are shown for graphic representation. For species axes loadings, see Appendix A.

The restored sites also had substantially different plant community composition than the reference sites (A = 0.16, $p < 0.001$, Fig. 3). The nonmetric multidimensional scaling (NMS) ordination extracted two axes from the plant data set that explained 65% of the variation in plant community composition. Axis 1 explained 40% of this variation and primarily represented a life history gradient (Appendix A). Plots loading negatively on this axis (e.g., reference wetland plots) had a greater abundance of perennial species, and plots loading positively on this axis (e.g., solarization and topsoil-removal plots) had a greater abundance of annual species. Furthermore, many negatively loading species on axis 1 were only found in the reference wetlands. Axis 2 explained 25% of the variation and did not separate treatments clearly, but instead, the youngest restored site (2004 solarization, lower-right corner) was significantly different from all other sites. This site was dominated by native annual forb species, with the exception of the exotic annual grasses, *Lolium multiflorum* and *Poa annua*.

Belowground responses

Overall, both restoration treatments differed significantly from the reference wetlands in belowground processes; however, the topsoil-removal treatment generally had the most dramatic effects on soil properties compared to the reference wetlands (Figs. 5-7). In all treatments, the headspace concentrations of the greenhouse gases nitrous oxide and methane remained at atmospheric concentrations over the course of the two-hour field measurements (i.e., flux equaled zero), despite the water table being within 15 cm of the soil surface and typically much closer.

Ecosystem respiration was significantly higher in the solarization sites than the topsoil-removal and reference wetlands (Fig. 5A). Phosphate availability was also highest in the solarization sites, and lowest in the reference wetlands (Fig. 5B). The topsoil-removal treatment had approx-

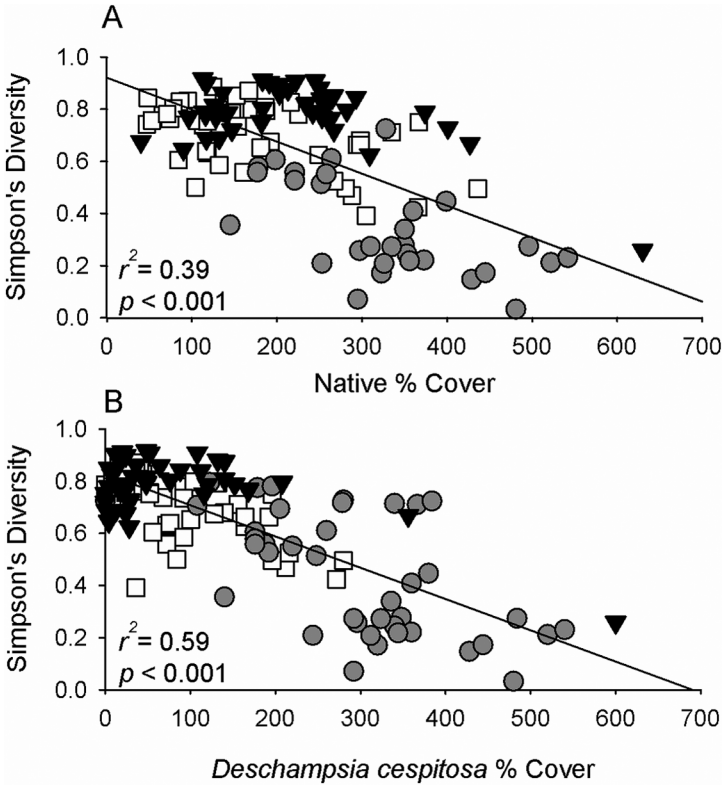

Fig. 4. Simpson's diversity vs. (A) percent native cover and vs. (B) percent *Deschampsia cespitosa* cover in all treatment plots (black: reference, gray: solarization, white: topsoil-removal).

imately half the total carbon and total nitrogen of the solarization and reference wetlands (Fig. 5C, D). Microbial biomass carbon, nitrogen, and phosphorus were lowest in the topsoil-removal sites, and highest in the reference wetlands (Fig. 5E–G). The solarization treatment had a slightly lower pH than the topsoil-removal and reference wetlands (Fig. 5H). In addition, bulk density was marginally higher in the topsoil-removal sites (mean = 1.46 g/cm^3) than in the reference wetlands (mean = 1.21 g/cm^3, $p = 0.09$), and soil moisture was marginally higher in the reference sites (mean = 32%) than in topsoil-removal sites (mean = 24%, $p = 0.09$). Soil texture and nitrogen availability did not differ among the treatments ($p > 0.16$).

Native and exotic grasses had approximately the same amount of colonization by arbuscular mycorrhizal fungi (AMF) (mean = 40%). AMF colonization differed among treatments but only for the native grasses (Fig. 6), where the topsoil-removal treatment had approximately 15% less colonization than the reference and solarization wetlands.

Environmental controls of plant community composition

Canonical correspondence analysis (CCA) revealed a significant relationship between plant community composition and edaphic factors ($p < 0.01$, Fig. 7). Axis 1 explained 12% of the variation in plant community composition, and axis 2 explained 7%, and species-environment correlations were 0.94 and 0.87 for axes 1 and 2, respectively. As in the NMS, axis 1 was primarily a perennial-annual gradient with the most negative loadings dominated by perennial species and the highest positive loadings dominated by annual species, particularly native annuals (see Appendix B). Soil variables loading most heavily on axis 1 included (in order of absolute magnitude of loading): phosphate availability, pH, microbial biomass, and to a lesser extent, percent clay. Axis 2 did not have a clear gradient

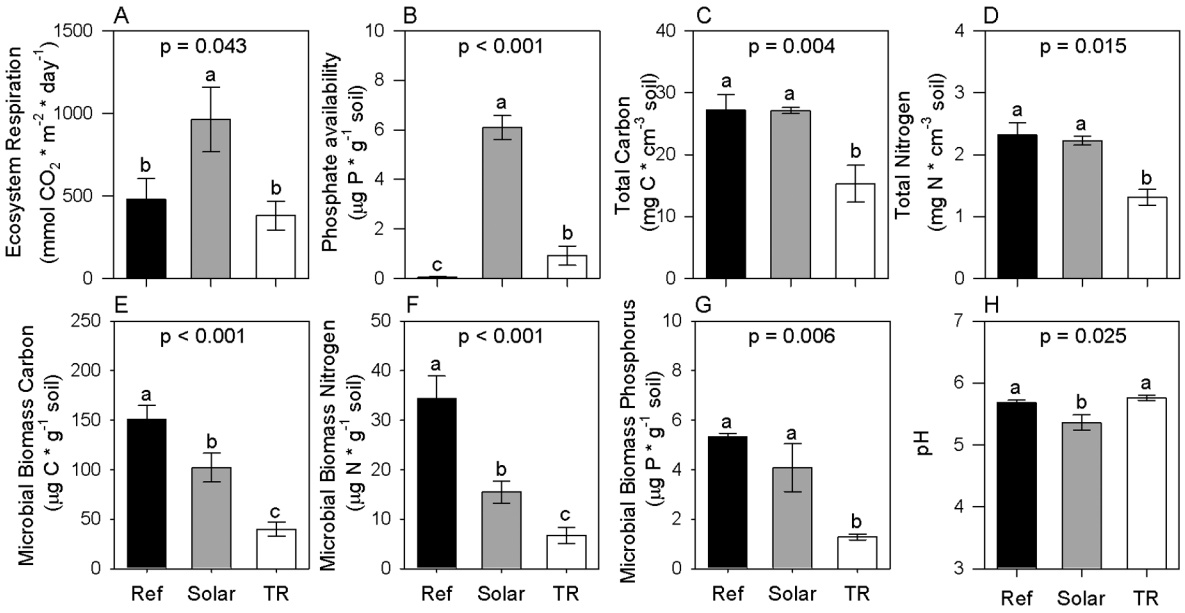

Fig. 5. Mean ecosystem respiration (A), phosphate availability (B), total soil carbon (C), total soil nitrogen (D), microbial biomass carbon (E), microbial biomass nitrogen (F), microbial biomass phosphorus (G), and pH (H) in the reference (Ref), solarization (Solar), and topsoil-removal (TR) wetlands. Error bars represent one standard error, and lower case letter differences indicate significant ($p < 0.05$) effects among treatments.

of plant functional groups. Soil variables loading most heavily on axis 2 included (in order): total carbon, bulk density, percent clay, percent moisture, and percent AMF colonization. Reference wetland plots tended to group in the lower left quadrant of community space, and restored plots tended to group in the upper middle of community space, with the exception of the young solarization plots (Coyote Prairie) which fell out in the lower right quadrant. Reference plots were distinguished by a high abundance of perennial species (as in the NMS) and were associated with higher microbial biomass and pH (i.e., more alkaline). Reference plots also tended to have higher total carbon, moisture availability, and AMF colonization than the restored plots, with the exception of Coyote Prairie which also loaded negatively on axis 2. The topsoil-removal plots loaded slightly more negatively on axis 1 than the solarization plots and were associated with higher bulk density and percent clay and lower total carbon, % moisture, and AMF colonization. The young solarization site was associated with the highest phosphate availability.

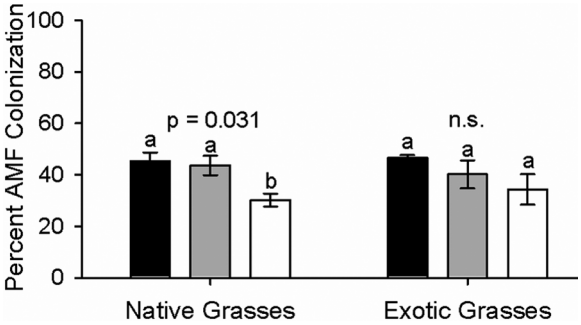

Fig. 6. Mean percent arbuscular mycorrhizal fungal (AMF) colonization in native and exotic grasses in the restored and reference wetlands. Error bars represent one standard error and lower case letter differences indicate significant ($p < 0.05$) treatment effects within a grass type.

Discussion

Despite the large variation in site history and subsequent management within each treatment type, we observed substantial differences in plant and soil properties among treatments. The restored sites differed from the reference wetlands both in plant community composition and

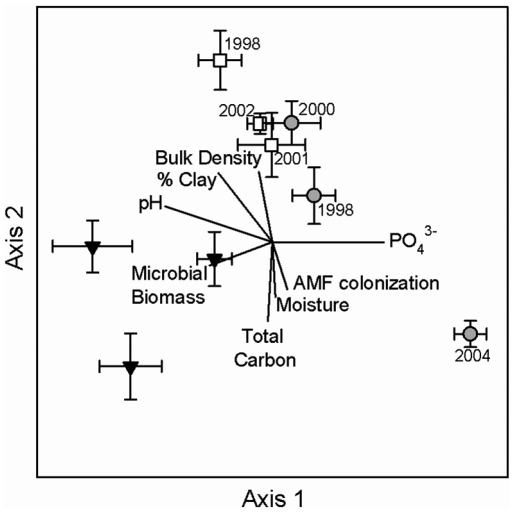

Fig. 7. Canonical correspondence analysis of fifty-three plant species using eleven environmental variables (pH, bulk density, percent moisture, ammonium, phosphate, nitrate, respiration, arbuscular mycorrhizal fungal (AMF) % colonization, microbial biomass P, total soil C, and % clay). Axis one and axis two explained 12% and 7% of the variation in plant community composition, respectively. Only vectors with a $r^2 > 0.25$ are shown. Although the analysis was performed on plots, the mean and bi-directional standard errors for each site are shown for graphic representation (black triangles: reference, gray circles: solarization, white squares: topsoil-removal). Year restored is included for the solarization and topsoil-removal sites. For species axes loadings, see Appendix B.

ecosystem function; however, the two site preparation treatments, topsoil-removal and solarization, varied in different ways. In the following paragraphs, we address each of our original hypotheses, highlight important mechanisms controlling plant community composition, and conclude with implications for restoration.

Our first hypothesis, that the removal of topsoil would have deleterious effects on ecosystem function and soil properties and thus be less productive than reference wetlands, was strongly supported. The microbial community was significantly reduced in the topsoil-removal sites, with lower microbial biomass and lower arbuscular mycorrhizal fungal (AMF) colonization of native grasses (Figs. 5 and 6). These sites had half the total soil carbon and nitrogen of reference wetlands (Fig. 5). Similarly, organic matter was drastically reduced following topsoil-removal in European wet meadows (Holzel and Otte 2003) and grasslands (Pywell et al. 2007). The topsoil-removal sites also had higher bulk density and lower gravimetric soil moisture than reference wetlands. Woodward (1996) attributed lower soil moisture following topsoil-removal to a decrease in soil porosity from compaction. In our previous research in wetland prairies, we found only minimal effects of site preparation on belowground responses, but none of the techniques tested (e.g., herbicide application) involved such intensive physical disturbance to the soil structure (Pfeifer-Meister 2008).

Likely as a consequence of these dramatic differences in edaphic conditions, the topsoil-removal sites had half the aboveground productivity (Fig. 2) and cover (Fig. 1) of the reference wetlands. Other studies in different kinds of wetlands have found similar results. In a United Kingdom wetland prairie, productivity was significantly reduced after topsoil-removal (Tallowin and Smith 2001), and in Germany, Patzelt et al. (2001) found plant cover continually decreased with greater depths of topsoil-removal in fens. Unlike cover, total and native species diversity was not lower in topsoil-removal sites, but instead was similar to reference wetlands on a 1 m^2 scale. Similarly, diversity was maximized in a grassland restoration following 5–10 cm of soil removal, but this was also accompanied by a decrease in productivity (Pywell et al. 2007).

Our second hypothesis, that solarization would result in high cover of native species and have less impact on belowground processes, was somewhat supported by our findings. The solarization sites had the highest mean native plant cover and significantly less exotic cover than the reference wetlands (Fig. 1). These sites were dominated by graminoid species, particularly native bunchgrasses despite similar seeding densities of the bunchgrasses in the two restoration treatments (Table 2, Fig. 2). Similar results were observed in a previous study of wetland prairie restoration in the region (Pfeifer-Meister et al. 2012) and in a California annual grassland (Moyes et al. 2005). Moyes et al. found that solarization significantly reduced cover of an exotic annual grass and increased survival of two native perennial bunchgrasses, but forb seedling density was significantly reduced. The decrease

in forb productivity that we observed (Fig. 2) appeared to be the result of native perennial bunchgrasses outcompeting forb species. These grasses contributed to a twofold increase in litter that, together with the high levels of bunchgrass cover, may have created an environment that reduced subsequent forb recruitment.

Many soil characteristics did not differ between solarization and reference wetlands as hypothesized, but we did detect some differences. Solarization sites had higher ecosystem respiration and phosphate availability, slightly more acidic pH, and lower microbial biomass carbon and nitrogen (Fig. 5). Other studies implementing solarization have found a decrease in the microbial community, with lower nematode abundance (Wang et al. 2006) and AMF infection (Bendavid-Val et al. 1997), but these effects were generally short-lived (weeks to months). We examined older sites (1–7 yr post restoration), so it was surprising that a decrease in microbial biomass was still detectable. This decrease was not as severe as that found in the topsoil-removal sites, and no decrease in AMF colonization was detected in the solarization sites. The prior land use (e.g., *Lolium multiflorum* fields) of the solarization sites could explain the higher phosphate availability, as these sites were fertilized regularly prior to restoration, particularly since phosphate availability decreased with age since restoration (Fig. 7).

We found partial support for our third hypothesis, that restored sites would have lower species richness and diversity than the reference wetlands and that this would be due to native perennial bunchgrasses excluding establishment of other species. Both restoration treatments (particularly solarization) had lower species richness (both on a 1 m^2 scale and totaled across the 15 subplots), but only the solarization sites had lower diversity (Fig. 1). The lower richness and diversity of restored sites than reference wetlands is a commonly observed phenomenon (Seabloom and van der Valk 2003, McLachlan and Knipsel 2005, Aronson and Galatowitsch 2008, Rey Benayas et al. 2009, Pfeifer-Meister et al. 2012). Somewhat surprisingly, we found no differences in native species richness and diversity on a m^2 scale, but the solarization treatment did have fewer native species when totaled across the 15 subplots.

We hypothesized that the mechanism for the lower diversity observed in the restored sites may be the dominance attained by the seeded native perennial bunchgrasses. Across all treatments, we observed a significant tradeoff between cover of *Deschampsia cespitosa*, the most common perennial bunchgrass, and diversity ($r^2 = 0.59$, Fig. 4). The solarization sites were dominated by this grass species and had the lowest overall diversity, whereas the reference wetlands had the lowest cover of *D. cespitosa* and the highest diversity. Results from other wetland and grassland studies suggest that this tradeoff between high native grass cover and diversity may be a generalizable trend (Heslinga and Grese 2010, McCain et al. 2010, Pfeifer-Meister et al. 2012).

Further research is needed to understand why restored sites are particularly vulnerable to native perennial bunchgrass dominance and reference sites are not. Potential mechanisms include (1) seed limitation within remnants as a consequence of historical losses of bunchgrasses, (2) the more variable microtopography of remnant prairies, or (3) inhibitory priority effects of the perennial bunchgrasses establishing initially at high densities in the restored wetlands. In California grasslands, seed limitation has been recognized as a primary obstacle to reestablishing native grasses and forbs (Hamilton et al. 1999, Seabloom et al. 2003). However, the reference wetlands in this study have maintained relatively high perennial bunchgrass cover (~50% of their relative cover) suggesting that seed limitation is not the dominant mechanism. Microtopographic heterogeneity has also been identified as a mechanism increasing diversity and richness in wetland communities (Vivian-Smith 1997, Araya et al. 2010). The reference wetlands in this experiment had much greater spatial variability with hummocks and deep channels, whereas the restored sites tended to be flat surfaces with little microtopographic variation. Consistent with this explanation, the reference wetlands exhibited greater site-level variability in plant community composition than did the restored sites (error bars of Fig. 3). Finally, restored sites are often seeded with high densities of competitive native perennial grasses to meet mitigation criteria of high native and low exotic cover (Oregon Department of State Lands

2011), which can lead to inhibitory priority effects, thus limiting subsequent establishment of other species (Young et al. 2005, Grman and Suding 2010). In a tallgrass prairie, communities with the highest initial cover of competitive native grasses lost diversity over a 16-year period, while communities with the lowest cover of these grasses were able to maintain diversity (Heslinga and Grese 2010). Similarly in our reference wetlands, the high diversity of established plants could limit the opportunity for native bunchgrass dominance. Future experiments could test these hypotheses by introducing topographic heterogeneity into restorations and by manipulating seed mixes to include varying levels of native bunchgrasses at different times post-site preparation. For example, partly based upon the results of this study, local wetland practitioners have begun seeding high densities of native forbs initially followed with low densities of native bunchgrasses 1–3 years later to promote both high native cover and diversity.

In addition to the many univariate differences among treatments, the ordinations revealed large differences in plant community composition and ecosystem function between the restored and reference sites (Figs. 3 and 7). Interestingly, the restored treatments did not substantially differ from one another in plant community composition, with the exception of the young solarization, though these sites differed from one another in total cover and productivity. Instead, a similar suite of species was found in all of the restoration sites, which may reflect the similar seed mixes used in these restorations (Table 2). Moreover, a different set of edaphic factors was more strongly associated with plant communities in the restored sites than in the reference wetlands (e.g., high microbial biomass, soil carbon; Fig. 7). In general, the restored sites had a higher abundance of annual species, whereas reference sites were dominated by perennial graminoids, forbs, and woody species (many of which were exotic, see Appendix A). This may reflect the young age of the restorations and that many early-successional species, particularly annuals, are still found in these wetlands.

The higher proportion of exotic species found in the reference wetlands (Fig. 2) could be a result of several mechanisms. It may be explained partially by the differences in initial site history and preparation, and subsequent management practices. Prior to restoration, these sites were agricultural fields that likely received extensive weed-control measures that depleted the seedbank. Moreover, post-restoration the restored sites also may have experienced more selective weeding of invasive species, as this is a typical practice within the Willamette Valley. However, this is likely not the only mechanism as we observed similarly low exotic cover and diversity in restored plots with no post-restoration management (Pfeifer-Meister et al. 2012). The lower proportion of exotics could also be a consequence of the young age of the restorations. Over time the restorations could accumulate more exotics as they disperse into the sites from elsewhere. Finally, the lower exotic cover and diversity could also be explained by the inhibitory priority effects of native bunchgrasses, suggesting that the restorations may be more resistant to invasion, although this comes at a cost of diversity. It is interesting to note, that although the reference wetlands had a large abundance of exotic species, native species were not excluded and were able to persist in relatively high abundances. Understanding what factors support this persistence of natives in the presence of exotics, and thus the maintenance of native diversity over time, has important implications for wetland restoration.

Conclusions

We found large differences between restored sites and reference wetlands in both plant community composition and ecosystem functioning, even with the relatively small sample size. Moreover, we observed important tradeoffs between the two site preparation treatments despite substantial differences in post-restoration management at each site. The removal of topsoil significantly altered ecosystem functioning, leading to substantially lower aboveground productivity, microbial biomass, AMF infection of native grasses, and total soil carbon and nitrogen than either the reference wetlands or solarization sites. However, these sites were more similar to reference wetlands in terms of diversity and species richness than solarization sites. The solarization treatment, on the other hand, appeared to have minimal effects on belowground responses and surpassed the reference wetlands in terms of native plant cover, particularly of

native perennial bunchgrasses, but these sites were substantially less diverse and speciose. In no case did restored wetlands, even up to 7 years after establishment, resemble high-quality reference wetlands in terms of plant community composition or ecosystem function, suggesting that mitigation for loss of natural wetlands may result in progressive loss of wetland function.

Our study highlights the importance of considering multiple criteria when determining the 'success' of mitigation projects. If only one criterion (e.g., high cover of native species) is examined, restorations could be deemed 'successful' despite having dramatically different ecosystem functioning or community composition than high-quality remnant prairies. Such simplistic metrics of success may not only gloss over the impacts of restoration treatments on key ecosystem functions, but also ignore important potential tradeoffs (e.g., if establishing high cover of native bunchgrasses suppresses overall species diversity). Further research is needed to better understand the mechanisms causing the tradeoff between diversity and native bunchgrass cover we observed, and why restored sites are particularly susceptible to native bunchgrass dominance. Establishing wetland prairie restorations that can sustain both high native cover and high species diversity over time with relatively low amounts of maintenance is a key challenge that remains to be solved.

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Supplemental Material

Appendix A

Table A1. Species axes loadings for NMS ordination of restoration treatments (see Fig. 3). Only significant indicator species ($p < 0.05$) are reported. Native (N) and exotic (E) origin, life history (A: annual, B: biennial, and P: perennial), and functional group (G: graminoid, F: forb, and W: woody) are given for each species. Axis loading values greater than 0.5 are in bold and values less than −0.5 are underlined and in bold.

Species	Axis 1 loading	Axis 2 loading	Species origin	Life history	Functional group
Hypericum perforatum	**−1.19**	0.17	E	P	F
Rosa nutkana	**−1.11**	0.14	N	P	W
Anthoxanthum odoratum	**−1.11**	−0.18	E	P	G
Fraxinus latifolia	**−1.10**	**0.65**	N	P	W
Zigadenus venenosus	**−1.07**	−0.28	N	P	F
Dichanthelium acuminatum ssp. *fasciculatum*	**−1.03**	−0.46	N	P	G
Crataegus monogyna x suksdorfi	**−1.00**	0.26	E	P	W
Sisyrinchium idahoense	**−1.00**	−0.09	N	P	F
Mentha pulegium	**−0.88**	−0.12	E	P	F
Leucanthemum vulgare	**−0.87**	**0.61**	E	P	F
Daucus carota	**−0.79**	**0.65**	E	B	F
Schedonorus arundinaceus	**−0.76**	**0.73**	E	P	G
Danthonia californica	**−0.75**	0.02	N	P	G
Symphyotrichum hallii	**−0.73**	**0.60**	N	P	F
Galium parisiense	**−0.71**	0.23	E	A	F
Potentilla gracilis var. *gracilis*	**−0.69**	**0.64**	N	P	F
Vicia tetrasperma	**−0.62**	0.40	E	A	F
Plantago lanceolata	**−0.61**	0.27	E	P	F
Sonchus asper	**−0.61**	0.23	E	A	F
Lotus formosissimus	**−0.60**	−0.13	N	P	F
Briza minor	**−0.58**	−0.04	E	A	G
Centaurium erythraea	**−0.54**	0.24	E	A/B	F
Rubus armeniacus	**−0.50**	0.34	E	P	W
Aira caryophyllea	−0.47	0.43	E	A	G
Linum bienne	−0.45	−0.11	E	A/B	F
Juncus nevadensis	−0.45	0.31	N	P	G
Leontodon taraxacoides	−0.36	0.29	E	P	F
Hypochaeris radicata	−0.27	0.32	E	P	F
Eriophyllum lanatum	−0.01	0.15	N	P	F
Myosotis discolor	0.06	0.34	E	A	F
Cirsium vulgare	0.07	**0.95**	E	B	F
Orthocarpus bracteosus	0.13	0.02	N	A	F
Microsteris gracilis	0.21	−0.31	N	A	F
Parentucellia viscosa	0.23	0.44	E	A	F
Juncus tenuis	0.23	−0.01	N	P	G
Wyethia angustifolia	0.23	0.15	N	P	F
Holcus lanatus	0.24	0.24	E	P	G
Grindelia integrifolia	0.24	−0.28	N	P	F
Deschampsia cespitosa	0.33	−0.09	N	P	G
Poa compressa	0.36	−0.30	E	P	G
Hordeum brachyantherum	0.38	−0.46	N	P	G
Lolium multiflorum	0.40	**−0.99**	E	A	G
Agrostis exarata	0.41	**−0.91**	N	P	G
Epilobium densiflorum	0.42	**−0.89**	N	A	F
Poa annua	0.42	**−0.95**	E	A	G
Carex densa	0.43	−0.23	N	P	G
Madia glomerata	0.44	**−0.93**	N	A	F
Plagiobothrys figuratus ssp. *figuratus*	0.44	**−0.86**	N	A	F
Moenchia erecta	0.45	0.09	E	A	F
Madia elegans	0.48	−0.05	N	A	F
Downingia elegans	**0.50**	−0.33	N	A	F
Epilobium brachycarpum	**0.50**	0.18	N	A	F
Deschampsia danthonioides	**0.54**	−0.20	N	A	G
Lotus unifoliolatus	**0.60**	0.41	N	A	F
Gnaphalium palustre	**0.61**	−0.14	N	A	F
Centunculus minimus	**0.66**	−0.01	E	A	F
Agrostis stolonifera	**0.71**	0.02	E	P	G

APPENDIX B

Table B1. Species axes loadings for CCA ordination of restored and reference wetlands (see Fig. 7). Native (N) and exotic (E) origin, life history (A: annual, B: biennial, and P: perennial), and functional group (G: graminoid, F: forb, and W: woody) are given for each species. Axis loading values greater than 1.0 are in bold and values less than −1.0 are underlined and in bold.

Species	Axis 1 loading	Axis 2 loading	Species origin	Life history	Functional group
Rosa multiflora	**−2.29**	0.77	E	P	W
Fraxinus latifolia	**−2.29**	**−3.66**	N	P	W
Plantago lanceolata	**−1.97**	**−1.23**	E	P	F
Leucanthemum vulgare	**−1.83**	−0.38	E	P	F
Potentilla gracilis var. *gracilis*	**−1.81**	−0.47	N	P	F
Daucus carota	**−1.75**	−0.14	E	B	F
Schedonorus arundinaceus	**−1.66**	−0.06	E	P	G
Eryngium petiolatum	**−1.65**	−0.58	N	P	F
Anthoxanthum odoratum	**−1.51**	**−1.37**	E	P	G
Dichanthelium acuminatum ssp. *fasciculatum*	**−1.32**	**−1.96**	N	P	G
Anagallis arvensis	**−1.25**	−0.83	E	A	F
Sisyrinchium idahoense var. *idahoense*	**−1.25**	−0.78	N	P	F
Vicia tetrasperma	**−1.24**	−0.59	E	A	F
Galium parisiense	**−1.22**	**−1.08**	E	A	F
Symphyotrichum hallii	**−1.21**	−0.38	N	P	F
Danthonia californica	**−1.20**	**−1.39**	N	P	G
Hypericum perforatum	**−1.18**	−0.01	E	P	F
Mentha pulegium	**−1.14**	−0.66	E	P	F
Centaurium erythraea	**−1.07**	0.30	E	A/B	F
Lotus formosissimus	**−1.03**	0.01	N	P	F
Crataegus suksdorfii	−0.94	**−1.68**	N	P	W
Hypochaeris radicata	−0.92	0.93	E	P	F
Rubus armeniacus	−0.86	−0.66	E	P	W
Zigadensus venenosus var. *venenosus*	−0.85	**−2.00**	N	P	F
Aira carophyllea	−0.83	0.06	E	A	G
Rosa nutkana var. *nutkana*	−0.69	−0.42	N	P	W
Briza minor	−0.68	−0.16	E	A	G
Juncus sp.	−0.58	0.27	N	P	G
Leontodon taraxacoides	−0.56	0.21	E	P	F
Eriophyllum lanatum	−0.47	**1.55**	N	P	F
Madia sp.	−0.44	**1.05**	N	A	F
Grindelia integrifolia	−0.39	**1.85**	N	P	F
Prunella vulgaris var. *lanceolata*	−0.31	−0.02	N	P	F
Juncus tenuis	−0.27	**1.64**	N	P	G
Holcus lanatus	−0.17	0.31	E	P	G
Lotus unifoliolatus var. *unifoliolatus*	−0.11	0.61	N	A	F
Cirsium vulgare	−0.07	0.06	E	B	F
Parentucellia viscose	−0.04	0.20	E	A	F
Madia elegans	0.09	0.84	N	A	F
Ranunculus sp.	0.10	**1.71**	N	P	F
Veronica scutellata	0.16	**1.42**	N	P	F
Microseris laciniata	0.20	0.99	N	P	F
Deschampsia cespitosa	0.28	0.82	N	P	G
Rumex salicifolius var. *salicifolius*	0.31	**1.97**	N	P	F
Agrostis stolliniferus	0.34	**1.94**	E	P	G
Epilobium brachycarpum	0.40	0.40	N	A	F
Vulpia bromoides	**1.07**	−0.17	E	A	G
Agrostis exarata	**1.54**	**−1.18**	N	P	G
Epilobium ciliatum	**1.62**	**−1.06**	N	A	F
Epilobium densiflorum	**1.67**	**−1.02**	N	A	F
Plagiobothrys figuratus ssp. *figuratus*	**1.73**	**−1.37**	N	A	F
Lolium multiflorum	**1.82**	**−1.39**	E	A	G
Madia glomerata	**1.98**	**−1.32**	N	A	F