

RESEARCH ARTICLE

Riparian vegetation composition and diversity shows resilience following cessation of livestock grazing in northeastern Oregon, USA

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Abstract

Riparian ecosystem restoration has been accomplished through exclusion of livestock using corridor fencing along hundreds of kilometers of streams in the western United States, for the benefit of riparian-obligate wildlife and endangered fishes. Yet, there are limited scientific studies that have evaluated more than short-term shifts in vegetation composition and diversity at a single location or handful of locations following grazing. We sampled riparian vegetation composition along 11-paired grazed and ungrazed (exclosed) stream reaches in northeastern Oregon. Exclosure ages ranged from 2 to >30 years and grazing treatments varied from light grazing every one out of three years to heavy season-long grazing. Species richness and diversity was higher in the ungrazed reaches ($p = 0.002$). The abundance of native sedges (*Carex* spp.) and broad-leaved forbs were also significantly ($p \leq 0.05$) greater in ungrazed areas. In contrast, exotic species adapted to grazing such as *Poa pratensis* and *Trifolium repens* were more abundant in grazed stream reaches. The prevalence of hydrophytic species significantly increased ($p \leq 0.01$) in ungrazed reaches, (based on wetland species indicator scores), indicating that wetland-dominated communities within the ungrazed stream reaches were replacing ones adapted to drier environments. The increased abundance of facultative and wetland-obligate species in ungrazed reaches compared to grazed reaches suggests that livestock grazing exacerbates those climate change effects also leading to warmer and drier conditions. Further, riparian-obligate shrub cover along the streambank was higher in 7 of 8 exclosures that were older than 5 years ($p = 0.05$). As a restoration approach, the inherent resilience of riparian ecosystems exhibited in ungrazed riparian zones suggest positive feedbacks to other beneficial ecosystem processes such as increased species and habitat diversity, increased carbon sequestration, enhanced allochthonous inputs and greater sediment retention, that would affect the aquatic and terrestrial biota, water quality, and stream morphology.

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Introduction

Riparian areas are zones of contact between land and water ecosystems, represented by mesic, productive environments bordering streams, rivers, lakes, and springs [1]. Whereas riparian zones comprise only 1–2% of landscapes in the western US, they provide habitat for more wildlife species than any other vegetation type [2]. For example, about 70% of the wildlife species in the Pacific Northwest of the western US depend on riparian areas for all or part of their life cycle [3]. It has been estimated that 204 (77%) of the 266 species of inland birds that breed in Oregon and Washington do so in riparian and wetland environments [3].

Riparian vegetation is a keystone ecosystem feature that exerts a strong influence on adjacent uplands and aquatic ecosystems. Riparian plant communities are integral to stream function/aquatic productivity, especially in low-order streams where they strongly influence stream temperatures [4] channel form [5], and the habitats of fish and aquatic invertebrates [6,7]. In addition, they are the predominant in-stream sources of nutrients and carbon via allochthonous inputs [7,8]. Through interactions of soil, vegetation, and water, riparian areas retain and filter sediments, stabilize stream banks, and moderate stream and groundwater flows through storage and flood attenuation. Productivity of riverine fish communities is determined by both habitat and food resources; factors that are intricately linked to the structure and composition of riparian zones [7].

Riparian zones and other palustrine/riverine wetlands are also important sinks of atmospheric carbon, underscoring their values for inclusion in climate change mitigation and adaptation strategies. Nahlik and Fennessy [9] reported that soils of palustrine/riverine wetlands of the USA had mean carbon stocks of 369 Mg C ha⁻¹ and that western wetlands stored 236 Mg C ha⁻¹. These stocks are about 3 to 6 times that of adjacent upland forests (≈61 Mg C ha⁻¹) in the Blue Mountains of Oregon (the location of this study; [10]).

Given the important ecosystem functions and ecological services provided by riparian vegetation, shifts in structure and composition would likely have far reaching effects on both adjacent terrestrial and aquatic ecosystems. In the western USA, livestock grazing is the most widespread land use on public lands and has been suggested to be a significant influence affecting riparian ecosystem structure, diversity, and function [11–13]. Cattle tend to prefer and congregate in riparian areas because of the abundant forage, proximity to water, relatively level terrain, and favorable microclimate, thus causing substantial damage to stream and riparian ecosystems [11,12,14].

Livestock grazing has been the most prevalent cause of ecological degradation of riparian/stream ecosystems in the Intermountain west [11,15,16]. Elmore and Kauffman [12], Beschta et al. [17] and Kauffman et al. [18] suggested that the cessation of livestock grazing in riparian zones of eastern Oregon was the single most ecologically and economically effective approach for restoring salmonid habitats.

Several studies have examined livestock effects on riparian vegetation including root mass [19], wetland species abundance [20], and vegetation structure [21,22]. Most studies that have quantified the vegetation differences between grazed and ungrazed stream reaches in a wide diversity of stream types in the Pacific Northwest have focused on the shrub component [21–23]. However, few studies have examined how livestock affect riparian vegetation composition as manifested in species diversity, and richness.

Kauffman et al. [24] suggested the first logical step in riparian restoration is the implementation of “passive restoration” defined as the cessation of those activities that are causing ecosystem degradation or preventing recovery. Cessation of livestock grazing via exclusion fencing along salmonid bearing streams has been a common passive restoration approach to fish and wildlife habitat restoration in the Interior Columbia Basin of Oregon and Washington.

Because the vegetation of riparian zones is adapted to frequent fluvial disturbances, many species possess adaptations facilitating a rapid recovery following both natural and anthropogenic disturbances [7,24].

The objective of this study was to quantify changes in the composition and structure of the riparian vegetation composition along 11 experimental streams where passive restoration (corridor fencing or livestock exclusions) had occurred. From measurements of species cover, we calculated composition, richness, and diversity in paired reaches that included livestock exclusion with an adjacent and geomorphically similar reach where the riparian zones were grazed by domestic cattle. We hypothesized that given the inherent resilience of riparian vegetation and physical shifts that occur due to livestock removal [19], the composition of ungrazed stream reaches would have a greater dominance of hydrophytic vegetation, as well as increased, species richness, and diversity.

Methods

To examine how streamside riparian vegetation differed between grazed and ungrazed stream reaches a total of 11 northeastern Oregon streams were selected. These streams were all tributaries of the Columbia River (Fig 1). Land tenure consisted both of public and private ownership. Each study stream consisted of two reaches, a grazed reach and an excluded (ungrazed) reach (Table 1, S1 Fig). Grazed reaches were those in which livestock grazing (principally cattle) was a dominant use in the riparian zone and surrounding uplands. Excluded reaches were those where livestock grazing had been eliminated through the construction of riparian exclusions or corridor fences. Riparian livestock exclusions are essential research tools for the study of ecosystem processes, recovery, and to better inform livestock management [21,25]. A major advantage of using small exclusions is that environmental site variability (precipitation, geology, flow regime, etc.) is practically the same for adjacent grazed and ungrazed areas, thus isolating the potential influence of livestock (or livestock removal) [20,25].

Exclusion ages at the time of sampling ranged from ~2 to 37 years (Table 1). Criteria for site selection included paired reaches (grazed and ungrazed) that were as geomorphically similar as possible, streams with salmonids, knowledge of the history of the exclusion, and owner permission. Our assumptions were that prior to the construction of exclusion fences the vegetation composition did not differ between reaches. The adjacent nature of sampled areas with identical pre-exclusion land use histories and similar geomorphic surfaces increased the likelihood that differences between grazed and ungrazed areas were largely due to current land use. The sampled exclusion fences were made of multiple strands of barbed wire or split rails which effectively exclude domestic cattle but not wild ungulates or other wildlife. As is the case for most livestock exclusions, occasional trespass grazing by cattle occurred for many of the sites and wild ungulates, such as Rocky Mountain elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*), had free access to all the exclusions.

Each grazed and ungrazed study reach was first delineated into pool-riffle channel units. Vegetation community composition was determined for each channel unit on both sides of the stream by calculating the percent cover of each plant species occurring in 1 x 4 m plots ($N \approx 40$ plots/reach). Plots were positioned so that its center was mid-way along a riffle or mid-way along a pool. Plots were then placed at the innermost edge on the green line which is the transitional point along a streambank edge where terrestrial vegetation dominates ground cover [26]. All plant species with a canopy cover 5% or more within the plot were recorded. Taxonomy largely follows that of Hitchcock and Cronquist [27].

From the plot data, we calculated species richness (number of species per experimental reach), species diversity, and similarity. Species diversity (H') was calculated using the

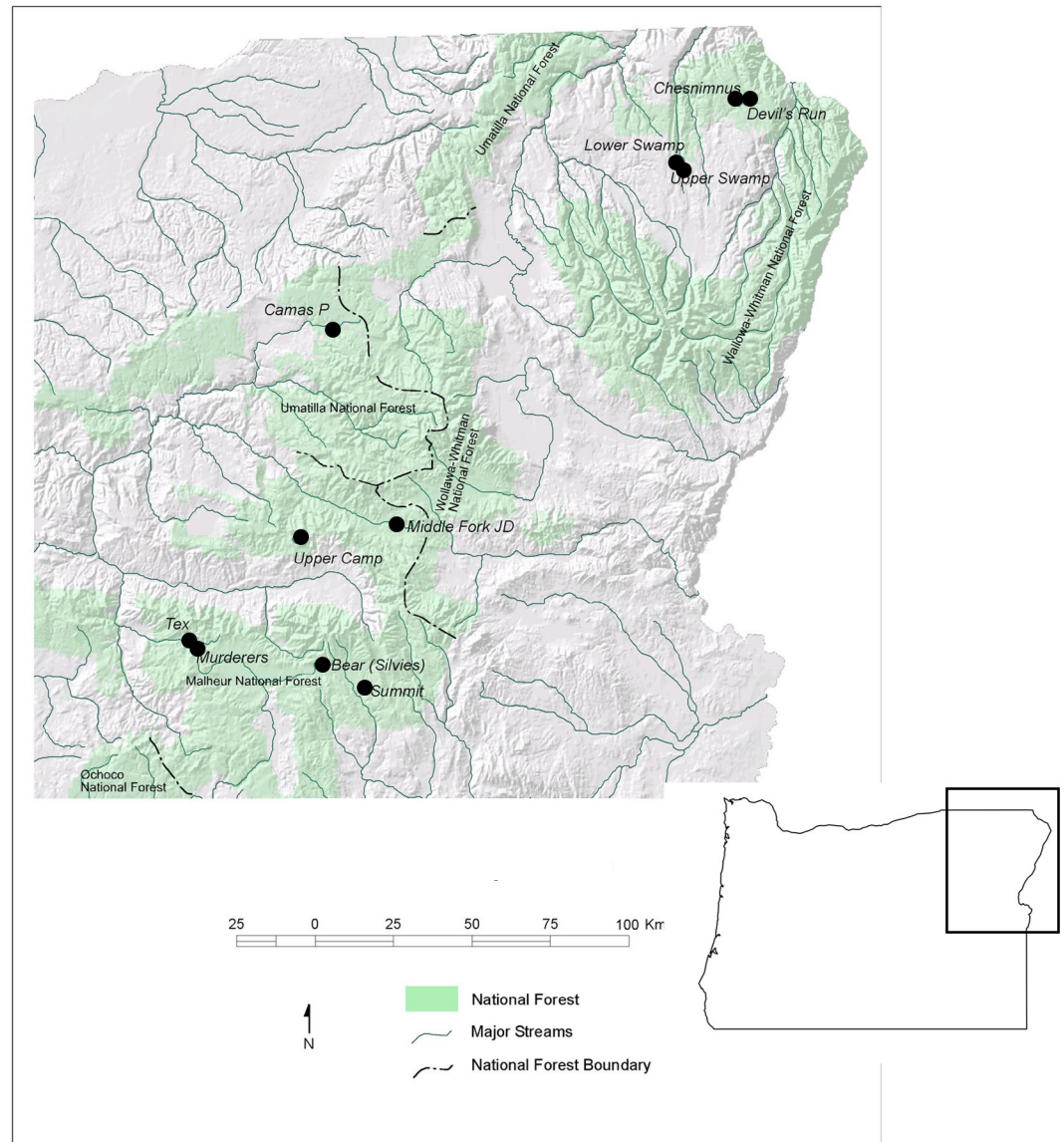


Fig 1. Location of the 11 study stream reaches selected for study in northeastern Oregon, USA.

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Shannon Index, where:

$$H = - \sum p_i \ln(p_i).$$

The quantity p_i is the proportion of cover of the i th species relative to the sum of cover for all species. We also report species diversity as the exponent of H' which is equivalent to the number of equally common species required to produce the value of H' [28].

The similarity between grazed and ungrazed reaches was calculated using Sorenson's quantitative measure of similarity [28]. Similarity ranges from 0 (no species in common) to 1 (all

Table 1. Site characteristics of the 11 stream reaches selected for study in northeastern Oregon, USA.

Site	Period of exclusion (years)	Site elevation (m)	Mean annual ppt (mm)	Drainage area (km ²)	Sinuosity (m/m)	Valley gradient (%)	Channel gradient (%)
Bear Creek (Silvies)	2	1554	686	39.2	1.55	0.99	0.64
Camas Creek	5	1240	635	95.3	1.22	0.72	0.58
Chesnimnus Creek	14	1305	483	40.5	1.27	1.77	1.39
Camp Creek	36	1467	635	16.4	1.33	3.43	2.58
Devil's Run Creek	10	1285	483	29.0	1.75	1.86	1.05
Middle Fk John Day	3	1292	533	97.6	1.91	0.43	0.23
Murderers Creek	30	1347	483	36.3	1.58	0.52	0.34
Summit Creek	22	1506	584	77.3	1.45	0.90	0.62
Lower Swamp Creek	13	1123	483	79.9	1.29	0.60	0.46
Upper Swamp Creek	13	1142	483	74.6	1.33	0.77	0.56
Tex Creek	23	1359	483	31.6	1.24	1.11	0.90

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species and their cover are identical). Similarity (C_N) was calculated using the formula:

$$C_N = 2jN/aN + bN$$

Where:

jN = sum of the lower of the two abundances (cover) of all species occurring on the grazed and exclosed reaches.

aN = The sum of plant cover in the exclosed reach.

bN = The sum of plant cover in the grazed reach.

The wetland species prevalence index, also referred to as the wetland score, was calculated for each grazed and ungrazed reach to determine predominance of hydrophytic (wetland) vegetation [29]. This prevalence index was computed by weighting the species cover from plots with index values for wetland indicator categories. Wetland indicator values were assigned to each species using the National list of plant species that occur in wetlands [30] (S1 Table). By assigning the composition to the wetland indicator scores we derived a wetland score for each grazed and ungrazed reach. These scores can range from 1 (all species wetland-obligate) to 5 (all species upland-obligate). The wetland prevalence index was calculated as follows:

$$\text{Wetland prevalence index} = \sum A_i W_i / \sum W_i$$

Where:

A_i = abundance (cover) of species i

W_i = indicator index value for species i

i = species

Riparian shrub and tree composition was measured via the line intercept technique. Two transects were established along the entire length of the sampled reaches; one on each side of the creek and running along the green line. The total length of these transects in the study reaches ranged from 188 to 688 m. All shrubs were identified to species. The cover of every individual shrub or tree overhanging the green line was measured regardless if there was overlap with other individuals (i.e., shrub cover can exceed 100%). From these measurements, woody plant composition and streamside cover was determined.

The total vegetation overstory and emergent (herbaceous) cover over the stream was measured along each channel unit. The overstory cover can not only include streamside vegetation but also tall trees (conifers) in adjacent uplands that may function as providing stream shade. This measure utilized a concave spherical densiometer. The densiometer was taped so that there was a “V” exposing only 17 of the grid line intersections following the methods of Platts et al. [31]. Cover was measured approximately 30 cm above the surface of the water, at approximately 30 cm from each bank as well as the middle of the stream. One reading at each bank was taken and four readings were taken in the middle of the stream. The four readings at the middle of the channel included readings upstream, downstream, towards right bank and towards left bank. The cover of emergent plants (principally Cyperaceae and Juncaceae) present in the channel, is the cover relative to the entire water surface area of the channel unit.

To statistically determine if there were differences between grazed and ungrazed treatments, the study reach was used to represent an experimental unit. Paired t-tests and Wilcoxon sign tests were used to test for differences in prevalence indices, diversity indices, and cover between grazed and ungrazed treatments [32]. Given the inherently high variation in composition, land use histories and differences in stream geomorphology, we assumed statistical differences existed when p-values were ≤ 0.10 but report the actual values. We used simple linear regression to assess the relationship between riparian vegetation variables (i.e., species diversity, individual species abundances, richness, and wetland prevalence index) with time since exclusion and channel gradient.

Results

The riparian plant communities sampled in this study were high in species richness and diversity. There were 128 plant species encountered with a cover of at least 5% in one of the micro-plots (S2 Table). At all sites, we found significant differences in vegetation composition and structure between the grazed and ungrazed reaches. The cover of native sedges (*Carex* spp.) was significantly greater ($p = 0.004$) in ungrazed areas (Fig 2). Forbs (broad-leaved herbs) were more prevalent in ungrazed reaches ($p = 0.05$) and shrub cover was significantly greater ($p = 0.05$) in ungrazed reaches that were >5 years old. Grazed areas had substantially higher bare ground (16%) compared to ungrazed areas (9.6%, $p = 0.13$) (Table 2). Mean cover of emergent vegetation present in the stream channel in ungrazed sites was over twice that in grazed reaches ($p = 0.07$) suggesting revegetation and narrowing of the stream channels.

Species richness ($p = 0.08$) and diversity ($p = 0.002$) was significantly greater in the ungrazed reaches (Table 3). The highest species richness was found in ungrazed reaches of Camp ($S = 50$), Camas ($S = 45$), Chesnimnus ($S = 45$) and Devil Creeks ($S = 45$). The greatest differences in species richness were in the heavily grazed Devil's Creek study reach where the ungrazed portion had 17 more plant species than the grazed portion. Species diversity ($\exp H'$) was as low 4.7 and 5.5 in the grazed reaches of the Middle Fork John Day and Murderer's Creek, respectively. However, the ungrazed reaches of these two streams had species diversity values of 14.6 and 12.7, indicating that livestock were limiting species diversity on these sites (Table 3). Similarly, there was a large difference in the species diversity in the grazed and ungrazed reaches of Summit Creek (9.1 and 17.7, respectively). Sites with the fewest differences included the recently established Bear (2 yrs) and Camas Creek (5 yrs) sites, as well as the forested Tex Creek (23 yrs). Tex Creek was a moderately constrained reach with a dense conifer overstory canopy and light grazing regime. Understory composition was most similar at this site (a similarity index of 0.73).

The changes in species richness and diversity reflect significant changes in species composition between the grazed and ungrazed reaches. Plant species composition were least similar

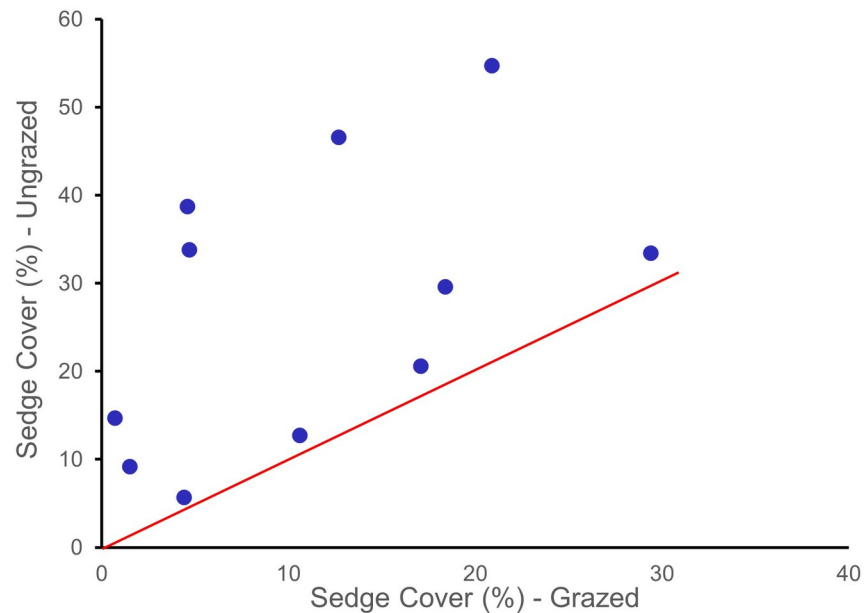


Fig 2. Comparison of sedge cover for 11 paired grazed and ungrazed riparian reaches in northeastern Oregon. If there was no change in the abundance of sedges between grazed and ungrazed areas the data points would be expected to fall on, or near the line. Data points above the line indicate a higher abundance of sedges in ungrazed areas compared to grazed reaches. The abundance of sedges in enclosures was significantly greater ($p = 0.004$) than in grazed areas.

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(0.34–0.38) between reaches of Devils, Lower Swamp, Middle Fork John Day, and Summit Creeks. These were all comparatively low gradient reaches where sedges and relatively hydric species were found in greater abundance in ungrazed areas. The relatively young age of some of these enclosures demonstrates that species composition shifts of the herbaceous component can occur in a relatively short period of time following cattle exclusion. We found the most similar composition between grazed and ungrazed sites to be in the forested reaches with a relatively high gradient (i.e., Tex and Camp Creeks) and at some of the recently established enclosures. Combining all sites in the analysis we found no strong relationships ($r^2 = 0.01$) between gradient and shifts in sedge composition. There were also no strong relationships between channel or valley gradients with the shifts in the parameters of diversity.

Wetland-obligate and facultative-wetland species were found in greater abundances in the ungrazed enclosures. Wetland species prevalence indices were consistently and significantly lower ($p = 0.01$) in the ungrazed reaches compared to the grazed reaches (Fig 3, Table 3). This indicates increased hydric conditions and soil moisture available for riparian plant use following cessation of grazing. Combining all sites, we found a statistically significant increase in native sedge (*Carex* spp.) abundance (largely wetland-obligate and facultative-wetland species, Fig 2) with concomitant declines in the abundance of the facultative exotic grass Kentucky bluegrass (*Poa pratensis*) (Fig 4). The only site where we did not find a shift towards wetlands species prevalence was at Tex Creek (a partially constrained forested reach; Fig 3).

The greatest shifts in wetland prevalence indices were in low-gradient reaches (e.g., Middle Fk John Day, Summit Creek, and Lower Swamp Creek). For example, at Summit Creek, wetland scores were 41% lower in ungrazed reaches (1.95) compared to grazed reaches (3.32); the streambank in the ungrazed reach was dominated by wetland-obligate and facultative-wetland species while the grazed reach was dominated by facultative and facultative-upland species.

Table 2. Herbaceous vegetation cover (%) and bare ground (%) of riparian vegetation life forms in 11 paired excluded (ungrazed) and grazed reaches in northeastern Oregon.

P-value	Percent cover with standard error in parentheses																							
	Bear		Cannas		Chesnimus		Devils		Lower Swamp		Upper Swamp		Mid Fk John Day		Murderers		Summit		Tex		Camp		All Sites	
	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed	Excluded	Grazed
0.004	29.6 (4.9)	18.4 (3.2)	20.6 (4.1)	17.1 (3.6)	9.2 (3.6)	1.5 (0.5)	14.7 (2.7)	0.7 (0.3)	38.7 (5.8)	4.6 (2.6)	33.8 (4.6)	4.7 (1.5)	46.6 (5.3)	12.7 (3.7)	33.4 (4.4)	29.4 (5.8)	54.7 (4.8)	20.9 (3.6)	5.7 (2.7)	4.4 (2.2)	12.7 (1.7)	10.6 (2.1)	27.2 (4.8)	11.4 (2.8)
0.375	2.2 (0.7)	9.5 (2.8)	8.0 (2.6)	4.2 (1.5)	0.4 (0.2)	0.3 (0.2)	0.9 (0.3)	0.4 (0.2)	14.9 (4.4)	0.4 (0.3)	13.5 (3.2)	0.9 (0.2)	14.2 (3.9)	1.6 (0.9)	51.8 (5.7)	68.6 (4.6)	10.2 (2.6)	6.5 (1.7)	0.1 (0.1)	3.3 (2.3)	26.7 (4.4)	18.0 (3.7)	13.0 (4.6)	10.3 (6.0)
0.156	23.1 (3.2)	30.3 (3.5)	37.9 (5.0)	33.9 (4.6)	33.1 (5.2)	33.0 (4.3)	41.9 (4.4)	58.1 (3.8)	39.8 (4.5)	68.1 (3.8)	35.9 (2.7)	35.2 (3.3)	37.5 (4.9)	66.5 (3.0)	42.0 (4.0)	30.6 (3.9)	11.1 (3.3)	11.1 (3.3)	41.3 (4.6)	35.6 (5.2)	52.5 (3.1)	61.9 (3.8)	36.0 (3.3)	42.2 (5.6)
0.048	49.0 (3.8)	68.7 (2.8)	40.5 (3.9)	41.6 (3.5)	50.5 (3.9)	36.2 (2.7)	59.5 (3.2)	46.0 (3.6)	35.2 (3.1)	20.4 (3.1)	43.1 (3.1)	31.7 (3.7)	48.5 (4.8)	28.0 (2.6)	50.9 (3.9)	21.1 (3.2)	43.9 (4.5)	50.4 (5.1)	61.6 (4.4)	40.4 (4.1)	74.3 (2.1)	67.6 (3.3)	50.6 (3.3)	41.1 (4.9)
0.129	25.4 (4.5)	9.6 (2.4)	25.1 (4.5)	19.7 (3.4)	14.3 (2.7)	24.1 (3.5)	4.7 (1.6)	12.2 (1.9)	1.7 (1.1)	8.0 (2.2)	0.4 (0.2)	35.2 (3.3)	15.9 (2.5)	15.4 (2.6)	4.4 (0.9)	6.0 (1.6)	11.1 (3.2)	23.4 (4.4)	1.9 (0.5)	10.9 (2.6)	0.6 (0.1)	10.0 (1.8)	9.6 (2.8)	16.0 (2.7)
0.067	1.4 (0.4)	0.5 (0.2)	5.3 (2.5)	6.8 (2.1)	0.6 (0.2)	1.0 (0.4)	3.1 (0.6)	0.8 (0.3)	23.3 (3.3)	2.5 (0.8)	11.8 (1.6)	2.9 (0.9)	13.8 (2.4)	12.8 (3.1)	13.3 (1.4)	8.2 (2.3)	3.6 (1.3)	4.4 (1.2)	3.7 (1.8)	0.6 (0.3)	5.3 (2.5)	1.4 (0.3)	7.8 (2.0)	3.8 (1.1)

Cover of herbaceous components are the means of 40 plots per experimental reach with standard errors in parentheses. Emergent (herbaceous) cover and canopy overstory cover is that which occurred over the stream channel. P-values are statistical results testing for differences between all excluded and grazed sites.

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Table 3. Plant species richness (S), species diversity (H' and exp H'), similarity (C_s), wetland species prevalence indices (WPI), and dominant species and cover (%) for paired excluded (ungrazed) and grazed stream reaches in northeastern Oregon.

Site	S	H'	exp H'	C _s	WPI	Dominant species (% cover)
Bear						
Exclosed	40	3.10	22.10	0.62	2.82	<i>Poa pratensis</i> (10), <i>Fragaria virginiana</i> (10), <i>Carex pellita</i> (9)
Grazed	41	3.02	20.54		3.00	<i>Equisetum arvense</i> (19), <i>Trifolium repens</i> (16), <i>Poa pratensis</i> (15)
Camas						
Exclosed	45	3.17	23.83	0.55	2.73	<i>Poa pratensis</i> (19), <i>Carex pellita</i> (7), <i>Juncus balticus</i> (5)
Grazed	45	3.11	22.42		2.89	<i>Poa pratensis</i> (15), <i>Trifolium repens</i> (7), <i>Phleum pratense</i> (7)
Chesnimnus						
Exclosed	45	2.80	16.48	0.41	2.60	<i>Equisetum arvense</i> (30), <i>Poa pratensis</i> (22), <i>Salix fragilis</i> (18)
Grazed	36	2.61	13.54		3.28	<i>Poa pratensis</i> (27), <i>Pseudotsuga menziesii</i> (11), <i>Trifolium repens</i> (11)
Devils						
Exclosed	45	2.90	18.09	0.35	2.68	<i>Myosotis scorpiodes</i> (32), <i>Agrostis stolonifera</i> (15), <i>Alnus incana</i> (10)
Grazed	28	2.17	8.76		3.57	<i>Poa pratensis</i> (37), <i>Trifolium repens</i> (19), <i>Phleum pratense</i> (17)
Lower Swamp						
Exclosed	36	2.74	15.50	0.34	2.50	<i>Agrostis stolonifera</i> (25), <i>Carex utriculata</i> (20), <i>Alnus incana</i> (18)
Grazed	34	2.02	7.50		3.04	<i>Alnus incana</i> (52), <i>Poa pratensis</i> (49), <i>Agrostis stolonifera</i> (10)
Upper Swamp						
Exclosed	35	2.92	18.46	0.42	2.46	<i>Agrostis stolonifera</i> (18), <i>Erigeron philadelphicus</i> (15), <i>Alnus incana</i> (13)
Grazed	30	2.67	14.37		2.53	<i>Juncus balticus</i> (13), <i>Poa pratensis</i> (9), <i>Trifolium repens</i> (9)
Mid Fk J. Day						
Exclosed	32	2.68	14.62	0.34	2.11	<i>Carex pellita</i> (30), <i>Solidago lepida</i> (15), <i>Deschampsia cespitosa</i> (15)
Grazed	23	1.55	4.71		3.71	<i>Poa pratensis</i> (64), <i>Solidago lepida</i> (11), <i>Carex pellita</i> (10)
Murderers						
Exclosed	32	2.54	12.70	0.59	1.86	<i>Juncus balticus</i> (44), <i>Poa pratensis</i> (23), <i>Carex utriculata</i> (21)
Grazed	21	1.74	5.45		1.63	<i>Juncus balticus</i> (67), <i>Carex nebrascensis</i> (27), <i>Poa pratensis</i> (24)
Summit						
Exclosed	37	2.88	17.74	0.38	1.95	<i>Carex nebrascensis</i> (19), <i>Carex pellita</i> (16), <i>Carex utriculata</i> (14)
Grazed	29	2.21	9.12		3.32	<i>Trifolium longipes</i> (31), <i>Poa pratensis</i> (10), <i>Carex pellita</i> (9)
Tex						
Exclosed	36	2.63	13.86	0.73	2.76	<i>Alnus incana</i> (54), <i>Poa pratensis</i> (16), <i>Symphyotrichum foliaceus</i> (11)
Grazed	39	2.53	12.59		2.92	<i>Alnus incana</i> (40), <i>Poa pratensis</i> (14), <i>Equisetum arvense</i> (8)
Camp						
Exclosed	51	3.01	20.21	0.63	2.86	<i>Poa pratensis</i> (34), <i>Alnus incana</i> (30), <i>Juncus balticus</i> (24)
Grazed	41	2.80	16.50		3.15	<i>Poa pratensis</i> (51), <i>Trifolium longipes</i> (26), <i>Juncus balticus</i> (16)
p-value	0.08	0.002	0.004		0.01	

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For example, *Carex* species (wetland-obligates) were most common in ungrazed reaches (55% cover) while facultative species *Poa pratensis* and *Trifolium longipes* dominated the grazed reaches (50% cover; Table 3). Hydric species such as *Carex* spp., *Glyceria* spp., and *Scirpus microcarpus* were more abundant in the ungrazed reaches while species more adapted to grazing and drier conditions (e.g., *Poa pratensis*, *Phleum pratense*, *Trifolium* spp., and *Taraxacum officinale*) were usually more abundant in grazed reaches (Fig 4). There was a mean 49% decrease in the cover of the exotic grass *Poa pratensis* in ungrazed reaches ($p = 0.03$, Fig 4).

Stream reaches also varied in their potential to support tree or shrub-dominated communities (Table 4). Streamside cover of woody vegetation ranged from 0.7% in the low gradient, meadow-dominated Middle Fork John Day to 129% in the relatively steep-gradient, forested Tex Creek. The most abundant woody species was Thin-leaf alder (*Alnus incana*), which was

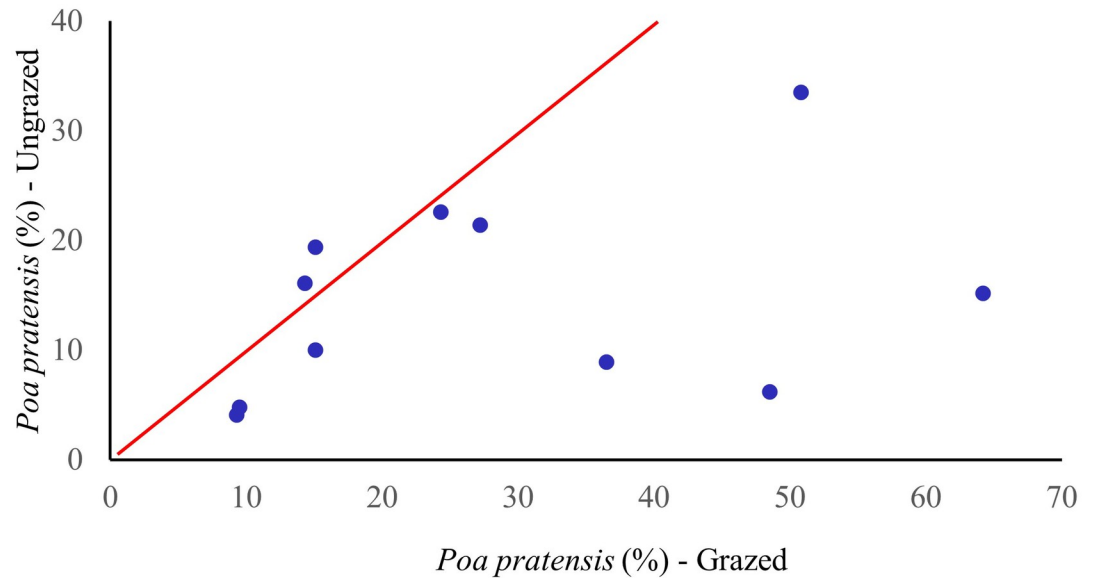


Fig 3. The relationship of wetland prevalence index for 11 paired grazed and ungrazed riparian reaches in northeastern Oregon. If there was no difference in the index between grazed and fenced areas the data points would be expected to fall on or near the line. Data points below the line indicates a greater abundance of wetland species in ungrazed areas compared to grazed reaches. There was a significance difference ($p = 0.01$) in the wetland indicator scores of grazed and ungrazed areas.

<https://doi.org/10.1371/journal.pone.0250136.g003>

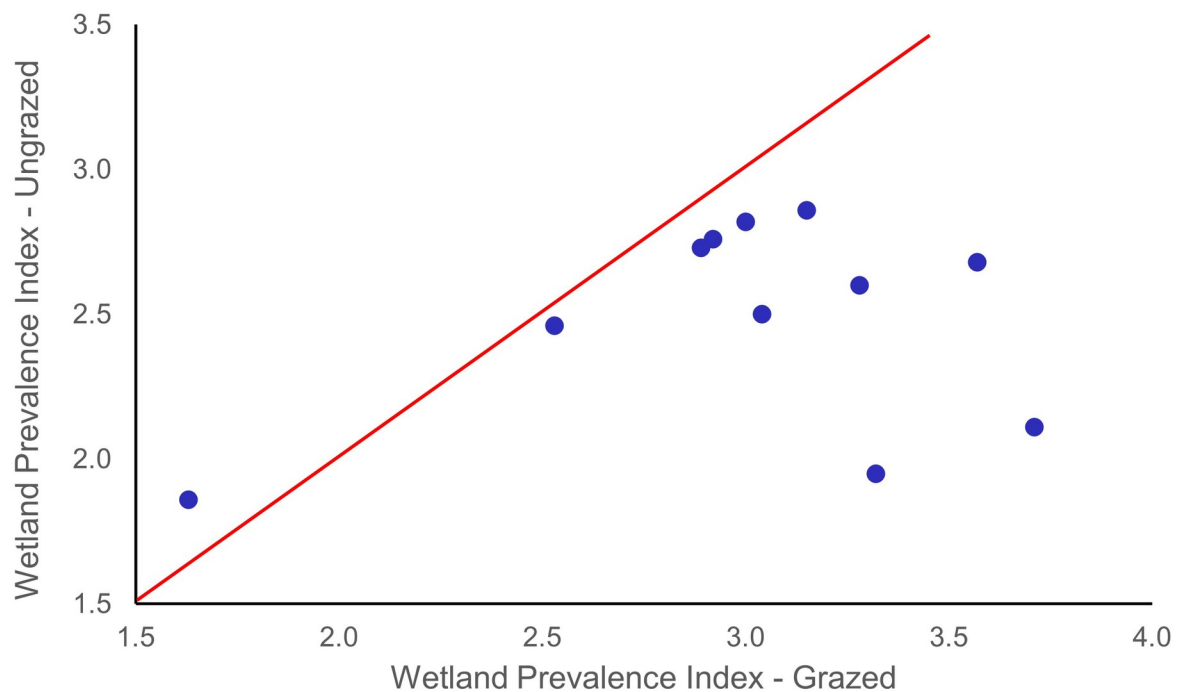


Fig 4. The relationship of the cover of an exotic grass, Kentucky bluegrass (*Poa pratensis*) adapted to herbivory, within 11 paired grazed and ungrazed riparian reaches in northeastern Oregon. If there was no difference in the abundance of this species between grazed and enclosed areas the data points would be expected to fall on or near the line. Data points below the line indicates a lower abundance of *P. pratensis* in ungrazed reaches compared to grazed reaches. The abundance of Kentucky bluegrass in was significantly less ($p = 0.03$) in ungrazed areas.

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Table 4. Shrub and tree cover (%) along the streambank (greenline) of 11 selected paired enclosed (Excl) and grazed (Graz) stream study reaches in northeastern Oregon.

Species	Wetland Indicator status	Bear		Camas		Chesinnmus		Devils		Lower Swamp		Upper Swamp		MF John Day		Murderers		Summit		Tex		Camp		
		Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	
<i>Acer glabrum</i> Torr.	FAC						0.3																	
<i>Alnus incana</i> (L.) Moench ssp. <i>tenuifolia</i> (Nutt.) Breitung	FACW	3.0	3.2	0.0	0.1	2.2	4.6	12.2	1.0	29.0	62.9	29.9	20.3				9.4	0.6	19.5	2.2	72.6	40.9	54.8	18.4
<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roemer	FACU									0.0	1.3													
<i>Artemisia tridentata</i> Nutt. ssp. <i>vaseyana</i> (Rydb.) Beetle	UPL																	0.0	1.3					
<i>Cornus sericea</i> L.	FACW					0.0	2.9	0.3	0.0					0.0	0.3						2.7	1.4	0.0	0.3
<i>Crataegus douglasii</i> Lindl.	FAC					7.6	16.4			0.0	0.9	0.2	0.0											
<i>Juniperus occidentalis</i> Hook.	UPL																					0.3		
<i>Larix occidentalis</i> Nutt.	FACU					0.0	0.4																3.0	3.6
<i>Pinus contorta</i> Dougl. ex Loud.	FAC	8.8	8.9	0.8	1.3			2.1	0.0	0.8	2.2						0.0	5.3	1.4	0.0	0.0	0.0	6.8	3.3
<i>Picea engelmannii</i> Parry ex Engelm.	FAC								1.1			0.00	4.00											
<i>Pinus ponderosa</i> P. & C. Lawson	FACU					1.9	0.0	2.0	0.0	0.0	1.1										0.5	3.7		
<i>Populus trichocarpa</i> Torr. & A. Gray	FAC					4.8	0.0																	
<i>Populus tremuloides</i> Michx.	FAC							0.8	0.0															
<i>Pseudotsuga menziesii</i> (Mirbel) Franco	UPL					0.0	23.7	0.0	1.1												1.7	0.0		
<i>Ribes aureum</i> Pursh	FAC											0.0	0.5											
<i>Ribes cereum</i> Dougl.	FACU					0.0	1.8					0.00	0.8										1.6	0.1
<i>Ribes hudsonianum</i> Richards.	OBL					1.3	4.1	6.5	0.0												20.6	13.6	6.4	2.7
<i>Ribes lacustre</i> (Pers.) Poir.	FAC					0.00	2.18	3.7	0.00			0.4	0.0									1.0	1.8	
<i>Rosa woodsii</i> Lindl.	FACU					1.3	0.6	0.1	0.0	0.0	1.4	0.0	1.4									0.4	0.7	
<i>Salix</i> spp (English willow)	FACW					20.8	0.0																	
<i>Salix bebbiana</i> Sarg.	FACW							0.9	0.0															
<i>Salix boothii</i> Dorn	OBL			2.3	0.0												0.7	1.0	0.0				0.0	0.3
<i>Salix exigua</i> Nutt. var. <i>exigua</i>	OBL					2.7	0.0												0.8	0.5	0.0		0.0	0.3
<i>Salix geyeriana</i> Anderss.	FACW	0.0	0.1	0.0	1.2									0.0	1.1	0.5	0.0	0.0	0.6	0.0	0.0	0.7		
<i>Salix lasianдра</i> Benth. var. <i>caudata</i> (Nutt.) Sudw.	FACW	0.2	0.3	0.0	2.5	0.7	0.0	0.0	0.9					0.7	0.2	1.0	0.0	0.3	0.1	2.1	1.9	0.4		

(Continued)

Table 4. (Continued)

Species	Wetland Indicator status	Bear		Camas		Chesnimmus		Devils		Lower Swamp		Upper Swamp		MF John Day		Murderers		Summit		Tex		Camp	
		Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz	Excl	Graz
<i>Symphoricarpos albus</i> (L.) Blake	FACU					0.0	0.5	4.8	0.0	0.8	4.8	0.6	0.9							4.9	8.8	0.0	4.0
Total shrub cover (%)		11.9	12.4	3.1	5.1	43.0	57.1	33.9	4.0	30.6	74.6	31.6	27.9	0.7	1.6	11.7	1.6	25.9	6.2	129.2	74.1	73.6	34.6
Riparian obligate cover (%)		3.2	3.6	2.3	3.8	32.2	11.6	19.9	1.9	29.0	62.9	29.9	20.3	0.7	1.6	11.7	1.6	20.6	3.5	103.2	59.6	61.5	21.8
shrub spp richness		3.0	4.0	2.0	4.0	9.0	11.0	10.0	4.0	3.0	7.0	4.0	6.0	1.0	3.0	4.0	2.0	4.0	6.0	7.0	13.0	7.0	9.0

The wetland Indicator status breaks down species in the following categories: Obligate-wetland (OBL), facultative-wetland (FACW), facultative (FAC), facultative upland (FACU) and obligate-wetland (UPL). The p values are statistical results testing for differences between all exclosed and grazed sites combined.

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present in 10 of the 11 sites. A total of 6 willow species (*Salix* spp.) were encountered in the study but never in great abundance. Overall, we encountered 28 shrub and tree species in the study with *Salix* spp. being present at all sites.

Total shrub cover was higher in ungrazed reaches for six of the 11 study sites ($p = 0.11$); riparian-obligate shrub cover was greater in ungrazed reaches for seven of the 11 study sites ($p = 0.06$). Cover differences can be largely explained by the age of the enclosure. Of the four study streams where cover was equal or less in ungrazed compared to grazed areas, 3 of them were less than 5 years old. For enclosures >5 years in age, riparian-obligate shrub cover was significantly greater ($p = 0.05$) in enclosures (39%) compared to grazed reaches (24%). The greatest differences in shrub cover were in the oldest 4 enclosures (>20 years). For example, woody vegetation cover at Summit creek (22 years) was 26% and 6% in ungrazed and grazed reaches, respectively, while woody vegetation cover at Camp creek (36 years) was 74 and 35%, respectively (Table 4). This finding indicates that 20 years or more of livestock exclusion may be required to allow significant recovery of woody vegetation. The benefits, ecosystem services, and values of the stream reaches excluded from livestock increase through time and may not be fully realized until decades after exclusion.

Discussion

Ecological restoration of riparian habitats is defined as the reestablishment of pre-disturbance riparian functions and related chemical, biological, and hydrological characteristics [33]. However, irreversible human impacts (e.g., soil loss, biotic invasions, air pollution), may preclude our capability to precisely re-create ecosystem structure and functions that previously existed. Thus, the goal of restoration projects is to ensure that the dynamics of natural ecosystem processes are again operating efficiently so that both ecosystem structure and functions can be recovered [33,34].

Passive restoration is defined as the halting of those activities that are causing degradation or preventing recovery [24]. Reviews of many in-stream restoration and enhancement projects throughout the western U.S. clearly reveal that passive restoration, especially the cessation of livestock grazing was the critical first step in successful riparian restoration programs [17,18,20,21,35]. The apparent resilience of riparian vegetation composition reflected in the significant increases in wetland-obligates and species diversity coupled with declines in exotic species and decreases in bare ground exemplifies the positive outcome of this passive restoration approach.

Cattle grazing appears to have maintained the presence of some exotic dominants at the exclusion of native species in most study reaches. In the absence of grazing, native graminoids and dicots increased in abundance while there was a concomitant decline in the exotic Kentucky bluegrass and Dutch clover (*Trifolium repens*). Kentucky bluegrass is a grazing-tolerant nonnative species that has invaded rangelands in the United States [36] and is currently a dominant in many riparian zones across the western USA. Kentucky bluegrass may reduce the genetic diversity of other species through habitat fragmentation as well as ecosystem species diversity and, therefore, resilience during future environmental stress events [36]. The prevalence of Kentucky bluegrass may partially explain the lower species richness and diversity in the grazed riparian reaches. We found that there was a decline in Kentucky bluegrass dominance in the ungrazed reaches (Fig 4) with a concomitant increase in species richness and diversity (Table 3). Schulz and Leininger [37] also found a decrease in Kentucky bluegrass in ungrazed riparian zones compared to grazed sites.

Willows, thin leaf alder, and black cottonwood (*Populus trichocarpa*) are important features of western riparian ecosystems and have multiple functional roles that influence biological

diversity, water quality/quantity, and aquatic/terrestrial food webs and habitat. While shrub response was most apparent in this study with long term absence of grazing (>10 years), the rapid inherent resilience of these species has been quantified. For example, after two years in the absence of livestock on Meadow creek, northeastern Oregon, significant increases in height, crown area, crown volume, stem diameter, and biomass were measured for willows, black cottonwood, and thin-leaf alder [22]. In addition, Brookshire et al. [23] reported that even relatively light levels of domestic livestock grazing, when coupled with wild ungulate browsing in riparian zones diminished both plant structure and reproduction of riparian willows. While we found recovery of riparian-obligate shrubs with only the removal of domestic cattle, Averett et al. [38] reported even in the absence of domestic livestock, high densities of wild ungulates (especially elk) suppressed deciduous riparian woody plant establishment and survival.

Regardless of the differences in the manner and intensity in which livestock were grazed in the 11 sampled stream reaches, we found increases in wetland species and decreases in exotic species in the ungrazed reaches. This is similar to conclusions of a review by Elmore and Kauffman [12] that reported livestock exclusion was the most effective approach to restoring riparian ecosystems.

We hypothesized wetland-obligate and facultative-wetland species would increase in abundance in sites protected from grazing (exclosures). We found a significant 24% shift in the wetlands species prevalence index (WPI) towards wetland species in ungrazed sites (Table 3). The trends in compositional change between grazed and ungrazed reaches were similar regardless of individual grazing approaches and levels of utilization at each site. Comparing intact and degraded stream reaches in Northeastern Oregon, Toledo and Kauffman [39] reported a 29% shift in WPI (1.82 to 2.45) with a loss in wetland-obligate species and a concomitant shift to species more adapted to drier environments in degraded sites. Coles-Ritchie et al. [20] also reported a statistically significant shift in wetlands species abundance in exclosed compared to grazed riparian reaches in western riparian zones. Differences in the WPI would suggest that livestock activities have altered the vegetation as well as those environmental and edaphic conditions that determine which species occupy a site.

The shifts in composition due to exclusion may also be reflective of physical changes in soil properties associated with cessation of grazing. Kauffman et al. [19] found that soil bulk density was significantly lower, and soil pore space and soil organic matter was higher in exclosed, compared to meadows. The mean infiltration rate for exclosed dry meadows was 13-fold greater than in grazed dry meadows (142 vs. 11 cm/h, respectively), and for wet meadows the mean infiltration rate in exclosures was 2.3 times greater than in grazed sites (80 vs. 24 cm/h, respectively). Livestock removal was found to result in significant changes in soil, hydrological, and vegetation properties that, at landscape scales, would likely have great effects on stream channel morphology, water quality, and the aquatic biota. For example, Kauffman et al. [19] estimated that under saturated conditions, a hectare of wet meadows with the pore space measured in the exclosed wet-meadow communities would contain 121,000 L/ha (121 Mg/ha) more water in only the surface 10 cm of soil than those in the grazed wet-meadow communities.

The composition of vegetation in the ungrazed riparian areas suggest a number of synergistic effects occur when livestock are excluded. In addition to vegetation composition shifts, Kauffman et al. [19] reported that total belowground biomass (TBGB), consisting of roots and rhizomes in dry meadows dominated by Kentucky Bluegrass was over 50% greater in exclosures (1105 and 652 g/m² in the exclosed and grazed sites, respectively). In exclosed wet meadows dominated by sedges, the TBGB was 62% greater in ungrazed compared to grazed sites (2857 and 1761 g/m², respectively). However, the Kauffman et al. [19] study may be

underestimating true shifts in below ground biomass associated with livestock exclusion. As we found shifts in composition from facultative species (Kentucky bluegrass) to wetland-obligate species (sedges), relevant comparisons may be that of the root mass in grazed dry meadows to that of enclosed wet meadows (i.e., a potential increase in root mass of 156% associated with exclusion).

The source of much of the energy, carbon, and nutrients of headwater streams originates from streamside vegetation [40] and both riparian meadows and forested reaches represent an important source of allochthonous materials for aquatic systems [41]. During peak flows when streamside communities are inundated, plant materials from meadow-dominated reaches become a source of organic C and nutrients to the stream. Ungrazed sites likely have high levels of organic inputs into aquatic systems for at least four reasons: (1) there is no removal of streamside vegetation via herbivory thus aboveground biomass is relatively high; (2) there is an increase in species of higher productivity (e.g., sedges compared to Kentucky bluegrass); (3) there are dramatic increases in root mass [19]; and (4) there is an increase in shrub and tree canopy with a concomitant increase in litterfall [23,41]. Increases in species richness and diversity also suggest there is likely an increase in the timing and composition of allochthonous inputs.

Shifts in ecosystem structure associated with livestock exclusion are not necessarily limited to vegetation or surface soils. Vegetation response to the exclusion of livestock by fencing (e.g., increased vegetation cover and structure, as well as reduced bare ground) are important factors associated with channel morphology. For example, Magilligan and McDowell [5] reported that livestock exclusion resulted in significant stream channel adjustments such that channels in ungrazed reaches were narrower, deeper, and had more pool area than the channels in grazed reaches. The vegetation composition within enclosures, as measured in this study, suggests an increased connectivity of riparian vegetation with their associated aquatic system.

While livestock exclusion was associated with a significant increase in sedges, broadleaved herbs, species richness, diversity, and the wetlands species prevalence, there was not a strong relationship with time since exclusion. These data suggest that some sites respond more quickly than others, which is consistent with the concept of variable recovery trajectories after livestock exclusion [25,34].

Differences in species composition between grazed and ungrazed riparian reaches may reflect the cumulative effects of cattle grazing on species that are less adapted to herbivory (e.g., willows, cottonwoods, and other keystone vegetation species) coupled with soil trampling that lowers infiltration rates and water-holding capacities of riparian soils. Channel degradation associated with bank trampling [5] and the concomitant loss of root mass associated with herbivory [19,39] further results in drier conditions, and thus shifts in vegetation composition toward species adapted to drier environments (Fig 4). This suggests that cumulative livestock impacts exacerbate the increases in temperatures and changing hydrological dynamics associated with climate change that are resulting in drier conditions [42]. Dwire et al. [43] also reported that the functionality of many riparian areas had been compromised by water diversions and livestock grazing, which reduced their resilience to additional stresses that a warmer climate would bring. Removal of grazing began to reverse these effects, suggesting that cessation of livestock utilization of riparian zones is a viable approach to climate change adaptation for these important ecosystems.

Supporting information

S1 Fig. Paired photos of selected ungrazed (enclosed) and grazed reaches. The ungrazed reaches on the left and the grazed reaches are on the right.
(DOCX)

S1 Table. Indicator categories, probability ranges, and indicator index values for species occurrence in wetlands (Wentworth et al. 1988 [29]).

(DOCX)

S2 Table. Plant species encountered in the 11 study reaches. The scientific name is followed by the Alpha code used.

(DOCX)

S3 Table. Plant species cover (%) the 11 study reaches. Numbers are the mean and standard error based upon their cover in at least 20 2 X 5 m plots for each study reach.

(DOCX)

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