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Shrub Encroachment Following Wetland Creation in Mixedgrass Prairie Alters Grassland Vegetation and Soil

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Abstract

Wetland decline under post-European settlement and land use change across western Canada has led to mitigation strategies, including wetland creation. Created wetlands can trigger environmental change, including woody species encroachment, in turn altering vegetation and soil. We quantify changes in shrub abundance from prior to wetland creation (1949) until 60 years later (2012) within a Mixedgrass ecosystem of the Verger watershed in Alberta, Canada. In addition, we compare remaining grassland with areas colonized by shrubland on similar ecosites for differences in (1) plant composition, including native and introduced flora, (2) herbage yield and forage accessibility for livestock, and (3) soil properties (surface organic depth, bulk density, mineral nitrogen (N), and carbon (C) concentration). Repeat photos show *Shepherdia argentea* shrublands increased from 0 to 88 ha (to 1.15% of study area) following wetland creation, with the greatest increase in the last 20 years. Relative to grasslands, shrublands had lower total plant diversity but greater presence of introduced plant species. Shrub patches were 94% lower in herbaceous production, with 77% of shrublands non-utilized by cattle, collectively leading to reduced grazing capacity. Relative to grasslands, shrublands had a thicker soil surface mulch layer, and where cattle were present, had increased mineral soil N and C. Overall, shrub encroachment following wetland creation has markedly altered vegetation and soils in this once grassland landscape, with negative impacts on native plant diversity, herbage production and forage accessibility, and has implications for the management of shrub encroachment.

Keywords Carbon · Forage accessibility · Herbage production · Native plant diversity · Species invasion · Soil nitrogen

Introduction

Encroachment of woody species into grasslands is a worldwide phenomenon (Archer et al. 1995; Ratajczak et al. 2012) and was described in detail for North American semi-arid regions by Van Auken (2000). Changes from grassland to shrubland include progression from initial colonization, through suppression of the understory, and eventually transition to near monocultures of shrubs (D'Odorico et al. 2012). Several mechanisms have been implicated as causing encroachment, including climatic alteration (MacDonald 1989), changes in atmospheric CO_2 (Tjetjen et al. 2010), industrial nitrogen (N) deposition (Köchy and Wilson 2001), fire suppression (Van Auken 2000), over-grazing by livestock (Van de Koppel et al. 2002), and even small mammal impacts (Bestelmeyer et al. 2007). Both livestock (Fredrickson et al. 2006) and wildlife (Kramp et al. 1998) can facilitate woody species spread by consuming and transporting shrub seeds, and can markedly impact trajectories of vegetation succession (Connell and Slayter 1977).

As water limitations are a primary limiting factor for growth in semi-arid grasslands (Willms and Jefferson 1993), increases in water availability can contribute to woody encroachment (Darrouzet-Nardi et al. 2006). In select regions of the northern plains, wetland creation has been undertaken to mitigate habitat loss and aid recovering populations of several waterfowl species (Asamoah et al. 2011). These wetlands are created using water diverted from major rivers under agreements between private land owners and conservation organizations, or are the result of overflow (i.e., runoff) water that otherwise remains unused.

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Long-term effects of these wetlands on vegetation dynamics are complex (Asamoah 2008), though little is known about their impact on woody species. Where encroachment has occurred, shrub presence can alter light, water, and nutrient availability for the understory (Archer 1995; Köchy and Wilson 2000), which are key resources for grassland vegetation (Chapin 1980). Moreover, as disturbances, such as grazing and fire maintain grasslands (Collins et al. 1998), changes in the intensity and frequency of disturbance may further alter woody plant cover (Ratajczak et al. 2011; Riginos and Grace 2008).

Grasslands are increasingly being recognized for their importance in providing a wide range of ecological goods and services (EG&S) (Allred et al. 2015; Bengtsson et al. 2019). However, the contrasting impacts of encroachment on EG&S in northern temperate semi-arid grasslands remain poorly understood, including changes in forage production and quality, floral diversity, and grassland carbon (C) storage. Bai et al. (2009) determined that areas colonized by the shrub western snowberry (*Symphoricarpos occidentalis*) did not alter soil organic matter relative to intact native grassland within the Canadian prairies, despite having greater aboveground shoot mass and a large root mass. Other investigations have found shrub encroachment can increase soil C relative to grasslands (Lett et al. 2004). The most common symptom of encroachment is a decline in herb biomass (Köchy and Wilson 2000; Bork and Burkinshaw 2009) that can reduce grazing capacity for livestock (Dye et al. 1995; Burkinshaw and Bork 2009). Additional impacts include reduced plant diversity (Bork and Burkinshaw 2009), though the opposite has also been found (Ratajczak et al. 2012).

Shepherdia argentea (thorny buffaloberry) is a shrub or small tree (2–5 m high) native to western North America that is found in the Canadian prairie and parkland regions. Belonging to the Oleaster family (*Elaeagnaceae*), this shrub is many-branched, has stems up to 10 cm in diameter, and can grow to 60 years in age (Looman 1984). Hansen and Hoffman (1988) described *Shepherdia argentea* as forming dense, nearly impenetrable thickets. Belowground, *Shepherdia argentea* has a taproot, with several rootstocks branching off the crown in the top 15 cm of soil, and is a symbiotic N-fixer (Looman 1984). In North Dakota *Shepherdia argentea* was described as a pioneer species invading grasslands (Hladek 1971). Hansen and Hoffman (1988) characterized non-disturbed *Shepherdia argentea* shrublands in Montana as either having an understory of Kentucky bluegrass (*Poa pratensis*) and Pennsylvania pellitory (*Parietaria pennsylvanica)*, or forming dense thickets with western snowberry.

Dittberner and Olson (1983) considered *Shepherdia argentea* as poor forage for cattle, presumably due to a high alkaloid content (Ayer and Browne 1970) and abundance of thorns (Looman 1984), even though nutritionally the protein content of *Shepherdia argentea* is sufficient to maintain cattle during summer (Erickson et al. 1981). In Montana, *Shepherdia argentea* provided cover for livestock and wildlife (Hansen and Hoffman 1988). *Sheperdia argentea* is browsing tolerant (Looman 1984) and relatively unpalatable to livestock, with several studies indicating this species can increase with moderate grazing (Klebenow and Oakleaf 1984).

Here we document the historical expansion of *Sheperdia argentea* following the creation of wetlands undertaken in the mid 1900s intended to increase waterfowl habitat in the Mixedgrass Prairie. In addition, we assess the impact of this invasion on several vegetation and soil metrics. Specific objectives were: (1) to quantify the progressive changes in shrub extent over a 63-year period following wetland development, (2) characterize the impact of shrub presence on herbage production, understory plant diversity and composition, as well as on topsoil characteristics, and (3) determine the impacts of shrub encroachment on associated opportunities for livestock grazing.

Materials and Methods

Study Area

We evaluated the abundance and impact of encroachment by *Shepherdia argentea* on the University of Alberta Mattheis Research Ranch (MRR), situated in the Dry Mixedgrass Prairie of SE Alberta, Canada (50°53’ N; 111°57’ W). The MRR is ~5100 ha in size, and comprised largely of non-cultivated grasslands with interspersed wetlands. The climate is strongly continental, with long, cold winters and short, warm summers. The area has a mean temperature of 4.2 °C and received an average of 348 mm of precipitation annually over the prior 30 years, with 77% falling during the growing season (April—September, inclusive). During 2014 when field sampling occurred, April through August rainfall was 218 mm, 3% above the long-term norm. Soils vary from Orthic Brown Chernozems on level loamy plains, to Rego Brown Chernozems on rolling sand dunes.

Beginning in 1949, Ducks Unlimited Canada (DUC) constructed wetlands on the western part of the ranch as part of the Verger wetland project, which now occupy nearly 400 ha of the MRR. These wetlands are inundated with water each summer starting in May from an ephemeral creek that carries runoff water from irrigated fields upstream. Water is distributed throughout the growing season using natural channels and constructed canals. Created wetlands are jointly managed by DUC and the MRR under formal agreement to provide habitat for wildlife. Up to 725 cow-calf pairs graze for up to 10 months annually in a rotational grazing system on the MRR, with two primary herds using 10 or more paddocks each. Each pasture is subject to one or two grazing periods of about 10 days per paddock, with pastures containing abundant wetlands typically receiving two grazing periods. In 2012 the average stocking rate of cattle was 0.67 AUM per hectare, where an AUM (animal unit month) is the amount of feed needed to support a 454-kg cow, with or without a calf, for 1 month.

Native grasslands that are unaffected by water addition are comprised of a mix of native grasses such as needle-and-thread grass (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), junegrass (*Koeleria macrantha*), blue grama grass (*Bouteloua gracilis*) and sandgrass (*Calamovilfa longifolia*). Wetland creation is known to have increased the abundance of introduced plant species, including those of agronomic and weedy origin (Asamoah 2008). *Sheperdia argentea* has become increasingly common near created wetlands.

Landscape Assessment

Historical aerial photos were obtained for the MRR for the years 1949, 1970, 1991, and 2012, to quantify *Shepherdia argentea* shrublands. Photos ranged from 1:30,000 to 1:40,000 in scale, and were in black and white for all years except the final date. As photos did not cover the entire study area at all dates, only the area encompassed by all imagery was used. The resulting area covered 4279 ha, or 86% of the MRR. Photos were georectified using ARCMAP GIS 10.1 and the ESRI online resource basemap in the coordinate system NAD 1983. For the 2012 photos, 13 control points per image were used for rectification, reducing mapping error to less than 5 m. Georectification of older images was more complex due to limited visible landmarks. As a result, the 2012 images were used as a base-map for previous years to facilitate georectification. Photos from the 2012 image were cut with the Analysis tool Extract by Mask, and merged with the data management tool Mosaic to New Raster. Resulting pixels were the same as the input pixels, as were the cell sizes and color settings. For the Mosaic operator, the blend function was used (ESRI 2014). Using the 2012 mosaic as a base-map, eight control points were established on each earlier photo. To minimize errors during rectification, control points were distributed over all images while avoiding edges and areas with large differences in elevation, which were rare. Final images from 1991, 1970, and 1949, derived from cutting and merging photos, led to first order root mean square error values of <10, 11, and 15 m, respectively.

After georectification and image merging, a polygon shapefile layer was created to map *Shepherdia argentea* for each year by manually tracing each visible shrub patch. After creation of a shapefile for each year, the total area of shrub polygons was calculated. In addition, the mean size of shrub patches was calculated.

Field Sampling

A sample of 30 patches of *Shepherdia argentea* was selected for field assessment in 2014. A stratified random approach during selection ensured accessibility of patches as well as representative distribution. Sampling was further stratified within each location to compare open grassland (i.e., areas lacking shrubs) together with a paired shrub patch as subplots, separated by 15 m. Patches were selected only if subplots were on similar ecosites (i.e., the same slope, aspect, elevation, drainage). Each of the 30 shrub-dominated subplots was further assessed for evidence of cattle disturbance (i.e., recent defoliation, tracks, dung deposition), with evidence of grazing found in 19 subplots. For these 19 subplots, shrubland sampling was further divided into sub-subplots of cattle disturbed and non-disturbed areas, and allowed for the differentiation of shrub presence alone from the additive effect of cattle on shrublands.

Data were collected in each resulting plant community ($N = 76$ total) between July 15 and August 30, 2014. Within each sub-subplot, foliar cover of all herbaceous plant species (nearest 1%) was assessed in 1 m^2 quadrats, along with litter abundance and exposed mineral soil. Foliar shrub cover was assessed for all subplots within shrub patches, and stem density counted. Following composition assessment, herbage was harvested at 2-cm height, separated into grasses and forbs, and dried at 55 °C to obtain dry matter values.

Within each subplot, two randomly located soil cores (3.18-cm diameter) were extracted using a JMC Backsaver plunge soil corer (JMC Soil Samplers, Newton, IA, USA). The depth of the overlying surface organic mulch layer was measured at removal (cm), and the top 10 cm of mineral soil retained. Duplicate cores were combined per subplot, dried at 55 °C and weighed, and later passed through a 1.7-mm sieve to remove roots and rocks.

Finally, for each shrub patch, the relative area (%) comprised of high stem density conditions (≥ 3 stems m^{-2}) was estimated within the patch. Estimations were made on each patch to interpret cattle use, including the spatial proportion (%) of the patch with evidence of cattle disturbance. In addition, the accessibility of the shrub patch for cattle was classified from 1 to 10, with 1 being highly inaccessible and 10 being highly accessible.

Soil Assessment

Soil samples were assessed for bulk density (g cm^{-3}) using dried weights and known soil volumes. Soil mineral organic matter was determined using loss-on-ignition by heating a pre-weighed glass vial with a known amount of soil to 360 °C for 2 h, and reweighing after ignition at a standardized temperature. Separate soil samples were ground to 0.1 mm size in a MM200 Retsch Ball Mill (Verder Scientific, Haan, GE), and 0.3 g subsamples analyzed for N and C concentration with a Leco Truspec® CN Auto-Analyzer (LECO, St. Joseph, Illinois, USA). To assess pH, 40 g of soil was combined with 80 ml of deionized water and the 1:2 slurry shaken for 30 min before being assessed with a Model 710 Thermo Orion pH meter (Cole-Parmer Canada, Montreal, QC, Canada). After samples settled overnight, the soil-water solution was pipetted and filtered through Q5 Fisherbrand filter paper, and electrical conductivity (EC) measured on the filtrate with an AP75 Fisher Scientific Accumet™ Portable Conductivity/TDS Meter (Thermo Fisher Scientific, Vantaa, Finland); data were converted to dS m^{-1} for analysis.

Data Analysis

To determine temporal changes in shrub abundance we compared the landscape area containing shrubland among successive sampling years. Shrub patch metrics were characterized using descriptive statistics. For each subplot (and sub-subplot where present), herb richness was determined for all plant species, as well as by individual growth forms (shrubs, forbs, and grasses). In addition, species were stratified based on whether they were of native origin (endemic), or introduced, based on the USDA Plants Database (https://plants.sc.egov.usda.gov/java/). Shannon's diversity was determined for all species, as well as for introduced species using the formula: $H' = -[\Sigma(\text{all species})_{pi} \times (\ln p_i)]$, where pi is the proportion of total cover comprised of species 'i', and ln is the natural log of $_{pi}$ (Kent and Coker 1992).

To evaluate shrub impacts on understory vegetation (plant richness, diversity, and herbage biomass) and soil characteristics (mulch depth, and mineral pH, OM, EC, C, and N), we first conducted a one-way mixed model analysis of variance using SAS software v.9.3 (SAS 9.3 Users Guide 2012) to compare shrubland attributes with those in adjacent grasslands on the same ecosites, with site as the random factor. Next, we compared shrub patches with and without evidence of cattle presence

($n = 19$ paired sub-subplots) to assess localized cattle impacts. All data were checked for normality using a Shapiro–Wilks test ($P < 0.05$), and a Levene's test conducted to assess equality of variances. Relationships between soil and vegetation variables were evaluated using linear regressions run in SAS software. Unless otherwise noted, significance was set at $P < 0.05$ for all analyses.

Herb cover of all species from each subplot was assessed using multivariate techniques with PC-ORD v.5 (McCune and Grace 2002). A Multi-Response Permutation Procedure (MRPP) was used to test for treatment differences between the grassland plots ($n = 30$), shrublands with no cattle disturbance ($n = 30$), and shrublands with cattle disturbance ($n = 19$), using a Sorensen distance metric. A Nonmetric Multi-Dimensional Scaling (NMDS) ordination was performed on vegetation composition data using a Sorensen distance metric. Ordinations condense complex vegetation data from multiple locations into simplified-dimensional space by seeking underlying structure in the data. The final analysis used 50 runs with real data and 249 with randomized data.

Last, regressions were done between herb mass and shrub cover, separately for each of the shrubland areas with and without evidence of cattle presence, to assess how the understory directly varied with overstory conditions ($P < 0.05$). Pearson correlations were also conducted to explore relationships between select soil and vegetation metrics.

Results

Shrubland Extent and Patch Properties

Mapped shrubland initially increased from 4.8 ha in 1949, comprising only 0.1% of the study area, to 18.5 ha in 1970, representing an annual increase of 0.7 ha. Shrub expansion continued at the same rate through 1991 (total of 32.7 ha), but then expanded more rapidly at 2.1 hectare per year through 2012 (to 77 ha). By 2012, 1.8% of the MRR was occupied by *Sheperdia argentea* (Fig. 1). Shrub increases were particularly evident early on in the western portion of the study area adjacent to wetlands first created in 1952. Larger increases on the eastern portion of the property were not evident until 1970 (Fig. 1).

Average shrub patch size in 2012 was 0.07 ha (706 m^2), with a range of 0.01–0.5 ha. Mean patch size also increased from 1949 (145 m^2) to 1991 (370 m^2). Mean shrub canopy cover within patches was 55% during the 2014 field assessment, but ranged from 10 to 90%. Shrub canopy cover was also lower ($P < 0.001$) in areas with evidence of cattle presence (+cattle = 46.1 ± 3.2% vs. −cattle = 68.7 ± 3.2%).

Plant Community Responses

A total of 101 different plant species were found during sampling, including 66 forbs, 24 grasses, and 11 shrubs, of which 15% were ruderals (annuals and biennials). Across all species, 75 were of native origin and 26 were introduced (i.e., non-endemic). Total richness in shrublands was 31% lower ($P < 0.001$) than in neighboring grasslands, primarily due to a reduction in native species (grassland = 7.5 vs. shrubland = 4.0 species m^{-2}; $P < 0.001$), rather than those of introduced origin (grassland = 3.4 vs. shrubland = 3.5 species m^{-2}; $P =$

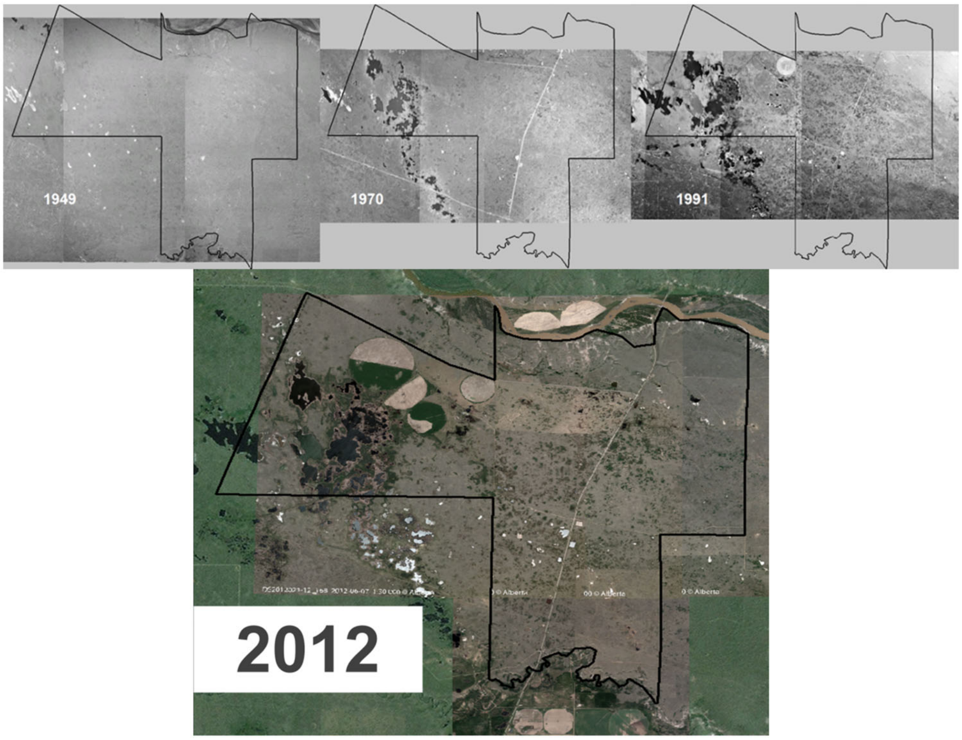

Fig. 1 Resulting aerial photo collages of the MRR between 1949 and 1991 (top) following wetland creation in a region of the Dry Mixedgrass Prairie in SE Alberta, Canada, and again in the final year of sampling of 2012 (bottom). The study area boundary is depicted by the bold line

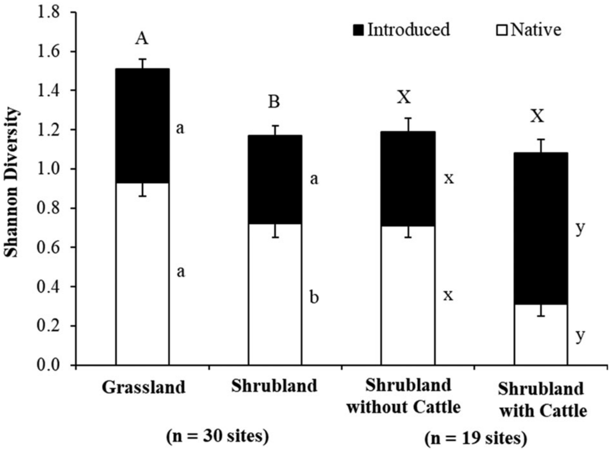

Fig. 2 Comparison of mean Shannon's diversity (±1 SE) between grassland and shrubland areas (left columns), as well as shrub areas with and without cattle presence (right columns), further partitioned by the contribution of native and introduced plant species. Differences in total diversity within each pair are denoted by uppercase letters, while lower case letters distinguish differences between treatment areas within a diversity component, all at $P < 0.05$. Data collected in 2014 from 79 locations at the Mattheis Research Ranch in SE Alberta, Canada

0.78). Within shrublands, presence of cattle grazing did not alter total richness ($P = 0.75$), nor the contribution of native ($P = 0.09$) and introduced species ($P = 0.28$) to richness. Among growth forms, shrublands were lower in both grass richness (grassland = 4.3 vs. shrubland = 1.1 species m^{-2}; $P < 0.05$) and forb richness (grassland = 6.1 vs. shrubland = 4.5 species m^{-2}; $P < 0.05$), which was only partly offset by a modest increase in shrub richness (grassland = 0.5, vs shrubland = 1.8 species m^{-2}; $P < 0.05$).

Shannon's diversity, which incorporates richness and evenness, remained lower ($P < 0.01$) in shrublands compared to grasslands, a response attributed to reduced diversity of native vegetation ($P < 0.001$) rather than introduced vegetation ($P = 0.07$) (Fig. 2). While no difference in total diversity was evident within shrublands based on exposure to cattle ($P = 0.46$), areas impacted by cattle had 56% less native diversity ($P = 0.046$), which in turn, was offset by 60% greater diversity of introduced vegetation ($P = 0.01$) (Fig. 2).

Unlike richness and diversity, total native plant cover remained similar between grassland (47.2%) and shrubland (51.7%) habitats ($P = 0.54$). Introduced plant species had lower cover ($P < 0.001$) in shrublands lacking cattle grazing (15.3%) compared to adjacent grasslands (44.6%). Within shrublands, the presence of cattle led to a sharp reduction in native plant cover (−cattle = 47.5% vs. +cattle = 5.6%; $P < 0.001$), with a tendency for more introduced plant cover instead (−cattle = 18.1% vs. +cattle = 28.1%; $P = 0.09$). Across all shrublands sampled, the total cover of introduced species was unrelated to overstory shrub cover in areas unaffected by cattle ($R^2 = 0.007$; $P = 0.66$), but increased with declining overstory shrub cover in patches disturbed by cattle ($R^2 = 0.26$; $P = 0.02$) (Fig. 3).

A summary of the MRPP evaluating vegetation composition showed differences among all three treatments ($P < 0.001$), although the comparison of grassland and shrubland

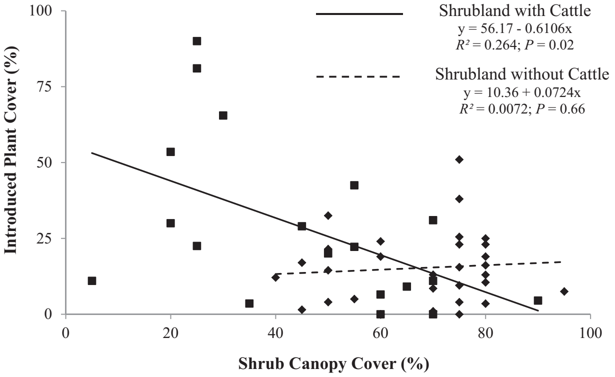

Fig. 3 Relationship between total introduced plant cover and shrub canopy cover of *Shepherdia argentea* within patches of shrubland either without evidence of cattle grazing (◆), or with evidence of cattle grazing (■). Data were collected in 2014 from 49 shrub patches at the Mattheis Research Ranch in SE Alberta, Canada

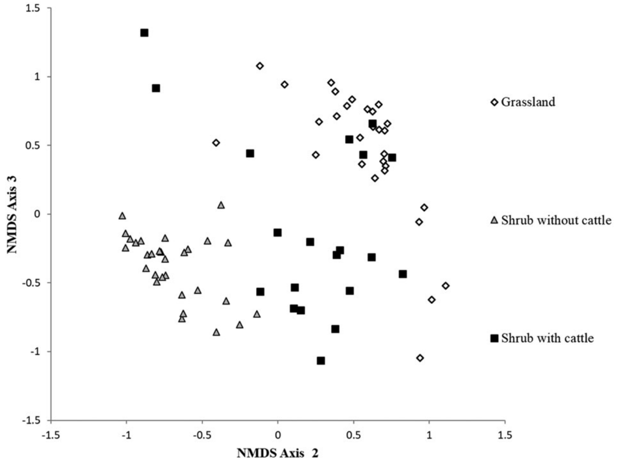

Fig. 4 Joint biplot of the NMDS ordination depicting vegetation composition responses in relation to the two axes accounting for most of the variation in composition. Data were collected in 2014 from 79 sampling quadrats at the Mattheis Research Ranch in the Dry Mixedgrass Prairie of SE Alberta

unoccupied by cattle exhibited the greatest homogeneity within groups ($A = 0.18$) and the strongest differences among treatments. Results of the NMDS ordination resulted in a final 3-dimensional solution with final stress of 16.6. The first three axes accounted for 13.8, 34.9, and 22.6% of variance in understory composition. Joint biplots revealed that grassland and non-disturbed shrubland subplots were each individually clustered but distinctly separated from one another, while shrubland sub-subplots grazed by cattle were positioned between the other treatments (Fig. 4). Shrublands, particularly those subject to grazing, were commonly associated with a decline in major native grasses and an increase in the cover of introduced plant species (Table 1).

Herbage Biomass and Livestock Use

Herb mass in grasslands averaged 326 g m^{-2}, the majority of which (74%) was graminoids (Fig. 5). Graminoids and forbs were both lower ($P < 0.001$) in shrublands, where total herb mass was only 19 g m^{-2}. Within shrublands, herb biomass was modestly elevated ($P = 0.078$) by cattle grazing (53 vs. 22 g m^{-2}), specifically due to an increase in grass biomass ($P = 0.03$) rather than forbs ($P = 0.27$), but remained far below that of open grasslands (Fig. 5). Regression of total herb mass against shrub cover revealed divergent responses depending on whether shrublands were occupied by cattle (Fig. 6). While no relationship was evident between herb biomass and shrub cover in areas without cattle ($R^2 = 0.02$; $P = 0.46$), shrubland with cattle use exhibited increased herb biomass as shrub cover declined ($R^2 = 0.25$; $P = 0.03$).

The median accessibility of shrub patches to cattle was 3 (1–10 scale of increasing accessibility). An average of 23% of each shrub patch had evidence of cattle occupation, though this ranged from 0% (no occupation) in 11 patches, to a maximum of 85%. Cattle were less likely to occupy shrublands with high shrub stem density ($P < 0.001$); on average, 70.5% of shrub patches without cattle presence were categorized as high stem density (≥3 stems m^{-2}), while only 0.4% of areas disturbed by cattle had high stem density.

Data on the area of shrubland in 2012 were combined with field data from 2014 on herbage mass differences among treatments to estimate shrub encroachment impacts on cattle carrying capacity. Shrub presence decreased carrying capacity by 280 AUMs. While most of this loss (264 AUMs) was due to declining herbage, another 15 AUMs were lost due to poor access to forage associated with cattle being unwilling or unable to enter shrub patches.

Soil Responses

Grasslands and adjacent shrublands differed only in the amount of exposed mineral soil and depth of the overlying mulch (organic) layer (Table 2); shrublands lacking cattle activity had 73% less mineral soil than grasslands, and a mulch layer that was 42% thicker. However, added presence of cattle in shrublands had further impacts on underlying soils. Cattle increased exposed mineral soil from 2 to 31.5% in shrublands ($P < 0.001$) and reduced mulch depth by 51% (−cattle = 2.56 cm vs. +cattle = 1.25 cm; $P = 0.004$). Cattle presence also increased soil bulk densities within shrublands (+cattle = 1.52 ± 0.03 g cm^{-3} vs. −cattle = 1.36 ± 0.03 g cm^{-3}; $P = 0.001$). Last, shrublands with cattle had 32% greater total soil N (+cattle = 0.25 ± 0.02% vs. −cattle = 0.19 ± 0.02%; $P = 0.05$).

Select soil conditions were strongly related to vegetation characteristics. Within grasslands, soil OM was positively

Table 1 Summary of those plant species and their abundance (% cover) with at least 1% mean cover in relation to at least one of the three habitats examined, including grasslands, shrublands without cattle, and shrublands with evidence of cattle use

Origin	Species	Common name	Grassland	Shrubland	
				−Cattle	+Cattle
Native	Arctium minus	Bishop's cap	0	0.9	2.0
	Artemisa frigida	Pasture sage	1.7	0	0
	Aster ericoides	Many-flowered aster	1.1	0	0.1
	Blitum capitatum	Strawberry blite	1.7	0	0
	Calamovilfa longifolia	Sandgrass	9.3	0	0
	Carex pensylvanica	Pensylvania sedge	3.9	0.8	0.3
	Carex praegracilis	Clustered field sedge	4.3	0	0
	Chenopodium fremontii	Fremont's goosefoot	0.1	0.3	2.0
	Elaeagnus commutata	Silverberry	2.2	0	0
	Glycyrrhiza lepidota	Wild licorice	5.4	0.2	0.1
	Hordeum jubatum	Foxtail barley	1.0	0.7	0.8
	Parietaria pensylvanica	Pellitory	0	2.0	0.1
	Pascopyrum smithii	Western wheatgrass	2.2	0	0.1
	Rosa arkansana	Prairie rose	1.1	0.3	0
	Rosa woodsii	Wood's rose	0	2.8	0
	Shepherdia argentea*	Thorny buffaloberry	0	37.1	0.1
	Symphoricarpos occidentalis	Western snowberry	0.3	5.6	0.4
	Utica dioica	Common nettle	0	1.2	0.9
Introduced	Agropyron cristatum	Crested wheatgrass	1.4	0.2	0.4
	Astragalus cicer	Cicer milkvetch	1.4	0.3	0.3
	Axyris amaranthoides	Russian pigweed	0.4	2.0	5.1
	Bromus inermis	Smooth brome	0	1.2	0
	Cirsium arvense	Canada thistle	1.7	0.6	0.6
	Lappula squarrosa	Bluebur	0	2.7	1.8
	Medicago sativa	Alfalfa	1.0	0	0
	Melilotus alba	White sweet clover	3.3	0.1	0.4
	Melilotus officinalis	Yellow sweet clover	1.5	0	0.3
	Plantago major	Common plantain	0	3.2	1.8
	Poa pratensis	Kentucky bluegrass	27.4	1.0	9.0
	Sinapis arvensis	Field mustard	0	0.1	1.3
	Sonchus arvense	Perennial sowthistle	6.0	1.1	1.3
	Taraxacum officinale	Dandelion	0.8	0.1	1.6
	Thinopyrum ponticum	Tall wheatgrass	1.2	0	0

*Indicates seedlings and young shrubs found in the undrestory

related to introduced plant species cover ($r = +0.407$; $P = 0.03$), but not the cover of native vegetation ($P = 0.36$). Soil C in shrublands was positively related to herbaceous biomass, particularly the mass of forbs, but only within those shrublands exposed to cattle ($r = +0.717$; $P = 0.0005$).

Discussion

Shrubland Dynamics

The photo analysis indicated that this area initially comprised of Dry Mixedgrass Prairie and lacking shrubs underwent a slow but steady increase in *Shepherdia argentea* between 1949 and 2012. Although surface water introduction was exclusively from the SW portion of the property, initial shrub establishment appeared to occur on the eastern side of the study area, from where it promptly spread into sub-irrigated grasslands to the west. Expansion in the latter coincided closely with initial flooding starting in 1952, and progressed steadily thereafter. While ongoing natural changes in climate, specifically rainfall, have the potential to contribute to shrub expansion, long-term growing season precipitation data (April through September inclusive) for the study region suggest mean rainfall has been relatively stable over the study period. For example,

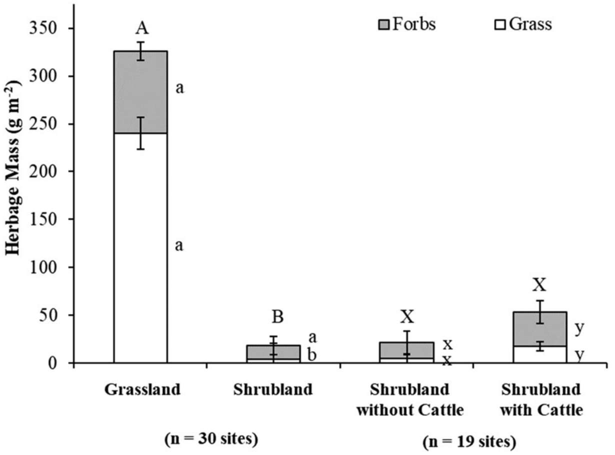

Fig. 5 Mean herbaceous biomass (±1 SE) within grassland and shrubland areas (left columns), as well as shrub areas with and without cattle presence (right columns), furthered partitioned by the contribution of dominant growth forms. Significance of total biomass within each pair is denoted by uppercase letters, while lower case letters distinguish differences among individual growth forms, at $P < 0.05$. Data collected in 2014 from 79 locations at the Mattheis Research Ranch in Alberta, Canada

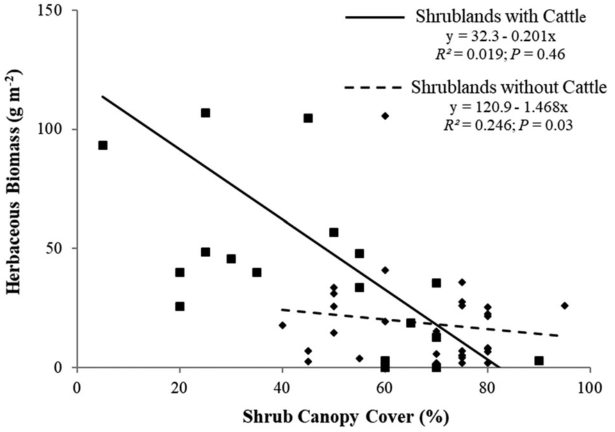

Fig. 6 Relationship between total herb biomass and shrub canopy cover within patches of shrubland either with evidence of cattle grazing (■), or without evidence of cattle grazing (◆). Data were collected in 2014 from 49 shrub patches at the Mattheis Research Ranch in SE Alberta, Canada

Table 2 Comparison of soil physical and chemical attributes among paired plots relative to the absence and presence of shrubs during the 2014 field sampling. Significance is based on ANOVA, with bolded values indicating $P < 0.05$

		Habitat type			
Soil Attribute	*n*	Grassland	Shrubland	SE	*P* value
Bare soil exposure (%)	30	7.30	2.00	4.23	<0.0001
Mulch depth (cm)	30	1.91	2.71	0.14	0.0002
Bulk density (g cm^{-3})	30	1.40	1.34	0.03	0.13
Soil carbon (%)	30	1.57	1.55	0.09	0.86
Soil nitrogen (%)	30	0.21	0.20	0.01	0.80
Soil OM (%)	30	2.56	2.55	0.12	0.95
Soil EC (dS m^{-1})	30	1.29	1.21	0.20	0.79
Soil pH	30	6.19	6.06	0.19	0.64

mean growing season precipitation prior to 1970 was 232 mm, which slightly increased to 249 mm between 1970 and 1990, and then declined to 245 mm between 1991 and 2012—the final assessment period.

Wetland assessments by DUC at the time of wetland renovation in 1988 (unpublished report) documented high levels of cattle disturbance within existing wetlands, and this could have aided shrub expansion, particularly given its unpalatable nature (Klebenow and Oakleaf 1984). Soil disturbed by cattle while feeding at productive wetland edges could create microsites favorable for colonization by new vegetation, including disbursing seed of *Shepherdia argentea*, thereby providing new locations for the shrub to expand from. Similarly, birds are known to aid woody plant expansion via seed dispersion (Prather et al. 2017). While fires every 20–25 year historically controlled woody vegetation across this region of western Canada (Wright and Bailey 1982), fire is now uncommon in the Mixedgrass Prairie, especially with widespread public concern for infrastructure and human safety, and this has likely aided encroachment by this particular shrub.

Spatial expansion by *Shepherdia argentea* over an extended period, such as occurred here has not been previously documented to our knowledge. However, a closely related tree species, Russian olive (*Elaeagnus angustifolia*) that is non-native to North America has been implicated as a species of concern in western Canada due to its ability to invade into riparian ecosystems (Collette and Pither 2015). Both these species demonstrate a wide-ranging tolerance for moisture and soil conditions (Collette and Pither 2015), and thus pose a similar concern for invasion. While the maximum potential for *Sheperdia argentea* expansion in this landscape remains unclear, it is likely constrained by moisture availability given its absence in arid grassland more distant from irrigated or sub-irrigated wetlands. Conversely, areas with excessive moisture are also less likely to be encroached and constrain the maximum distribution of this shrub, much like glossy buckthorn (*Rhamnus* spp.) in the Alleghany Plateau of Pennsylvania, which preferred well-drained areas of the landscape (Williams and Krock 2012).

Soil and Understory Vegetation Responses to Shrubs

Relative to adjacent grasslands on the same ecosite, shrub encroached areas had marked differences in soil and vegetation. While most soil attributes were similar between grassland and shrubland habitats, encroached areas had less bare soil and a thicker organic mulch layer, both reflecting the high input of surface debris (leaves and twigs) from the shrub canopy. Previous studies of shrub encroachment in the Mixedgrass Prairie suggest that expansion of woodlands such as *Shepherdia argentea* may increase soil N and C storage (Springsteen et al. 2010). Shrublands comprised of *Shepherdia argentea* may be particularly productive in these environments because of its N-fixing ability that is estimated to be as high as 136 mg m^{-2} d^{-1} in mid-summer (Vlassak et al. 1973). Despite the differences in surface organic matter found here, mineral soil OM and N levels remained similar between grassland and shrubland habitats, consistent with shrub encroachment in Kansas (McCarron et al. 2003).

Herbage biomass was markedly (94%) lower in all (non-grazed) shrublands than grassland, with both grasses and forbs declining, though grasses decreased to a greater extent. Herbage decreases can be attributed to direct competition for light, water, and nutrients, as shown in other grasslands invaded by shrubs (Bork and Burkinshaw 2009). However, the abundant amount of moisture from adjacent wetlands suggests the limiting factor for herbage growth here may be light or nutrient availability, rather than moisture. The relatively closed canopy (>50%) found in non-grazed shrublands could markedly reduce growth of herbs normally reliant on high light levels. Notably, shrublands with cattle had a reduced shrub canopy, and therefore presumably had increased light in the understory, but also greater soil N, the combination of which coincided with a modest increase in herb biomass.

Along with herbage mass, plant species composition changed markedly in response to shrub encroachment, and included widespread reductions in the floristic diversity of grasses and forbs. Furthermore, reduced herb cover, richness and diversity was disproportionately more apparent among native flora. The relatively closed canopy stands of *Shepherdia argentea* appeared to restrict the ability of native herbs to survive under these conditions, including dominant native grasses, such as *Hesperostipa comata* (needle and thread), *Pascopyrum smithii* (western wheatgrass), *Bouteloua gracilis* (blue grama), and *Koeleria macrantha* (Junegrass). This is not surprising given the typical environmental conditions native flora evolved under within these relatively sparsely vegetated semi-arid grasslands, including ample light availability. In contrast, shrub encroached areas had much greater representation of introduced plant species, presumably those able to cope with the altered environment in the understory. This response is consistent with other studies reporting shrub-induced increases in exotic species (Grant et al. 2020).

Many introduced species were either disturbance adapted ruderals, or species capable of surviving in the altered microenvironment. As many of the species documented were weedy in nature, and not deliberately introduced to the area, the vector for their arrival remains unknown. Potential mechanisms for their introduction include as seed arriving in flood water, air-borne seed rain from adjacent cultivated agricultural lands, or through the introduction of supplemental feed for livestock, as well as the cattle themselves acting as agents of dispersal. Not surprisingly, while *Shepherdia argentea* was the dominant shrub in shrubland patches, these areas also contained other woody species found in only low abundance in neighboring arid grasslands, including western snowberry (*Symphoricarpos occidentalis*), *Rosa acicularis* (prickly rose), and *Rosa woodsii* (woods rose). Overall, these widespread vegetational shifts highlight the substantial ecological changes that shrub encroachment can impart within grassland landscapes influenced by wetland development.

Cattle Use of Shrublands

Presence of cattle in shrublands altered both soil and vegetation, supporting the importance of grazing animals in altering vegetation succession (Connell and Slayter 1977). Shrub communities accessed by the cattle had greater bulk density, likely a direct compaction response to hoof impact. We observed cattle congregating within shrublands, presumably to escape high temperatures (>30 °C) or biting insects in mid-summer, and coupled with moist soil conditions, this high stocking density of animals is likely to cause soil compaction (Donkor et al. 2002). Bulk densities in these areas exceeded 1.5 Mg m^{-3} and could pose a problem for root growth (Sheoran et al. 2010). Concentrated cattle use in shrublands also increased soil N levels, likely due to abundant urine and fecal deposition from cattle (Bélanger et al. 2015), which combined with ongoing N addition through fixation by *Shepherdia argentea*, would further alter competitive dynamics within the understory of shrublands. This result is consistent with the notion that grazing can enhance ‘islands of fertility’ in arid environments (Allington and Valone 2014).

Cattle also impacted herbage mass within shrub patches. While shrublands without cattle presence had the least herbage, subplots with an increasingly open canopy were associated with greater biomass, particularly of grasses. This indicates that where cattle were able to enter and occupy shrublands, they at least partly limited the extent of shrub development, in turn increasing understory growth. While this modest increase in herbage was insufficient to offset the overall effect of shrub encroachment, it does highlight the impact of large herbivores in potentially limiting shrubland development.

Although cattle presence reduced shrubs and increased herbage, cattle also further altered vegetation composition in shrublands. More specifically, cattle presence increased plant diversity, though this increase was primarily due to introduced species, presumably those that had higher grazing tolerance; in contrast to introduced species, native species declined in diversity. Thus, the combined effect of shrub encroachment in altering resource availability, together with the acute disturbance of concentrated cattle activity, appeared to further place native flora at a competitive disadvantage. Maron and Connors (1996) reported invasive weed increases brought on by N-fixation by native shrubs, which could be a contributing factor here. Of even more importance potentially, N enrichment from cattle excrement could explain why dense shrub stands with limited cattle presence had greater native plant diversity than adjacent shrub patches where cattle had opened up the shrub canopy.

Shrub Encroachment Implications for EG&S

Our findings illustrate the potential tradeoff in EG&S within these once sparsely vegetated native grasslands following shrub establishment. While the original intent of establishing wetlands was to provide brood habitat for waterfowl, and thereby offset ongoing wetland loss across the prairie pothole region (Asamoah et al. 2011), water introduction is also known to have sharply altered grassland vegetation dynamics (Asamoah 2008). In the current study area this is exemplified by increased shrublands, which in turn, contributed to both reductions in native species richness and diversity, and an increase among introduced (non-native) plant species, thereby posing a further threat to native grassland conservation, and potentially their obligate wildlife species. As one of the most threatened ecosystems globally (Hoekstra et al. 2005; Henwood 2010; Carbutt et al. 2017), conservation of temperate grasslands is a significant goal of land managers. In Alberta, while as much as 43% of native Mixedgrass Prairie remains (Adams et al. 2013), this region continues to be under pressure from land use conversion and industrial development. Wetland establishment within these otherwise arid landscapes appears to be contributing to the decline of native grasslands, in part by facilitating shrub encroachment, but also changing prairie vegetation towards non-native species (Grant et al. 2020).

Our field data demonstrates that once established, *Shepherdia argentea* can directly alter the ability of these landscapes to support cattle grazing, which remains the most widespread land use in the region. Shrublands inhibited use by cattle, presumably due to the thorny nature of *Shepherdia argentea* (Looman 1984), and even more-so led to decreases in herbage productivity, both of which could result in lost economic opportunities. While the extent of this decline remained modest here (i.e., 280 AUM across 4279 ha), this nevertheless amounts to a reduction of forage equivalent to supporting 50 cow-calf pairs over a 5.5 month grazing season. As this wetland complex is not the only one established and maintained in the region, with as many as 900 irrigation fed wetlands covering 33,358 ha (DUC, unpublished data), and forms a significant component of the provincial wetland loss mitigation strategy (Alberta Environment 2007), a full spatial accounting of these impacts is needed to understand how these agricultural landscapes may be impacted.

Changes in native grassland conservation and forage loss should also be put into context with respect to the impacts of wetland creation and associated shrub encroachment on other EG&S, including any benefits thereof. For example, while not quantified here, shrublands were observed to provide novel habitats in this agro-ecosystem, including cover for many wildlife species. *Shepherdia argentea* shrublands held high numbers of western jackrabbit (*Lepus townsendii*), pheasant (*Phasianus colchicus*), and several ungulates, such as whitetail deer (*Odocoileus virginanus*), elk (*Cervus elaphus*), and moose (*Alces alces*). As these ungulates rely extensively on browse, the increase in shrubland may improve foraging opportunities for these populations, a benefit that remains unquantified. Moreover, mast crops of *Shepherdia argentea* were observed to support select bird species, such as cedar waxwings (*Bombycilla cedrorum*) in winter. However, these wildlife species may also be different from those that historically used the original Mixedgrass Prairie, as obligate grassland birds are reported elsewhere as declining with shrub encroachment (Grant et al. 2004; Anderson and Steidl 2019). Shrublands also provide structural cover for livestock to escape extreme weather conditions, including heat in summer and cold winds in winter. In addition, while shrublands associated with wetland development may reduce grazing opportunities, the wetlands they arise from have been associated with high levels of primary production, particularly of graminoids and associated hydrophytic species, with additional benefits to forage quality (Asamoah 2008). This increased plant growth may enhance C sequestration, for example, by as much as 3.25 t CO_2-equivalence per hectare per year, even after adjustment for methane emissions (Badiou et al. 2011). Similarly, *Shepherdia argentea* shrubs represent another form of C storage, and a full accounting of the amount of C stored in both wetlands and accompanying shrublands is needed to understand this benefit. Finally, while created wetlands may not produce large numbers of breeding waterfowl (Asamoah et al. 2011), they nevertheless provide critical habitat during waterfowl migration to ensure survival (Janke et al. 2019). Ultimately, the collective impacts of shrub encroachment are complex, and depend on many inter-related ecosystem goods and services related to wetland development.

An important question that arises under the ongoing creation and maintenance of wetlands, is if shrub encroachment is considered undesirable, then what strategies are available to reverse this process? In general, little is known on how this species can be controlled in this environment. Options such as prescribed burning are problematic, in part due to the fire adapted nature of many shrub species (Fuhlendorf et al. 2011), and more importantly, the risk fire poses to infrastructure and public safety in an arid ecosystem. Similarly, intensive livestock grazing may have a role in limiting *Shepherdia argentea*, particularly if applied to browsing livestock, such as goats, which are more likely to browse on the shrub and impact its population. Herbicide control is another option, but unlikely to be used due to the close proximity of shrub patches to wetlands. Last, it is possible that alteration to flood water management, such as the amount and timing of inundation, may also alter shrub establishment and spread.

Conclusions

We have shown that wetland establishment in this northern temperate Dry Mixedgrass Prairie has led to increasing shrub encroachment over a 63-year period. Albeit gradual, shrubland increases, in turn, have altered understory vegetation and soil properties. These changes include a reduction in biodiversity, particularly native flora, and their replacement with introduced plant species, as well as changes to soil surface properties. In addition, reductions in herbage biomass, coupled with limitations in livestock use of shrublands, has led to a modest decline in livestock grazing potential, the predominant land use of the region. Overall results of this study demonstrate that created wetlands and the shrub encroachment they cause are likely to alter many ecosystem attributes within these semi-arid grasslands, and ultimately these responses should be weighed off against the direct benefits of these shrublands, including increased landscape diversity, the provision of unique wildlife habitat, and potentially improved C sequestration.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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