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RESTORATION AND NOVEL COMMUNITY STRUCTURE: INVESTIGATION OF A
RESTORED PRAIRIE IN BOULDER, COLORADO

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ABSTRACT

Factors that contribute to long-term persistence of restored natural areas remain largely unstudied. In Boulder, Colorado, a tallgrass prairie was mined and used as a gravel pit for 50 years before it was drilled with native grass species in 1998. The ecosystem was then allowed to revegetate without intervention. A study in 2004 investigated the sensitivity of plant community structure to nutrient manipulations. Authors of the study argued that low carbon and nitrogen levels at this site contributed to a novel, low-diversity plant community that was resistant to invasion by nonnative species. I reassessed the site in 2016 to determine whether native species persisted, and whether carbon and nitrogen content of these soils had recovered to nearby, undisturbed soil levels. Native grasses declined from 92% relative cover in 2004 to 45% in 2016. A single planted grass, *Sporobolus airoides*, a plant known to thrive in alkaline soils, dominated both study years. *Bromus tectorum*, increased its coverage by 20%, contributing to a reduction in species diversity. Soils at this site showed a nonsignificant (0.15%) increase in soil carbon in the top 10 cm of soils, suggesting that the sequestration capabilities of this ecosystem were not effective in the 12-year interval between measurements. These results suggest that novel soils can produce novel vegetation communities, but initial establishment of desirable native species has been replaced by opportunistic species better adapted to current climate conditions. Restoration managers must consider the potential impact of climate variability, increasingly prevalent invasive species, and degraded soil structure to ensure the health of novel ecosystems.

INTRODUCTION

Scientists and stakeholders alike are becoming more interested in remediating degraded ecosystems because healthy ecosystems benefit humans economically, physically and

emotionally, yet anthropogenic disturbances are pervasive. (Firn et al., 2013; Hobbs et al. 2006; Tolvanen and Aronson, 2016; White, 1979; Johnson and Miyanishi, 2007). Ecosystems are inherently resilient, which implies that they are able to absorb ecological changes and still persist, but measurements of resilience and ecosystem health are difficult to standardize (Johnson and Miyanishi, 2007; Thom). These discrepancies make ecological restoration projects, defined by the Society for Ecological Restoration (2004) as “the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed,” dynamic and unique to each system.

The value of proper ecological restoration is increasingly important as changes in global and regional climate accelerate local changes in plant and soil communities (Harris et al., 2006; Corlett, 2016). Vulnerable or resource-limited ecosystems are especially sensitive to these unpredictable changes. Plant distributions in semi-arid grasslands are particularly reliant on variability in temperature and precipitation due to limited summer precipitation (Oppenheimer and Wilcove, 2009). Given that restoration success can be interpreted as the re-establishment of native species (Thorpe and Stanley, 2011), grasslands can be difficult to restore.

Climatic factors and invasive species influence soil nutrient cycling, which help determine terrestrial productivity and function (Corbin and D’Antonio, 2004; Gasch et al., 2015). Anthropogenic disturbances inevitably change soil characteristics (Shrestha and Lal, 2011), and these changes influence the plant community structure. Restored mining sites are known to produce soil conditions that differ from historical values. Mining removes soils and overburden to access deeper minerals, and this movement of soil disrupts microbial processes, subsurface hydrological regimes, and local vegetation (Shrestha and Lal, 2011). The new altered soils that are formed through mine restoration projects are relatively young and very different from their original states (Shrestha and Lal, 2011). Surface mining is considered to be one of the most

drastic forms of habitat disturbance (Gasche et al., 2015; Fischer and Fischer, 2006). Previously mined sites are challenging to restore because they have experienced a high degree of soil structure disturbance (Shrestha and Lal, 2011). Once revegetated, RMSs are likely to evolve into unique ecosystems unlike the natural surrounding areas. These sites provide examples of ‘novel ecosystems’ that feature new assemblages of plants and changes in ecosystem functioning as a result of deliberate human action (Seastedt et al., 2008; Hobbs et al. 2006). These impacted ecosystems often complete unique successional pathways that are resilient to change (Suding et al., 2004).

Few studies examine the long-term effects of post-mining soils. Many restoration projects are constrained by high cost and time requirements, and this results in minimal-involvement projects that rely on successional patterns to restore the ecosystem. One restoration project at a post-mining site in Boulder, Colorado, followed this trend. To facilitate succession-like revegetation, this relict tallgrass prairie was drilled with native grass seeds in an attempt to facilitate ecosystem restoration. Cherwin et al, (2009). surveyed the plant and soil community in 2004 at this site and reported the presence of a low-nutrient soil and the dominance of native grasses on a species-poor area. The site has not been monitored since that study. My study re-investigates the community composition of this area in order to observe how this system has evolved and/or persisted. If restoration is working, the state of the ecosystem (species richness, presence of natives, soil nutrients) will have improved and this site will be more similar to native prairies. I seek to answer:

1. How has the community structure in this unusual ecosystem changed over time?
2. Have seeded native grasses maintained their dominance?
3. As predicted by Cherwin et al., is this system resistant to invasion by nonnatives?

METHODS

Study Site

Data was collected on the University of Colorado's "South Campus," a 308-acre plot of land alongside Highways 93 and 36, on the southeast boundary of the city of Boulder (40°00'N, 105°16'W). Because of its proximity to the turnpike, this plot was colloquially called 'Turnpike Pit.' Typically, most precipitation falls in the spring and early summer in this continental climate (Prevéy and Seastedt, 2007). The average annual precipitation is 51.4. The soils at this site are classified as Sandy Loam with 1.22% carbon and 0.09% nitrogen and an average pH of 6.85 (Davies, unpublished data).

This site was most likely a relict tallgrass prairie prior to mining (Bennet, 1997). According to records from the Colorado Department of the Interior, Colorado Mine Land Reclamation Division, topsoil from this site was removed in order to create a depression that was filled with gravel and moraine debris in the 1950's. Removed topsoil was stored for over 40 years while mining of gravel continue on-site until 1998, when gravel was removed and original soil was replaced. Replaced topsoil formed an "A" horizon approximately 12-18cm deep (Cherwin et al., 2009; Seastedt and Suding, 2007). In 1998 the site was drilled with a mix of nine native grass species, including the cool-season (C3) grasses, *Poa compressa*, *Agropyron smithii*, *Elymus trachycaulus* and the warm season (C4) grasses *Sporobolus airoides*, *Bouteloua gracilis*, *Bouteloua curtipendula*, *Buchloe dactyloides*, *Panicum virgatum* and *Andropogon gerardii*. Observations in 2004 note that the spatial distribution of species from original seeding rows still existed and vegetation was dominated by planted grasses, composing 92% of relative vegetation cover. Another ~20 species composed the remaining 8% cover (Cherwin et al., 2009). Warm season species, dominated by *S. airoides*, made up 60-90% of total cover in 2004 (Cherwin et al.,

2009), and the combination of species was described as a semi-arid, mixed grass community (Seastedt and Suding, 2007). Non-planted species may have invaded this site from nearby fields or were contaminated in the seed mix.

Experimental Design

In 2001-2004, Cherwin et al. investigated how resource availability and plant community structure affect cover and richness of species at the post-mining site 'Turnpike Pit.' Their design involved nutrient additions and reductions in carbon, phosphorus, nitrogen and grass cover (Cherwin et al., 2009). My study compares plant species composition in unmanipulated control plots from their analyses to species coverage data in the 2016 growing season, May-July.

A block of 100m² was selected within the revegetated South Campus area. This area was sampled using a 0.25m² 6x6 point-intercept quadrat, where intersections of string marked 36 precise sample locations. A pin flag was dropped at each intercept point and up to two species were recorded, if present, at each intercept point. Thus, each quadrat represents one plot with 72 potential species observations. A measuring tape and random number generator guided the placement of the quadrat within the site, with 1m-minimum buffers between each sample. Three groups of 25 plots (n=75) were assessed over three time periods, yielding a total of 5400 data points. Sampling rounds represent early, middle, and middle-late summer periods from June-July, 2016. Additional sampling rounds were planned in accordance to the Cherwin et al. study design, but early dry-down and total senescence of summer plants prevented me from collecting useful data.

Soil Analysis

To interpret changes in plant community composition, soils and nutrients were analyzed. Average total carbon and nitrogen concentrations were measured in the top 10cm of the soil

using CHN machines that combust soil and measure elemental gases produced. In 2004, nutrients were measured using combustion on a Carlo-Erba CHN analyzer (Carlo Erba Instruments, Milan, Italy). In 2015 and 2016, C and N were determined using Thermo Finnigan EA 1112 Series Flash Elemental Analyser (Thermo Fisher Scientific, Inc., Waltham, Massachusetts, USA) (Matejovic, 1997).

Species Richness and Cover

Species richness and abundance values were calculated for each of the plots observed in 2004 and 2016 (n=32 and 72, respectively). Absolute cover data described each species' average percent coverage per plot, including the presence of bare soil, rock or debris. Relative cover data described the cover of each species as a percentage of total plant cover. Samples were pooled into three general timeframes for observation: Early, middle, and middle-late summer. A fourth collection timeframe was planned for early August, but most plants had senesced, dried out, or died by late July.

Statistical analyses

Statistical analyses were performed using SAS version 9.4 (SAS 2013). In order to assess differences between study years, we transformed the data using the arcsine square root transformation. SAS GLM (made for unbalanced designs) conducted TTEST procedures to assess differences in native seeded species and *S. airoides*. Differences in *Bromus spp.* cover were analyzed with the nonparametric Wilcoxon rank-sum test (Wilcoxon Mann-Whiney U-test) because the arcsine square root could not homogenize variances between the two samples. Descriptive statistics related to abundance, compared numbers with those used by Cherwin et al., 2009.

RESULTS

My data suggest that the plant community structure did change as *Bromus spp.* increased cover (Supplemental Figure 3) and seeded native species lost cover (Table 1; Figure 1), which allows us to reject the null hypothesis.

	R-squared	Mean Square	F	p
Seeded Native Grasses	0.5	5.2	134.1	<0.0001
<i>Sporobolus airoides</i>	0.009	0.04	0.9	0.3

Table 1. Statistical indices for GLM tests. Seeded Native Grasses (*P. compressa*, *A. smithii*, *E. trachycaulus*, *S. airoides*, *B. gracilis*, *B. curtipendula*, *B. dactyloides*, *P. virgatum* and *A. gerardii*) and *Sporobolus airoides* data were transformed by arcsine square root transformation to correct for irregular distribution and then analyzed with SAS GLM procedure.

Plant Community Structure

The plant community structure of the Turnpike Pit site changed from 2004 to 2016. In particular, the relative cover of seeded native grasses reduced coverage with respect to year (Figure 2; $F=161.1$, $p<0.0001$; Supplemental Figure 1). Only seven of the nine originally seeded grass species were present in 2004, but the two missing species (*Elymus trachycaulus* and *Poa compressa*) were observed in 2016 (2.7 and 4.1% relative cover, respectively). In 2016 only five of the nine originally seeded species (*Sporobolus airoides*, *Elymus trachycaulus*, *Bouteloua gracilis*, *Poa compressa* and *Agropyron smithii*) remained. This decline in native grasses contributed to a decline in gamma species richness, from 25 to 14 species (sum of 32 and 75 samples, respectively). Average plot species richness in 2004 was measured at 10.1 ($n=32$, std error <0.25) and in 2016 at 4.9 ($n=75$, std error=0.16). Twelve of the species observed in 2004 were no longer present at the 2016 study sample, although 3 new species (including two originally seeded grasses) appeared in 2016 (Figure 2). *S. airoides* was present in all but one plot

in 2016 (making up an average of 45.7% of relative cover), followed by *Bromus tectorum* and *Bromus japonicus* (20.6% and 9.2% respectively) (Figure 2). Today, patterns of original seeding rows are still detectable, but spaces in between rows are primarily filled with *Bromus tectorum* and *Bromus japonicus*.

These three species accounted for the majority of relative cover. In 2004, the three most abundant species were *S. airoides*, *A. smithii* and *B. gracilis*, all of which were part of the original seedbank (Figure 2). The distribution of *Sporobolus airoides* did not change between years ($F=0.9$, $p=0.3$; Supplemental Figure 2), while *Bromus spp.* did change with respect to year ($p<.0001$; Supplemental Figure 3).

Total vegetation cover reduced from 112% in 2004 to 82.6% in 2016 ($n=32$ and 75 , respectively). This implies that in 2016 more rock/litter/bare ground samples were recorded and in 2004 there was a tendency to observe two species per hit.

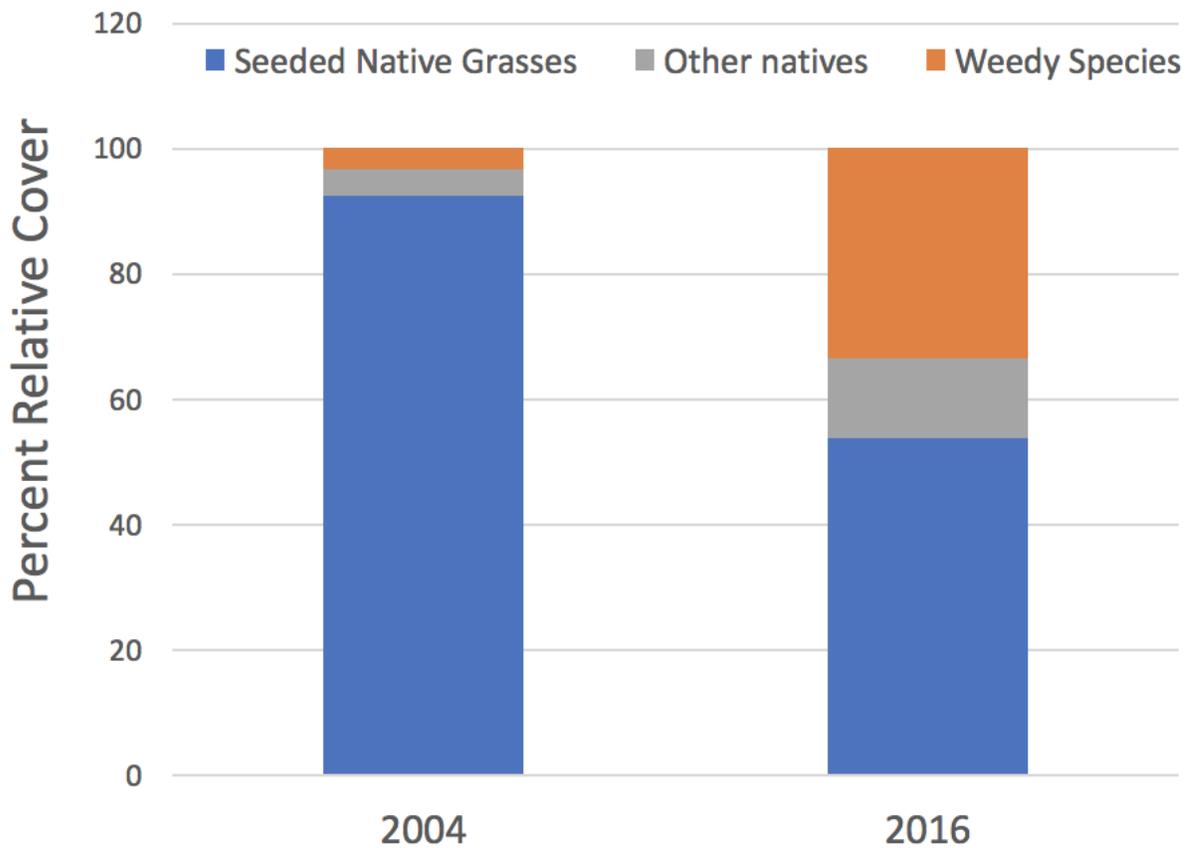


Figure 1. Community Composition of “Turnpike Pit,” a revegetated post-mining site, in 2004 and 2016. Seeded native grasses include *P. compressa*, *A. smithii*, *E. trachycaulus*, *S. airoides*, *B. gracilis*, *B. curtipendula*, *B. dactyloides*, and *P. virgatum*. Weedy species are defined as non-native species and include *Bromus tectorum*, *Bromus japonicus*, *Lepidium campestre*, *Lactuca serriola*, *Cichorium intybus*, and *Convolvulus arvensis*. Other native species include other grasses and forbs native to Colorado. Data transformations revealed a significant decrease in seeded native grasses ($F=161.1$, $p<0.0001$).

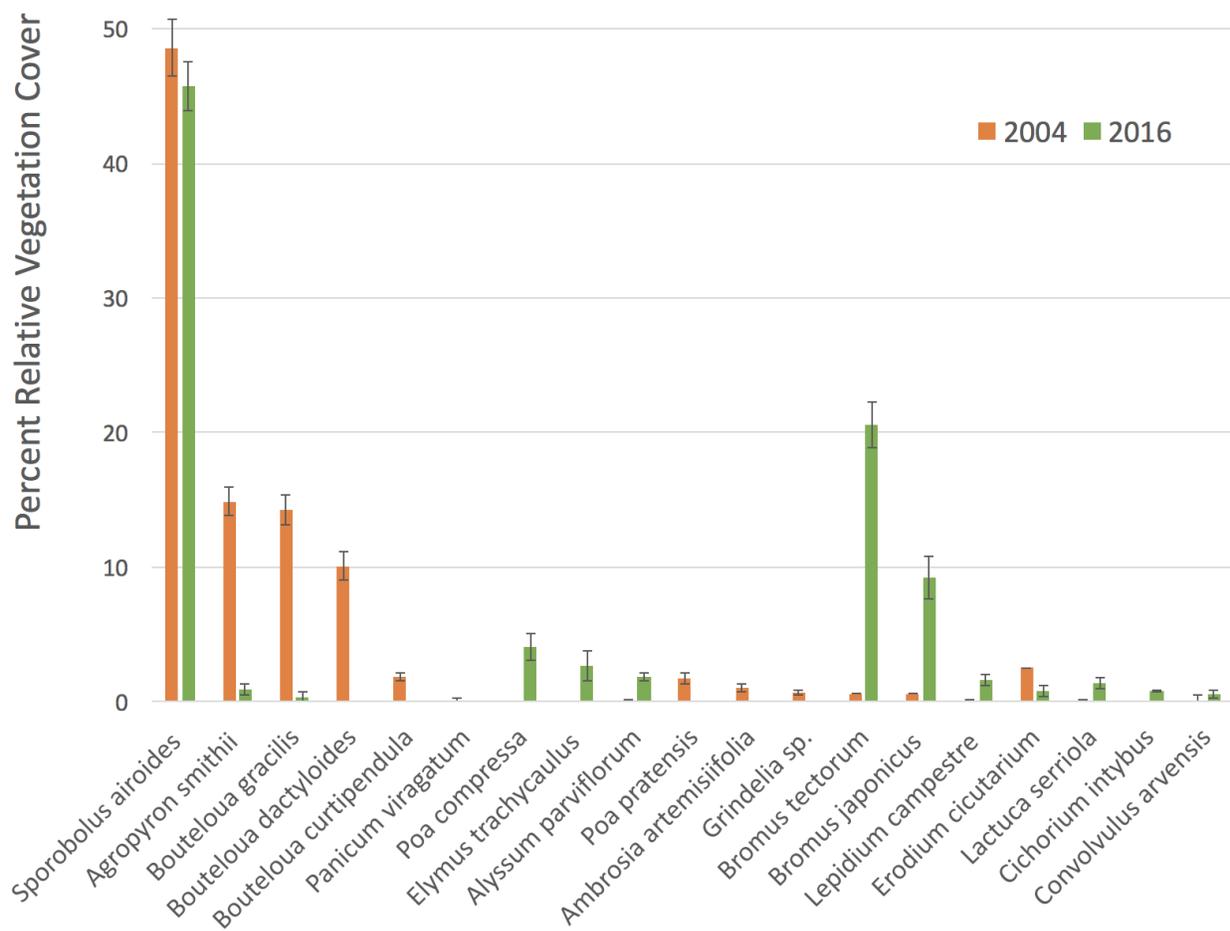


Figure 2. Mean relative vegetation cover in 2004 and 2016 (n=32 and n=75, respectively) for all identified species. To aid visualization of community changes, seeded native grasses (*S. airoides*, *A. smithii*, *B. gracilis*, *B. dactyloides*, *B. curtipendula*, *P. virgatum*, *P. compressa* and *E. trachycaulus*) are featured on the far left, other native non-planted species (*A. parviflorum*, *P. pratensis*, *A. artemisiifolia* and *Grindelia sp.*) in the middle, and weedy species (*B. tectorum*, *B. japonicus*, *L. campestre*, *E. cicutarium*, *C. intybus*, and *C. arvensis*) on the right.

Soil Analysis

The surface horizon of this site is not representative of neighboring semiarid grassland soils. Measurements of the top 10cm of the soil in 2004 and 2016 revealed Carbon and Nitrogen

levels that are less than half of the nearby prairie levels (Figure 3). The average C:N ratio in 2004 was 12.4, 13.38 in 2016, and 11.52 in the native plot (Figure 3).

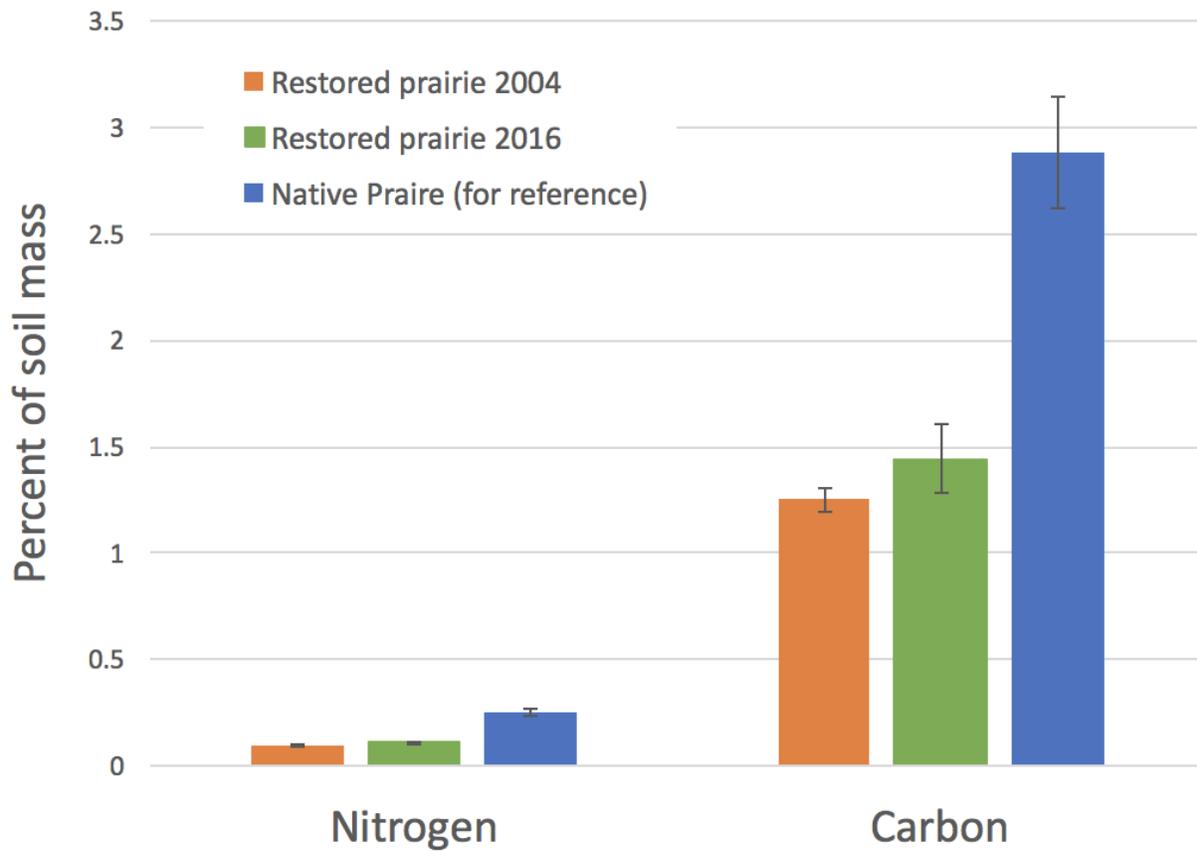


Figure 3. Average percent of nitrogen and carbon in the top 10cm of soil in revegetated soil in 2004 and 2016, and at similar, undisturbed reference prairie in 2012 (n=82 for 2004, n=10 for 2016 and n=11 for Native Prairie). Native reference prairie data obtained by Beals et al. (in review).

DISCUSSION

The Turnpike Pit restoration area is representative of a novel ecosystem because it contains new species combinations as a result of human action (Hobbs et al., 2006). In the 12

years between study efforts, this area experienced a decline in intentionally seeded grasses (Figure 1; Table 1). In contrast to Cherwin et al.'s observations, this system was not resistant to invasion by nonnative species (Figure 1). This site continues to diverge from soil and species characteristics of nearby native grasslands (Cherwin et al., 2009; Beals et al., unpublished results), likely due to the unusual seed mix that site managers started the revegetation with. This seed bank featured locally native species, but *S. airoides*, the singular dominant species in both study years (Figure 2), is not known to dominate other Boulder communities (Cherwin et al., 2009). *S. airoides* is the only warm-season C4 grass that thrived at this site (Figure 2), perhaps because of its ability to tolerate saline soils and drought (Ferrero-Serrano et al., 2008; Mealor and Hild, 2006). *S. airoides* is frequently used in restoration projects to help stabilize soils and accumulate toxic compounds (Ferrero-Serrano, 2008; Mealor and Hild, 2006), and this may be why it was included in the original seed selection despite lack of local abundance. While providing important vegetation cover, it is difficult to assess the relative ecosystem services of this species. It is difficult to say whether the dominance of *S. airoides* benefits this ecosystem or harms it, and further research should investigate the competitive interactions between *S. airoides* and other native and introduced plant species.

The advantage of *Sporobolus airoides* in this restoration may have been aided by the unusual soil conditions (Figure 3) created by standard mining reclamation procedures, which made Turnpike pit not representative of neighboring native semiarid grassland soils (Cherwin et al., 2009; Reed et al., 2007). The replacement of native pre-mining topsoil is mandated by the Surface Mining Control and Reclamation Act (SMCRA) because these soils provide native plant material, organic matter, and microorganisms that help re-establish nutrient cycling (Zipper et al., 2013; Macdonald et al., 2015). Although this restoration project reapplied 12-16cm of the

original topsoil to the site, it sat in storage for 40 years. Nutrient content and biological quality of topsoil is reduced during long-term storage, and its value as a ‘living resource’ decreases with time (Macdonald et al., 2015). This management may have contributed to the low Carbon and Nitrogen profile of our system (Figure 3). Interestingly, the low-nutrient soils apparently favor C4 species like *S. airoides* (Ferrero-Serrano, 2008), but only one of the four other planted C4 species, *Bouteloua gracilis*, was found in 2016, and its cover was negligible (0.3% relative cover, Figure 2). Predictions of soil carbon recovery in post-mining has been documented in some restoration systems (Vindušková and Frouz, 2012), but this recovery reported elsewhere was not observed in my study (Figure 3). Instead, soil carbon sequestration processes appear to be slow, if present at all. Future studies should look re-investigate nutrient controls on disturbed grasslands and how restoration projects may be able to better aid ecosystem resiliency.

Many invasive annual grasses have life history traits that enable them to use limiting soil nutrients more effectively than native grasses (Chambers et al., 2016). This competitive advantage is enhanced by anthropogenic disturbances that create gaps in vegetation cover for exotics to establish themselves in (Corbin and D’Antonio, 2004). *Bromus tectorum*, also known as cheatgrass, is particularly well-suited to the heavy winter precipitation patterns of Colorado grasslands because its shallow roots and fast growth rate allow it to harness water and nutrients in early spring before native plants are active (Knapp, 1996; Chambers et al., 2016; Prevéy and Seastedt, 2015). The increasing pervasiveness of cheatgrass (Figure 2; Supplemental Figure 3) is concerning because it is an example of an Invasive Alien Plant (IAP) which drives ecological change as it alters ecosystem functions and services (Richardson et al., 2000; Richardson and Gaertner, 2013). *B. tectorum* can increase fire frequency and severity, manipulates nutrient cycling, and reduces plant diversity (Prevéy and Seastedt, 2015; Knapp, 1996). The increasing

abundance of *B. tectorum* (Figure 2; Supplemental Figure 3) may explain some of the changes in community structure as the ecosystem is manipulated and moisture for later-growing species is usurped by *B. tectorum*.

The community composition of semiarid grasslands is largely influenced by the timing and amount of annual rainfall (Rao et al., 2011; Dietrich and Smith, 2016; WU,). 2016 was a drier year than 2004 and experienced its typical spike in spring precipitation a month earlier than in 2004 (Supplemental Figure 4). Precipitation during the 2004 growing season (April-August) was almost double than that of 2016 (43.7cm vs. 23.8cm), which may have led to higher ecosystem productivity (Dietrich and Smith, 2016). High winter precipitation (including precipitation from November and December) and drier summers, as is seen in 2016 (Supplemental Figure 5), retard mid- and late-summer herbaceous species and favor nonnative species that germinate in early spring (Lesica and Kittelson, 2010; Prevéy). Many of these winter-active species, such as *Bromus spp.* can take advantage of precipitation earlier in the season, causing earlier dry-downs (Prevéy and Seastedt, 2014; Bush et al., 2007). The Turnpike Pit site experienced an extremely early dry-down in July of 2016, when species found in the Cherwin et al. study would normally peak in abundance. The exact cause of widespread plant death in July, 2016 was not identified, but reduction in growing season precipitation (Supplemental Figure 4) and slightly-hotter-than-average July temperatures (Supplemental Figure 5) may have influenced flowering phenology and survival.

Once an ecosystem has gone through fundamental change, new relationships between abiotic and community factors make it difficult to return to past states of existence (Suding et al., 2004). Restoration projects often create new assemblages of plants that are not predicted under historical circumstances, and these systems are potentially adapted to new conditions, persistent,

and resistant to change (Firn, Price and Whalley, 2013; Suding, Gross and Houseman, 2004; Johnson and Miyanishi, 2007). My study area evolved into an unusual community (Figure 1) with unique soil characteristics (Figure 3) that are new to this landscape. Given that most restoration projects leave their sites to revegetate naturally (Corbin and D'Antonio, 2004), it is difficult to say whether manipulation of this site through soil nutrient additions or active re-seeding could have prevented the encroachment of weedy species like *Bromus spp.* Future restoration projects should attempt to rebuild native soils and should monitor long-term trends, including climatic trends, which may reveal insights into how we can fix many of the world's destroyed ecosystems. Either more proactive management actions are necessary, or stakeholders will have to accept the mixes of native and non-native vegetation that are best adapted to current and future environmental controls.

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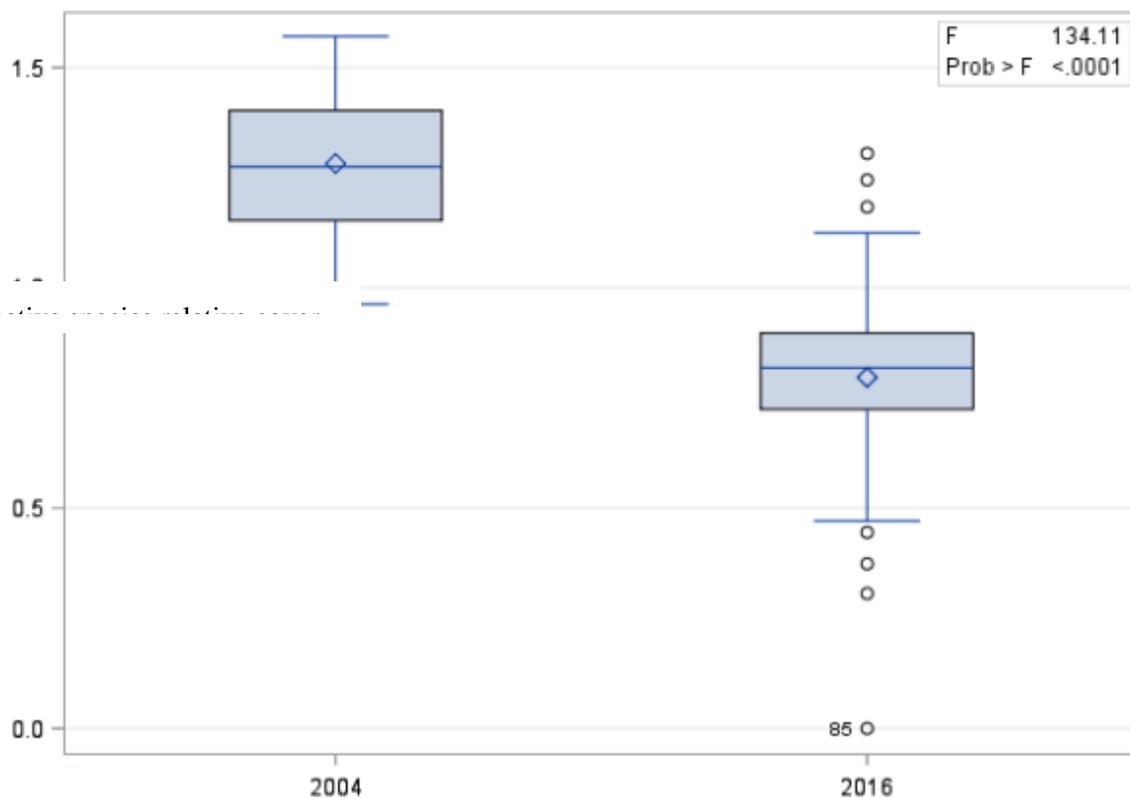
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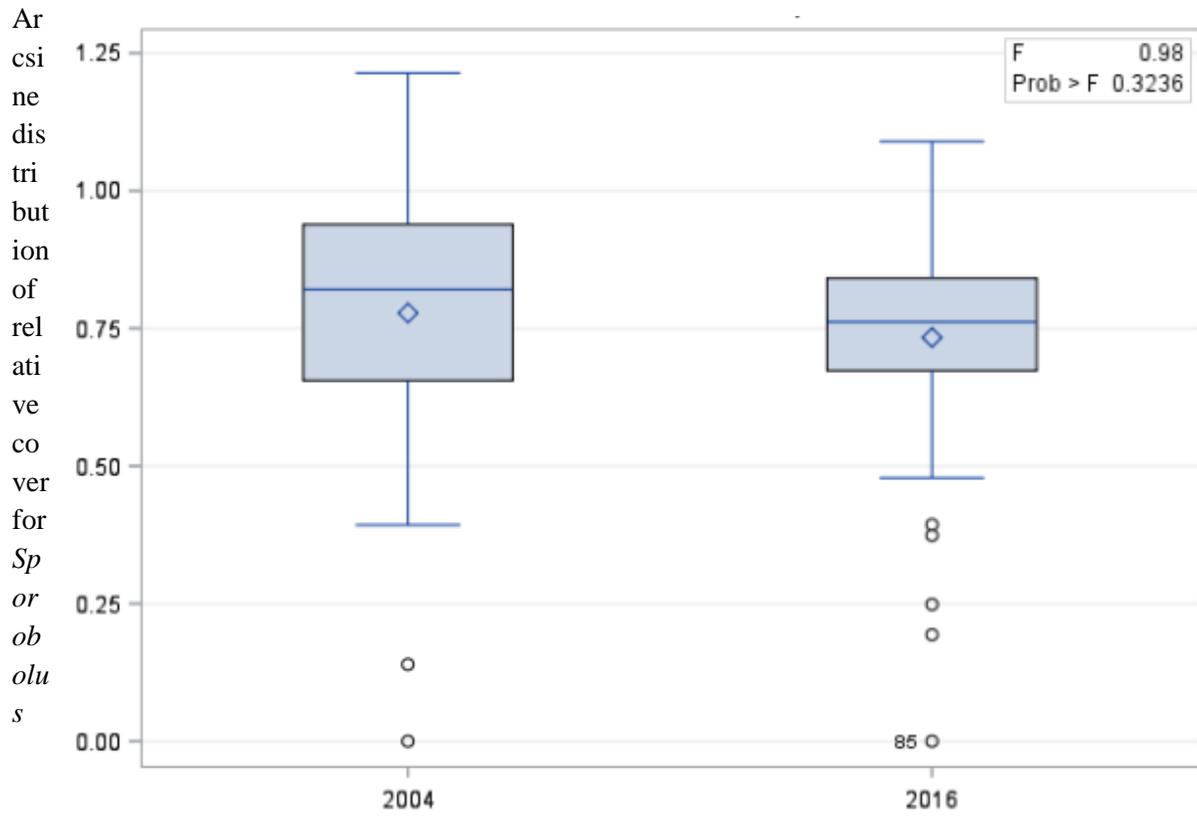
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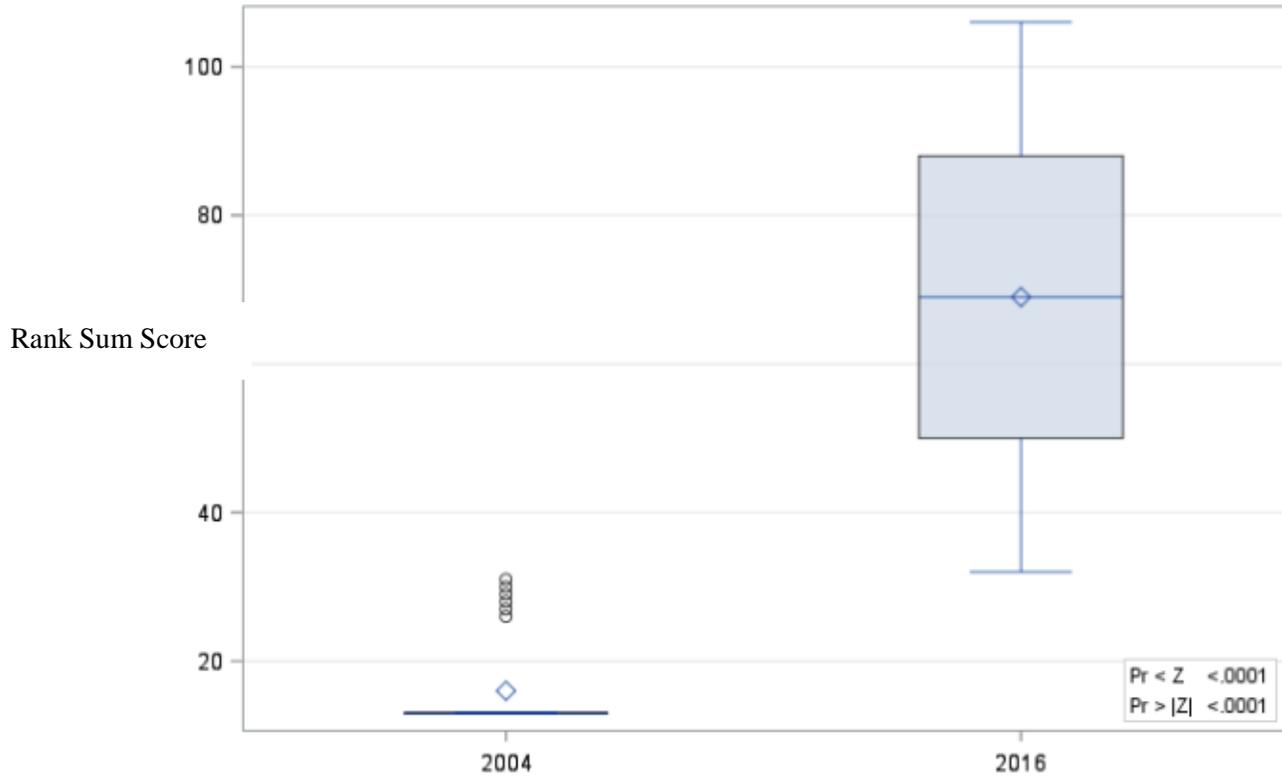
SUPPLEMENTAL FIGURES



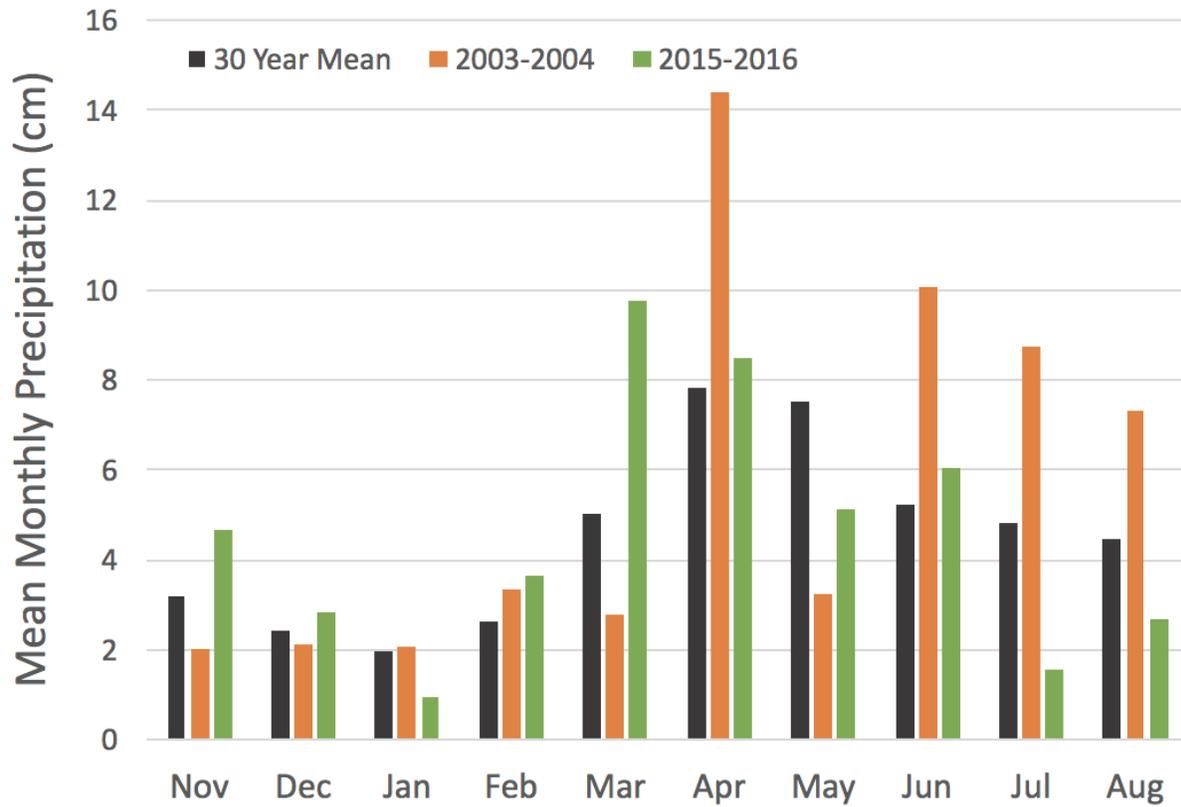
Supplemental Figure 1. Arcsine square root transformation of seeded native species cover, including *S. airoides*, *A. smithii*, *B. gracilis*, *B. dactyloides*, *B. curtispindula*, *P. virgatum*, *P. compressa* and *E. trachycaulus* (F=134.1, p <0.0001, df=1).



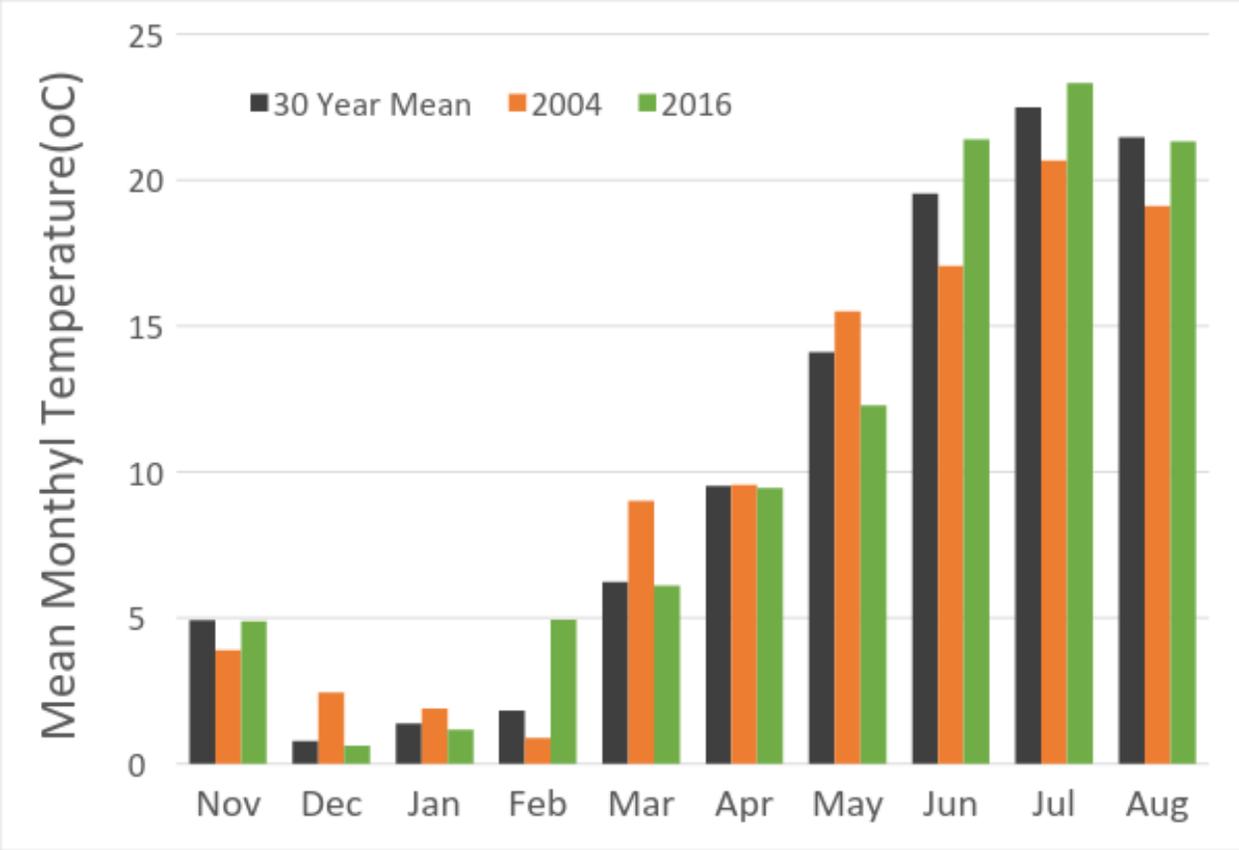
Supplemental Figure 2. Arcsine square root transformation of relative cover of *Sporobolus airoides* in 2004 and 2016 (F=0.9, p=0.3, df=1).



Supplemental Figure 3. Distribution of Wilcoxon scores for *Bromus spp.* The mean score for 2004 was calculated at 16.0 and at 69.0 in 2016 \pm 143.03 (S=496.0, One-sided PR < Z < 0.0001)



Supplemental Figure 4. Mean monthly precipitation in Boulder, Colorado in 2004, 2016 and over a 30 year average. Total precipitation in the 2003-2004 timeframe was 56.0cm and 45.7cm in the 2015-2016 timeframe. Data compiled from NOAA (2017).



Supplemental Figure 5. Mean Monthly Temperature in Boulder, Colorado in 2004 and 2016.

Months leading up to the growing season (December and November) are featured to help explain winter conditions that affected annual species. Data gathered from NOAA.