5-2014

The equitable contributions of environment, management and restoration status on grassland diversity and composition

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THE EQUITABLE CONTRIBUTIONS OF ENVIRONMENT, MANAGEMENT AND RESTORATION STATUS ON GRASSLAND DIVERSITY AND COMPOSITION

by

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A THESIS

Presented to the Faculty of

The Graduate College at the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree Master of Science

Major: Biological Sciences

Under the Supervision of Professors Jean Knops and Chad Brassil

Lincoln, Nebraska

May, 2014

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University of Nebraska, 2014

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Plant composition is controlled by a combination of environmental, biotic, historical and management factors. Although there has been much focus on restoring grassland diversity, it is unclear which factors and/or interactions of factors are constraining diversity in grasslands and the relative influences of different factors. We measured soil fertility, soil texture, grazing intensity, fire frequency and plant cover in 694 plots, located within 33 remnant and restored fields in managed grasslands in the central Great Plains. Using univariate (general linear model) and multivariate (PERMANOVA) analyses, we identified significant factors and their relative contributions to plant richness, evenness, floristic quality index (FQI) and composition.

We found that species richness declines with nitrogen across all fields; however, remnant fields have higher species richness for any level of soil nitrogen. Remnant fields also have significantly more soil nitrogen than restored fields. Increased grazing intensity correlates with increased richness. Conversely, evenness and FQI are only affected by burn frequency. We found species composition is equitably controlled by environment, management and restoration status, explaining over one-third of the total variation. Soil nitrogen has the largest effect on composition but it is not exponentially greater than soil texture, grazing intensity, fire frequency and restoration status.

We performed an indicator species analysis to identify species associated with each environmental and management factor. Indicator species analysis reveals that the differences in environment and management maintain high beta diversity; the extremes of every factor maintain plant communities with similar floristic quality indices (FQI) and proportions of native/exotic species. Our results reinforce the premise that a complexity of drivers control ecosystems; no single management factor or environmental factor controls plant composition. Maintaining a diversity of management intensities and regimes helps sustain plant diversity across a variable landscape.

Acknowledgements

I would like to thank the large group of people who made this possible for me. Jean Knops, for bearing with my unending questions and for your support through this process. In addition to being the general awesome numbers guy on this project, my co-advisor, Chad Brassil, swooped in at the critical hour and nurtured my growth as a writer and scientist. Travis Hinkelman provided much needed statistical support and R-coding.

Trevor Johnson, Xiaoan Zuo, Wenjin Li, Kayla Tarr and Ryan Tompkins provided assistance in the field and lab. Thanks for all the laughter, guys! The Nature Conservancy and the Crane Trust allowed access to their grasslands as well as general field support and resources. I would like to thank Chris Helzer of The Nature Conservancy for being a constant source of humor, support and a shining example of the type of ecologist I would like to be.

To my lab mates, Kyle Funk and Yi Yang, thank you for all the discussions (scientific and otherwise), hilarity and margaritas. Cathleen McFadden, Rachael Wells, Afton Miller, Kilee Haase and Charlie Hubenka, the number of meals, ice cream runs, phone calls and general life support you have provided for me in the last four years kept me afloat, thank you.

My brother, Russ Powers, was a rock to lean on as well as a continuous source of free wild meats! Finally my parents, Pat and Geri Powers, have provided encouragement, support and love since day one, thank you.

Grant Information

This work was funded by funding from the Nebraska Game and Parks State Wildlife grants, Nebraska Environmental Trust, Sigma Xi, UNL Center for Great Plains and UNL School of Biological Science research grants.

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Introduction

For decades, scientists have struggled to understand the mechanisms that control plant communities observed in nature. It is clear that multiple factors contribute to the structure of communities. The factors that control diversity and composition fit into three broad categories: abiotic environment, biotic processes and disturbance. Identifying the factors which impact plant species diversity is a first step, but we must also explore the relative strength of influences from different factors to best guide conservation and management of plant communities. Studies which examine multiple abiotic drivers of diversity and their relative contributions to plant diversity and composition are scarce, but do find differences in the effect strengths of environment and management. For example, in hedgerows, abiotic variables, management factors and origin together explained about 17% of the variation in species composition, while spatial configuration only explained about 3.8% (Deckers, Hermy & Muys 2004). In long leaf pine forests, historical land use, historical connectivity and canopy cover explained 35% of variation in composition while factors like shrub density and current patch size were not associated with composition (Brudvig & Damschen 2011). They also found that management factors affected remnant and restored sites differently; in historically forested sites, overstory thinning had no effect but was a key driver of composition in post-agricultural forests (Brudvig & Damschen 2011). These studies demonstrate the need to quantify the relative impacts of environment, management and restoration status on composition; we need to know how much environment and management control diversity.

The main factors affecting managed grasslands are soil characteristics, restoration status and disturbance regime, i.e. grazing and burning (Briggs & Knapp 1995; Baer *et al.* 2003; Polley, Derner & Wilsey 2005; Anderson 2006). The studies establishing the importance of these factors mostly focus on their significance in predicting univariate indices of diversity, like richness, Shannon diversity or evenness. In three studies which examine relative effects, several aspects of management and environment have differing relative impacts on plant composition in managed grasslands (Klimek *et al.* 2007; Marini *et al.* 2007; Grman, Bassett & Brudvig 2013).

Among soil characteristics, soil nitrogen is an important determinant of plant communities, and grasslands are a classic example of the effects of fertilization on community structure. As nitrogen availability increases, many nitrophilous, non-native C3 grasses increase in dominance (Isbell *et al.* 2013). These grasses are efficient at capturing and utilizing soil nitrogen and form dense colonies with relatively high vegetation, effectively eliminating light to any short stature species. For example, nitrogen deposition explained 55% of the variation in species richness in British grasslands; species associated with infertile conditions were quickly lost with increased nitrogen deposition (Stevens *et al.* 2004).

Although the relationship between productivity and diversity varies widely globally (Adler *et al.* 2011), North American grasslands show clear patterns of decreased diversity with increased productivity (Mittelbach *et al.* 2001). A negative relationship between fertility and diversity poses a risk to prairie communities, as human inputs of nitrogen to the environment increase (Vitousek *et al.* 1997). Atmospheric deposition of nitrogen is especially a problem in the Midwestern grasslands of the United States, where ammonium deposition derived from row crop agriculture has substantially increased the total atmospheric nitrogen deposition in the last couple of decades (Krupa 2003).

In addition to soil fertility, other soil characteristics, such as soil texture, may have substantial effects on soil structure and plant-soil relations. For example, soil texture affects water holding capacity and soil organic matter, can be a key determinant of species richness, and also has been linked to the dominance of exotic species (Parton *et al.* 1987; Stohlgren, Schell & Vanden Heuvel 1999; Hanson *et al.* 2008). Sandy soils are less efficient at soil carbon storage than finer silty soils and therefore contain less soil organic matter (Parton *et al.* 1987). In one grassland study, soil texture was a key determinant of total and native only species richness (Stohlgren, Schell & Vanden Heuvel 1999), however, another study found no effect of soil texture on richness but it was a predictor of the dominance of exotic species (Hanson *et al.* 2008). The direction and significance of soil texture on richness and composition may be site specific and the size of its relative influence on composition is unclear.

Disturbance can lead to altered community composition with decreased species richness and diversity and is especially important in areas with a history of disturbance (Hobbs & Huenneke 1992). Management activities that mimic natural disturbances are often used on grasslands to enhance diversity, productivity and reduce woody and exotic species invasion (Hobbs & Huenneke 1992). In grasslands, prescribed fire and livestock grazing are used in place of wild prairie fires and native grazers, such as bison.

Grazing studies have shown a significant effect on composition, at moderate stocking rates, cattle graze preferentially on grasses and ignore most forbs, reducing grass dominance and productivity (Milchunas & Lauenroth 1993). As grass biomass is removed, understory forbs get more sunlight, bolstering growth and reproduction. The presence of large herbivores also accelerates the nitrogen cycle; altering both physical soil properties by compaction through trampling, and the quantity and quality of nutrients available for plants (Schrama *et al.* 2013). Moderately grazed grasslands have greater plant species diversity than non-grazed or infrequently grazed fields possibly because of light exclusion by long-lived grasses which dominate in undisturbed landscapes (Collins *et al.* 1998). For example, species richness and diversity at grassland sites in both North America and South Africa were highest in grazed versus ungrazed sites, with increased cover of forbs and decreased grass cover (Koerner & Collins 2013).

Worldwide, fire is a formative disturbance that structures the composition of ecosystems. The absence of fire can lead to biome shifts from grasslands to savannah or forest (Bond & Keeley 2005). However, the impact of fire on species diversity and richness is often dependent on study area and scale. In South African grasslands, species richness was unaffected by fire frequency but species composition was markedly different between burned and unburned sites (Uys, Bond & Everson 2004). Alternatively, eucalypt forests displayed a strong increase in diversity in the absence of fire (Gosper, Yates & Prober 2013). Uncovering the direction and relative strength of fire dynamics will help guide active management decisions.

In grasslands, prescribed burning is an increasingly common management activity. Periodic fire removes all aboveground standing biomass and litter, creating open soil space and ample light for plants, especially species that may have been suppressed but present in the understory (MacDougall & Turkington 2007). This leads to higher plant richness and diversity in areas with sporadic burning (Hobbs & Huenneke 1992). In fireprone landscapes, the suppression of fire leads to species loss, as seen in remnant grasslands in Wisconsin (Leach & Givnish 1996). However, the effects of fire can be detrimental as well, annually burned areas may have lower total species richness than unburned or grazed only areas as fire tolerant C_4 grasses become more dominant (Collins *et al.* 1998). If burning is present, the frequency of fires affects ecosystem response, diversity in annually burned grasslands may decline in diversity, peak in moderately burned grasslands and decline again with infrequent fires (Collins & Wallace 1990; Blair 1997).

In North American grasslands, restoring row crop agriculture fields to native species is a common conservation goal, but achieving and maintaining plant diversity at the level of healthy remnant grasslands is problematic. Remnant fields are often higher in species richness, diversity and evenness than restored fields, and are frequently lower in exotic species richness and relative biomass than restored fields (Martin, Moloney & Wilsey 2005; Polley, Derner & Wilsey 2005). These inequalities in plant composition may be due to the drastic differences in environmental characteristics between remnant and restored fields. Leaching, loss of soil organic matter and annual removal of plant biomass have reduced total soil nitrogen and carbon in cultivated fields (Bowman, Reeder & Lober 1990; Baer *et al.* 2002). Cultivation also changes species composition of arbuscular mycorrhiza and may exclude rare fungal species that may be important for the success of uncommon prairie plants (Stover *et al.* 2012). Additionally, effects of the soil seed bank may be constraining diversity in abandoned agricultural fields, which have fewer species and fewer seeds from native species compared to undisturbed grasslands (Schott & Hamburg 1997). Although seed is added to many restoration projects, there may be lingering effects of a low density and low diversity seed bank in restored fields. In total, restored grasslands often have less resource heterogeneity, overall poorer soil fertility, fewer fungal species to help extract soil nutrients, a smaller soil seed bank and less plant diversity, all of which may be barriers to restoring diverse plant communities.

To reestablish grassland ecosystems, we need to examine the environmental differences among sites so that we can mitigate the conditions that limit diversity and ecological function. Restored fields and fields with high nitrogen may support fewer species, while active grazing and burning can increase richness and evenness. The relative effects of environment versus management are fairly unexplored. Do historical and environmental factors override the effects of management? Or is current management the main predictor of species diversity and composition?

To address these questions, we must investigate the magnitude of effects of current management strategies on species diversity and composition, as well as the measure the influence of environment. Comparing the amount of control of management and environmental factors on diversity and composition and investigating interactions among these factors is essential to understanding and overcoming the constraints on plant diversity in both remnant and restored grasslands. Although the relative effects of soil nitrogen and soil texture on composition have begun to be explored, we found no studies investigating the separate relative contributions of restoration status, burn frequency and grazing intensity (Klimek *et al.* 2007; Marini *et al.* 2007; Grman, Bassett & Brudvig 2013).

Historically, the Platte River Basin was open, bison-grazed grassland; tree establishment was controlled by grazing, periodic fire, and flooding (Johnsgard 2008).

By the late 1860s, most bison herds were exterminated and permanent settlements established. Because grasslands in the floodplain are relatively flat, with abundant accessible water on highly fertile soils, most were converted to agricultural production. However, cattle grazing remains an important common practice in the area and is the main reason why, relative to other areas in Great Plains, a substantial part of the landscape is uncultivated prairie. The remaining grasslands are mostly conservation sites nested within an agricultural landscape dominated by large scale row-crop agriculture, mostly corn and soybeans.

Platte River grasslands are an ideal area to examine the relative roles of environment, management, and restoration status on multiple measures of plant diversity. This data is essential to develop successful grassland management and optimally use different management strategies in relation to varying environmental conditions. Our objectives were to first explore the relative impacts of soil texture, soil fertility, grazing intensity, burn frequency and restoration status on plant composition and diversity. And second, to investigate the importance of interactions between these factors. Specifically we addressed the following questions; across all fields, how important are management activities in comparison to environment and restoration status? Do restored and remnant fields have similar soil characteristics and do they respond similarly to management activities?

Methods

Study Area

Our study area is located in mixed grass prairies in the Platte River Basin of south central Nebraska, USA (98°34'57"W, 40°44'17"N). Several non-profit agencies have acquired property in the region to restore and preserve ecologically valuable grasslands. The Nature Conservancy (TNC) owns 2,000 hectares and the Crane Trust (CT) owns 4,000 hectares in this area.

Study fields are located along a 32 km stretch of the Platte river; fields are within the flood plain on lowland terraces (within 8 km of the river's edge), generally flat; with an average elevation of 567 m. Sites are in the Great Plains ecoregion with a continental climate; growing season is 6 months long, April-October, with mean maximum and minimum temperatures of 25.3°C and 12.3°C and mean annual rainfall of 658 mm; all climate data are 30 year averages (CLIMOD 2014).

These prairies are dominated by warm season grasses but species diversity is mostly comprised of cool season grasses, sedges (due to lack of flowering head, most sedges were identified only to genus *Carex*) and forbs (Table 1).

We collected observational data from a total of 33 grasslands, 25 owned by TNC and 8 CT fields. Conservation fields are managed with controlled burns, cattle grazing and infrequent haying. In comparison to non-conservation grazed fields, which are infrequently or never burned, conservation fields have a high burn frequency at 0.2-0.6 burns/year, and lower intensity grazing. Although most fields have relatively low stocking rates of 0-1.7 AUM/acre, the CT has infrequent periods of intense grazing in wetter meadow sites with 3.0-3.7 AUM/acre. Fifteen fields are restored (restoration year varies from 1988-2005) and 18 fields are remnant grasslands.

Vegetation sampling

In order to capture the heterogeneity of soils and management within a field, we established 21 plots within each field, for a total of 694 permanent plots within 33 fields.

The average field size is 94 acres, ranging from 15-369 acres. In most fields, plots were systematically placed on 3 transects to maximize the spread of plots across the field, while minimizing the travel time to plots within each field. Transects were placed equidistance from each other and from the edge of the field, they were usually oriented North-South. A typical transect was comprised of seven equally spaced plots. There were multiple fields that were not square shaped. In order to place plots evenly across the field, we placed unequal numbers of plots on transects of different lengths in 15 fields. Four fields required four transects. However, each field contained 21 plots; regardless of transect number or length.

All plots were 0.5 x 1 m^2. This size reduced the observer time to estimate species cover and is comparable to other studies (Inouye *et al.* 1987; Miles & Knops 2009; McGranahan *et al.* 2012; Li, Zuo & Knops 2013). We used a square plastic frame, constructed of 1 cm wide round PVC pipe, covering the 0.5 m^2, placed using the two metal plot markers.

Every plant species was identified following Kaul *et al.* 2006 and questionable identifications were verified by the state botanist. The abundance of each species was visually estimated; cover estimates totaled to 100% for each plot. All cover estimates were integers. Two researchers visited plots together and independently estimated percent cover for each species, estimates were compared and a single cover value agreed upon. Four researchers formed two teams to record cover; team composition was not static. All researchers spent 3 days learning cover estimate method and plant species at the start of the 2010 field season. Cover estimates were recorded from early July to late August at the peak of warm-season plant production.

Richness, evenness, and floristic quality index were calculated for each plot and averaged to field (Molles & Cahill 1999). Floristic quality index (FQI) is a quantitative measure of community quality for an area; both species richness and an assigned coefficient of conservation value (C) for each species are included in FQI (Rooney & Rogers 2002). We split plot-level plant richness data into native and exotic species, averaged to field and analyzed as separate dependent variables. We examined the relative abundance of native species by dividing the cover of native species by total cover in each plot and averaging to field. For all multivariate analysis, we used field averages of cover data.

Soil Sampling

Soil type in this river floodway is highly variable, both within and among fields, due to differential deposition and erosion of sediment as the river location moves within the floodplain through time. This produces alternating strips of gravel, clay and sand at our sites.

Soil cores (2 cm x 10 cm) were collected in 2010. Five soil cores were extracted from within each plot; core locations were placed evenly inside the entire plot area. The five samples were combined, dried to 65° Celsius and sieved through 2 mm to remove larger gravel and root pieces. The resulting soil samples were used to determine soil texture, soil nitrogen and soil carbon. Soil particle size (percent silt, sand, and clay) was determined using the hydrometer method with 50 g soil (Elliot *et al.* 1999). Total nitrogen and carbon were analyzed using a dry combustion GC analysis on a Costech Analytical ECS 4010 with 20-25mg finely ground soil. We averaged the plot soil characteristics to determine field averages.

Scale

To explore if heterogeneity within a field may impact plant trends, we calculated a coefficient of variation (CV) for every continuous factor in each field and included it in our analysis of richness, evenness and FQI.

Management

Initially, we explored three current management activities; haying, grazing intensity and fire frequency. However, haying was not frequent or common enough at our sites for this analysis. In addition to fire frequency and grazing intensity, we included the restoration status of the field as a categorical factor. For fire frequency, management records from the 5 years previous to plant sampling, 2006-2010, captured more variation than a 3 year scale. While even longer time scales captured more variation in burn frequency, the decreasing impact of disturbance on vegetation through time prompted us to choose more recent management only. For simplicity, we also used a five year time scale for grazing intensity. Some management was performed at a subfield level; field averages were calculated as follows.

Grazing intensity was calculated using animal unit months per acre (AUM/acre), a common measure of herbivory in range science (Helzer 2010). AUM/acre records were obtained from the TNC and CT. Plot level AUM/acre was determined for each year and summed across a field to provide yearly value of AUM/acre for each field. We averaged the five yearly AUM/acre values for each field.

We created a proportional value for fire frequency by examining the number of plots burned in each field in each year. For example, if three of twenty one plots burned in a single year, the burn frequency for the field in that year would be 3/21 or 0.142. The yearly burn frequencies were averaged for each field across the five year history.

Data analysis

All of the observed correlations found using the following analysis methods are based solely on observational data. To simplify the presentation of results, we used causative language to describe relationships.

We used general linear models (GLMs) to test how soil and management influenced plant richness, evenness and FQI. We used standardized regression coefficients for ANOVA tables (type II) performed in R (Fox 2008; R Core Team 2013). Linear models were used and we tested all interactions between factors.

We tested how soil and management affected community composition using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Dissimilarity among plant composition in each field was calculated with the Bray-Curtis index. To visualize PERMANOVA results, we performed a non-metric multidimensional scaling (NMDS) (Kruskal 1964). NMDS also uses the Bray-Curtis index and shows the location of each field in two-dimensional space; axes are composites of plant species presence and cover. All PERMANOVAs and NMDSs were performed using the vegan package in R.

We used indicator species analysis in the labdsv package in R to identify species that were significantly abundant and had high fidelity to sites with specific management strategies (Dufrêne & Legendre 1997). Each continuous management or environmental factor was divided into two categories at the median of the values for our fields. For burn frequency, a large number of fields were never burned in the 5 year management average.

Therefore, one category of burn frequency is fields which have not been burned in over 5 years, while the other is fields which have been burned at least once in the 5 years previous to sampling.

Results

Soil

Soil texture within our 33 fields varied from clay loam to silty sand and covered 7 of 12 soil classes identified by USDA (appendix Figure A1). Because soil texture categories (sand, silt and clay) were highly inversely correlated (appendix Table A1), the first component of a principle component analysis (PCA), which captured 61% of the variation, was used as the soil texture factor in analysis.

Soil total organic carbon ranged from 0.08-6.5% and was highly correlated with soil total nitrogen, which varied from 0.01-0.56% among plots (appendix Table A1). Consequently, we used only soil nitrogen throughout the analysis, however, carbon showed the identical patterns. Carbon/nitrogen ratio varied much less, from 7.2 to 17.2 with a mean of 11.5. All soil and management terms are field averages of plot level observations.

Species richness, evenness and FQI

In total, we identified 187 unique species in 2010, with a range of 2 to 18 species per plot, and an average of 7.8 species. Evenness varied from 0.06 to 1.00 with an average of 0.59 per plot. Shannon diversity varied from 0.07 to 2.21 with an average of 1.20 per plot. FQI varied from 0 to 14.9 per plot with an average of 6.8.

We also tested the importance of within field variation for soil nitrogen, soil texture, burn frequency and grazing intensity by including the coefficient of variation (CV) calculated from the 21 replicated plots in each field. Only the CV of soil nitrogen had a significant impact, solely on richness, evenness and FQI were unaffected by any CV. We included the significant CV soil nitrogen in our analyses of richness, evenness and FQI to simplify the presentation of results.

Field average soil nitrogen, CV soil nitrogen, restoration status and grazing intensity significantly affect richness and explain about 60% of the variation (Table 2). Of these, average soil nitrogen has the largest impact on plant species richness. Fields with higher soil nitrogen CVs have lower species richness than fields with lower nitrogen CVs, i.e. fields that have more soil nitrogen variation among plots have lower species richness. Increasing average field soil nitrogen and the CV of soil nitrogen has negative impact on richness, unlike grazing intensity, which increases richness. Restored fields have, on average 2 less species than remnant fields.

In the analysis of species richness, evenness and FQI, no interaction terms between field averaged soil nitrogen, soil texture, burn frequency, grazing intensity and restoration status were significant, thus we use backward selection and present only the main effects (appendix Table A2).

Evenness was only marginally positively affected by burn frequency, with 16% of variation explained (Table 2). Average soil nitrogen, CV soil nitrogen, average field soil texture, grazing intensity and restoration status had no effects on evenness.

FQI showed nearly the same pattern as evenness; burn frequency had a marginal, positive effect on FQI, explaining 18% of the variation (Table 2). Average soil nitrogen, CV soil nitrogen, average field soil texture, grazing intensity and restoration status had no effects on FQI. In the FQI analysis, when we included both restoration status and soil nitrogen, neither was significant, whereas when only one factor was included, both were marginally significant. Thus we excluded the restoration status from the FQI analysis.

In the analysis of species richness, evenness and FQI, no interaction terms between field averaged soil nitrogen, soil texture, burn frequency, grazing intensity and restoration status were significant, thus we present only the main effects (appendix Table A2).

To summarize, species richness was affected by average soil nitrogen, CV soil nitrogen, restoration status and grazing intensity. In contrast, evenness and FQI were only affected by burn frequency.

Remnant versus restored grasslands

Species richness declines with increasing field average soil nitrogen (Table 2). At a given level of soil nitrogen, remnant fields have 2 more species than restored fields (Figure 1). We found that remnants, on average, have twice as much soil nitrogen as restored fields. Soil nitrogen captures some of the variation in restoration status that affects plant communities, but there is additional variability in restoration status which also affects plant diversity.

Native vs exotic species richness

Soil nitrogen has opposite effects on native species and exotic species. Native species richness decreases by half as nitrogen increases, a trend seen in total species richness as well. In contrast, exotic species richness increases by approximately 2 species across the range of nitrogen values (Figure 2). Because there are approximately 1/5 as many exotic species as native species, native species drive the trends that we see in total species richness.

Community composition

Soil nitrogen, restoration status, grazing intensity and burn frequency were significant drivers of composition, explaining roughly 1/3 of the variation (Table 3). Composition trends with soil texture (p=0.059). Nitrogen has the largest relative effect (R^2=0.125), but all other factors are roughly similar, with R^2 values of 0.041-0.068 (Table 3). In other words, environment, management and restoration status all had similar contributions to the compositional structure of our grasslands.

We found a significant relationship between field average soil texture and grazing intensity on composition, there were no significant interactions between average soil nitrogen, burn frequency and restoration status (appendix, Table A3). The significant interaction between soil texture and grazing intensity seems to indicate that the effects of soil texture are less important at high grazing intensities (appendix, Figure A2). We presented only main effects to avoid correlation between main and interactive factors and because of the difficulty of presenting the interactive effect visually.

Multiple species were identified as indicator species for high and low values of soil nitrogen, restoration status and grazing intensity. High burn frequency and sandy soil texture also had multiple indicator species. In contrast, fields which were burned infrequently had no significant indicator species and fields with silty/clay soil texture had only a single significant indicator species. A complete list of all significant indicator species for all factors is in appendix A4.1-5.

At low soil nitrogen values (0.06-0.23%), there were 15 indicator species; 11 low growing forb species and 4 graminoids. In contrast, high levels of soil nitrogen (0.23-

0.39%) were associated with 7 grass species and only 3 forbs. This is a common trend in nitrogen gradients, as competitive, tall grasses shade out short statured forbs in high nitrogen conditions (Tilman 1987). Because restoration status is correlated with soil nitrogen, we saw many of the same species in remnant/restored fields as in high/low soil nitrogen fields. Restored fields and low nitrogen fields had 10 common indicator species, restored fields had 6 indicator species not associated with low nitrogen sites. Remnant fields and high nitrogen fields had 10 indicator species in common, remnant fields also had 6 species not associated with high nitrogen fields. We saw no clear patterns in the indicator species unique to remnant or restored fields.

Sandy fields, ~73-90% sand, had 11 significant species; eight forbs and 3 graminoids. In silt/clay fields, ~58-72% sand, only a single forb species, *Physalis longifolia*, was significant. All indicator species in sandy fields are plants we would qualitatively associate with dry soils and so these trends may be driven by the water holding capacity as well.

There were no species associated with infrequently burned fields. In fields that were recently burned, there were 5 significant species, all generalist, small-seeded native species and one nitrogen fixing species. This is consistent with other remnant grasslands where nitrogen fixing and small seeded species were lost with suppression of fire, likely because these species are successful in post-fire environments, i.e. open, sunny areas (Leach & Givnish 1996).

In fields with low grazing intensity, indicator species were mostly forbs and highly palatable species in our system (Helzer, personal communication). Alternatively, in intensely grazed fields, unpalatable grasses dominate. Herbivore selectivity is a known driver of community composition in grasslands, here we see the increased intensity of grazing leading to communities significantly associated with species that cattle avoid (Brown & Stuth 1993).

Discussion

We found that average field soil nitrogen, soil texture, restoration status, burn frequency and grazing intensity explained 1/3 of the composition differences between 33 remnant and restored fields. Differences in soil (nitrogen and texture), restoration status and management (burn frequency and grazing intensity), were similarly important in explaining the composition differences. Therefore, it's clear that in our site, soil characteristics, management and restoration status all influence the plant diversity and structure of communities in managed grasslands. The relative contributions of environment, history and management are only beginning to be studied and understood across ecosystems and research sites (Brudvig 2011).

Soil nitrogen often has been identified as a significant driver of vegetation composition (Wedin & Tilman 1996; Cleland & Harpole 2010). However, only a few studies have examined the relative importance of soil nitrogen versus management factors. Two grassland studies that examined the relative importance of both management and environment (Klimek *et al.* 2007; Marini *et al.* 2007), found that management (which includes soil nitrogen) explained 1/4 to 1/3 of total vegetation composition variation, whereas soil phosphorous and other microsite feature like elevation, slope or solar radiation only explained a small amount of the variation. In both these studies, soil nitrogen was not examined independently of the other factors. In contrast to our study, the soil nitrogen gradient in these studies was created by fertilizing and was done simultaneously with other management actions, and soil nitrogen, grazing and haying were analyzed as a single management term. In addition these studies covered a much larger topographic gradient and because of the high atmospheric nitrogen deposition in Europe, the location of both studies, and additional nitrogen fertilization, phosphorous limitation is more common. In contrast, within North American grasslands, nitrogen is often the most limiting resource for productivity (Cleland & Harpole 2010).

Although restoration status and burn frequency are known drivers of species richness (Collins & Wallace 1990; Cousins, Lindborg & Mattsson 2009), evenness (Polley, Derner & Wilsey 2005; Heslinga & Grese 2010) and composition (Sluis 2002; Uys, Bond & Everson 2004), their relative influence on composition when compared to other management and environment is rather unstudied. We found restoration status and burn frequency had comparable impacts on composition as all other management and soil characteristics. The only study quantifying the relative influence of grazing intensity compared to other management or environmental factors on composition found that management, which included soil nitrogen and hay cutting frequency, explained an equitable amount of variation as the environmental factors measured, similar to our findings for grazing and soil characteristics (Klimek *et al.* 2007). (Grman, Bassett & Brudvig 2013) also explored the relative effect of management and soil and found that vegetation composition was equitably controlled by site age, soil heterogeneity, seed mix and the surrounding landscape type, which explained 36% of the site differences in composition. Soil texture did not have a significant effect on composition. This study also did not include site differences in soil nitrogen, burn frequency or grazing intensity. Thus, surprisingly, even though the identity of the specific management and soil factors differ, both management and soil often explain comparable amounts of variation in species composition among grasslands (Klimek *et al.* 2007; Marini *et al.* 2007; Grman, Bassett & Brudvig 2013). Thus, no single factor controls grassland vegetation species composition, and our results and the other studies cited above strongly support the hypothesis that many soil, management, historical and landscape factors control grassland composition and that the identity of which specific soil and management factors differs among sites.

We found, associated with differences in restoration status, soil nitrogen and grazing intensity, comparable numbers of native and exotic species and roughly similar average coefficient of conservatism (C) values, a measure of each species' fidelity to intact, high quality plant communities. In addition, we also found different indicator species and species composition associated with differences in restoration status, soil nitrogen and grazing intensity. Therefore, the combination of differences in soil, management and field history all contributed to environmental and site heterogeneity which increases different niches and results in higher beta diversity, without having clearly inferior fields low in conservation value and high in exotic species. This indicates that variability in soil, management and restoration status are ecologically valuable and should be maintained and incorporated into overall site selection and grassland management in order to maximize beta diversity. In other words, restored fields and nitrogen rich fields contribute unique niches that increase the overall diversity and increases niches available for plant species. Variation in grazing also contributes to increased overall species richness. In contrast, the lack of indicator species in infrequently burned field's points to little value of having unburned fields within our grasslands. Sporadic burning of all fields lowers litter accumulation and conserves valuable short statue forb species.

In our study we only explained 1/3 of the field differences in species composition. Other factors that we did not examine, such as site restoration age, seed mix and surrounding landscape type (Grman, Bassett & Brudvig 2013), also are likely to be important drivers of grassland composition and diversity. In addition, we only analyzed one year of species composition data and species composition can vary among years, both in response to climate variation (Mitchell & Csillag 2001) and ongoing successional changes (Connell & Slatyer 1977). Our study is also correlational, and although we had relatively high replication at both the plot-level and field-level, particularly in the number of remnant and restored fields over a large spatial scale (encompassing 32 km of river floodplain grasslands), we did not directly experimentally manipulate soil characteristics or management. Beyond experimentally testing the relationships we observed, an important next step is to evaluate the ecological function linked to species that are associated with each soil, and management factor. In other words, do restored fields maintain similar levels of ecological function? Are there like numbers of functional groups in high nitrogen and low nitrogen fields? Answering questions like these regarding both environment and management will further guide land managers to management practices that create and maintain not only plant diversity and composition, but the essential ecological functions that we rely on.

We found that species richness was affected by soil nitrogen, CV soil nitrogen, restoration status and grazing intensity, while evenness and FQI were only affected by burn frequency. In short, we found remnant fields with uniform low soil nitrogen which are moderately grazed and burned to have greater values in multiple measures of diversity. Exploring multiple measures of plant diversity can shed light on the varying effects of different factors on biodiversity (Ruiz-Jaen & Aide 2005; Anderson *et al.* 2011).

We found restored fields to have significantly lower soil nitrogen than remnant fields and also lower species richness. This is a common finding in restored grassland fields (Sluis 2002; Hansen & Gibson 2014). Both remnants and restored fields increase richness with less soil nitrogen, but restored fields are consistently lower in richness, regardless of soil nitrogen. Our inference on richness and nitrogen may be limited because the overlap in soil nitrogen in remnant and restored fields is fairly low and we measured total soil nitrogen, not the amount of mineralized nitrogen that is available to plants. Differences in species richness between remnant and restored field may be due to soil nutrients besides carbon and nitrogen, differences in soil microbe diversity or density, soil structure differences, effects of species pool and seed limitation (Janssens *et al.* 1998; Turnbull, Crawley & Rees 2000; van der Heijden, Bardgett & van Straalen 2008). Identifying the factors that constrain restored communities to relatively low richness values is critical, because although restored fields support a unique community with a range of conservation values, their deficiency in species richness could have implications for their ecological function. High diversity has been positively linked with a number of ecological functions including productivity and resistance to invasion (Hooper *et al.* 2005; Isbell *et al.* 2011).

Interestingly, while soil nitrogen varied between restored and remnant fields, we found management factors had the same effect regardless of restoration status. Across all fields, we found increased grazing to have a positive effect on species richness, as seen in many other grassland studies (Collins *et al.* 1998; Kruess & Tscharntke 2002; Pykala

2003). Light to moderate levels of grazing intensity increase species richness, grazing intensities high enough to see the negative impacts of "overgrazing" on diversity are not present in this site (Milchunas, Sala & Lauenroth 1988). We found that burn frequency had no effect on species richness but does affect evenness. This concurs with other grassland research where an increase in evenness was found with burn regime (Heslinga & Grese 2010). We also found a positive relationship between FQI and burn frequency, which was a result inferred in other grasslands (Jog *et al.* 2006).

Management implications

We see this study as a first step in evaluating the scope of various factors on plant community structure in managed grasslands. Although about 2/3 of explained variation explained in plant composition is controlled by abiotic factors and restoration status, management activities are significant drivers of composition. Additionally, management has positive effects on species richness, evenness and FQI.

Our analysis of species diversity indicates that fields with lower soil nitrogen and less variation in soil nitrogen have higher potential for species richness than high nitrogen fields. Indicator species analysis reveals that silty/clay fields are associated with a single common grassland species, while sandy fields support more diverse, uncommon species. To support both more species and rarer species, fields with lower soil nitrogen, less variance in soil nitrogen within the field and sandier soils should be prioritized for restoration and conservation. Additionally, we found moderate grazing intensities promote higher richness while moderate burn frequencies increase evenness and FQI. To support high species diversity at the field scale, moderate burn frequencies and grazing intensities are encouraged.

In contrast to field level recommendations, to support diversity on a landscape scale, having fields that vary in soil nitrogen content, grazing intensity and restoration status are essential to sustain a diverse pool of plant species. We found that diversity in soil characteristics, management strategies and restoration status increases available niche space that supports grassland diversity.

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Table 1. Field characteristics for 33 prairies. Average soil nitrogen and carbon, richness and soil textures values from 21 0.5x1 m^2 plots in each field. The species listed are ten most frequent species across all fields in 2010, if the species is also one of the 10 most abundant species found in a field there is an x.

Owner	Field area (acres)	Restoration year	% Soil Nitrogen (Ave ± S.E.)	% Soil Carbon (Ave ± S.E.)	% Sand	% Clay	% Silt	Mean field species richness	*Andropogon gerardii*	*Poa pratensis*	*Panicum virgatum*	*Medicago lupulina*	*Carex unidentified*	*Symphyotrichum ericoides*	*Equisetum laevigatum*	*Ambrosia psilostachya*	*Elymus canadensis*	*Panicum oligasanthes*
TNC	34	R*	0.341 (±0.016)	4.08 (±0.19)	71	4	25	5.7	x	x	x				x			
TNC	112	R	0.312 (±0.031)	3.51 (±0.35)	72	4	23	7.6	x	x	x		x					
TNC	369	R	0.265 (±0.020)	3.13 (±0.24)	64	10	26	7.0	x	x	x		x			x		
CT	229	R	0.224 (±0.023)	2.70 (±0.27)	80	3	17	10.2	x	x				x		x		x
TNC	56	R	0.272 (±0.023)	2.99 (±0.27)	69	7	23	8.3	x	x						x		x
TNC	125	R	0.381 (±0.026)	4.64 (±0.34)	73	6	21	7.8	x	x	x	x		x		x		
TNC	30	R	0.333 (±0.025)	4.13 (±0.23)	66	7	28	6.0	x	x	x	x	x					
TNC	168	R	0.225 (±0.024)	2.51 (±0.29)	74	4	21	8.4	x	x				x		x		x
TNC	157	R	0.230 (±0.026)	2.90 (±0.30)	73	6	21	10.0	x	x			x			x		x
TNC	67	R	0.232 (±0.015)	2.88 (±0.23)	78	5	21	6.9	x	x	x					x		x
TNC	214	R	0.314 (±0.020)	3.88 (±0.28)	71	8	21	8.6	x	x	x		x					
TNC	15	R	0.383 (±0.013)	4.64 (±0.13)	70	6	23	6.4	x	x	x		x		x			
TNC	55	R	0.121 (±0.010)	1.41 (±0.12)	82	5	13	10.6	x	x	x					x		x
CT	82	R	0.259 (±0.018)	2.91 (±0.21)	74	6	20	6.4	x	x	x	x			x	x		
TNC	138	R	0.333 (±0.013)	3.74 (±0.16)	75	5	20	7.8	x	x	x	x	x	x				
CT	83	R	0.213 (±0.014)	2.44 (±0.21)	82	5	12	9.2	x		x		x					
CT	122	R	0.306 (±0.019)	3.34 (±0.22)	79	5	16	9.1	x	x	x		x					
CT	96	R	0.262 (±0.026)	3.19 (±0.32)	79	7	15	8.6	x	x	x		x			x		
CT	97	1988	0.199 (±0.014)	2.43 (±0.16)	71	7	22	6.9	x	x	x							
CT	40	1992	0.168 (±0.013)	1.87 (±0.17)	68	7	25	7.6	x	x	x		x	x				
TNC	107	1994	0.251 (±0.011)	3.08 (±0.15)	58	10	33	6.3	x	x	x						x	
TNC	49	1995	0.168 (±0.011)	1.97 (±0.13)	69	8	23	6.9	x	x	x					x		
CT	65	1995	0.171 (±0.012)	2.00 (±0.15)	68	6	26	6.5	x	x	x		x					
TNC	23	1997	0.124 (±0.007)	1.43 (±0.09)	75	5	20	7.0	x	x	x						x	
TNC	28	1997	0.130 (±0.008)	1.65 (±0.13)	71	6	22	6.9	x	x	x							
TNC	19	1999	0.100 (±0.015)	1.03 (±0.16)	90	3	7	9.1	x							x		
TNC	71	1999	0.118 (±0.008)	1.34 (±0.10)	75	7	19	7.7	x		x	x		x			x	
TNC	64	2000	0.066 (±0.003)	0.70 (±0.40)	83	5	11	8.3	x									
TNC	67	2001	0.112 (±0.013)	1.24 (±0.14)	79	6	15	7.3	x	x	x	x					x	
TNC	69	2002	0.100 (±0.010)	1.07 (±0.12)	78	7	14	7.2	x		x						x	
TNC	108	2002	0.099 (±0.008)	1.09 (±0.10)	71	7	22	8.7	x	x	x							
TNC	30	2003	0.156 (±0.008)	1.72 (±0.10)	66	9	25	7.6	x					x			x	
TNC	120	2005	0.102 (±0.011)	1.18 (±0.14)	73	5	21	7.9	x	x	x						x	

Table 2. General linear model results using field history, soil and management explaining richness, evenness and floristic quality index (FQI). (n = 33 restored and remnant prairies, 21 plots/field). Environmental data and plant cover are 2010 plot data or field average data. Restoration status is a 0/1 relationship where remnant fields=0 and restored fields=1. Management records were collected at the plot-level and averaged to field level, management parameters shown are from 2006-2010. .p<0.1, *p<0.05, **p<0.005, ***p<0.0005.

Richness	**Estimate**	**Sum Sq**	**F value**	**p value**	
Restoration status	-2.06	9.13	15.56	0.00	***
Soil nitrogen	-1.15	8.98	15.30	0.00	***
CV nitrogen	-0.38	4.16	7.08	0.01	*
Soil texture	0.24	1.08	1.84	0.19	
Grazing intensity	0.37	3.92	6.68	0.02	*
Burn frequency	0.09	0.24	0.41	0.53	
Residuals		15.26			

Adjusted R^2: 0.59

Evenness	**Estimate**	**Sum Sq**	**F value**	**p value**	
Restoration status	0.02	0.00	0.32	0.58	
Soil nitrogen	-0.01	0.00	0.08	0.78	
CV nitrogen	-0.02	0.01	3.15	0.09	.
Soil texture	0.00	0.00	0.02	0.88	
Grazing intensity	0.01	0.00	0.50	0.48	
Burn frequency	0.02	0.02	5.55	0.03	*
Residuals		0.08			

Adjusted R^2: 0.16

FQI	**Estimate**	**Sum Sq**	**F value**	**p value**	
Soil nitrogen	-0.40	3.76	3.82	0.06	.
CV nitrogen	-0.13	0.47	0.47	0.50	
Soil texture	-0.17	0.75	0.76	0.39	
Grazing intensity	0.07	0.16	0.16	0.69	
Burn frequency	0.48	6.65	6.75	0.01	*
Residuals		26.60			

Adjusted R^2: 0.21

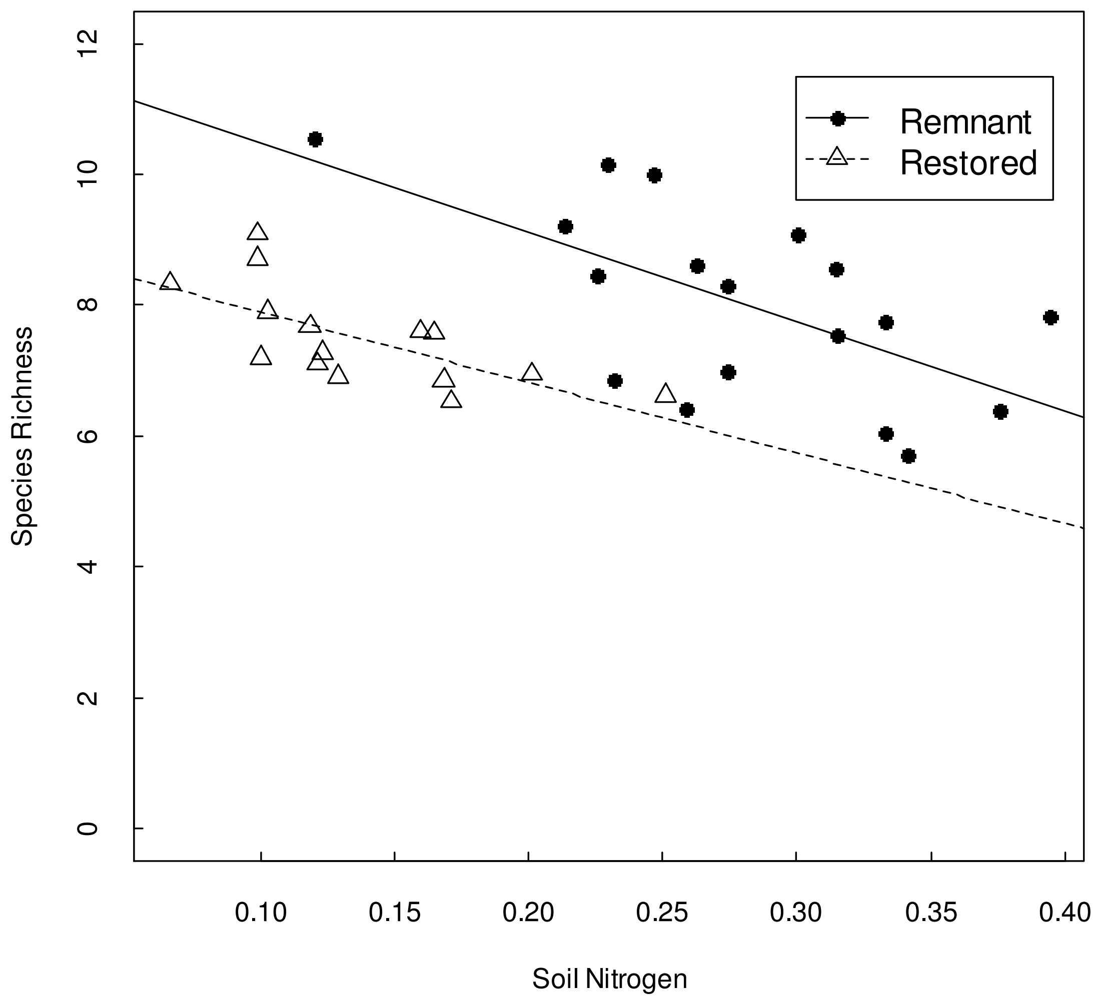

Figure 1. Species richness versus soil nitrogen, presented are the averages of 33 fields. All data are field averages from data collected from 21 plots/field in 2010. Linear regression lines from both remnant fields (F value= 10.13, p value=0.01*, R^2=0.35) and restored fields (F value= 11.07, p value=0.01*, R^2=0.42) are plotted.

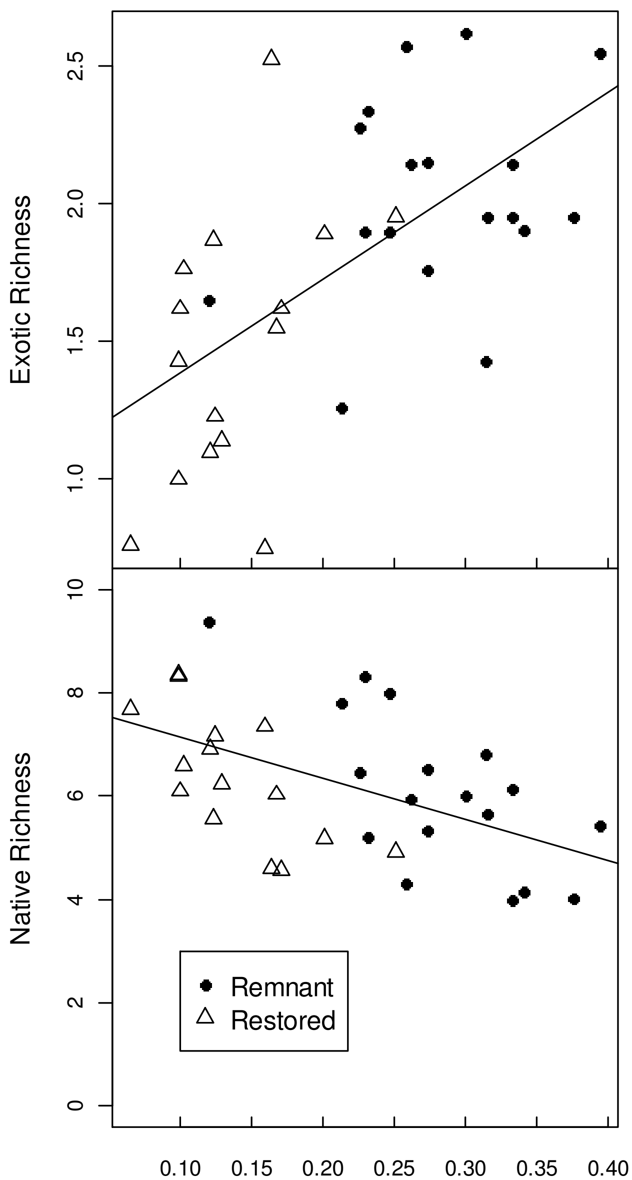

Figure 2. Native and exotic species richness versus soil fertility and for 33 fields. Linear regression lines for exotic richness (F value= 18.83, p value=0.00***, R^2=0.36) and native richness (F value= 11.52, p value=0.001**, R^2=0.25) are plotted.

Table 3. PERMANOVA results of environment and management impacts on plant composition from 33 grasslands. Environmental data and plant cover were collected at in 2010 at 21 plots/field and averaged for each field. Management records were collected at the plot-level and averaged to field level, management parameters shown are from 2006-2010. Restoration status is a 0/1 relationship where remnant fields=0 and restored fields=1. .p<0.1, *p<0.05, **p<0.005, ***p<0.0005.

	Df	**Sum Sq**	**F value**	**R^2**	**P value**	
Restoration status	1	0.355	2.715	**0.065**	0.004	**
Soil nitrogen	1	0.680	5.197	**0.125**	0.001	***
Soil texture	1	0.223	1.707	**0.041**	0.059	.
Grazing intensity	1	0.369	2.822	**0.068**	0.003	**
Burn frequency	1	0.274	2.097	**0.050**	0.024	*
Residuals	27	3.533		0.650		
Total	32	5.435		1.000		

R^2: 0.350

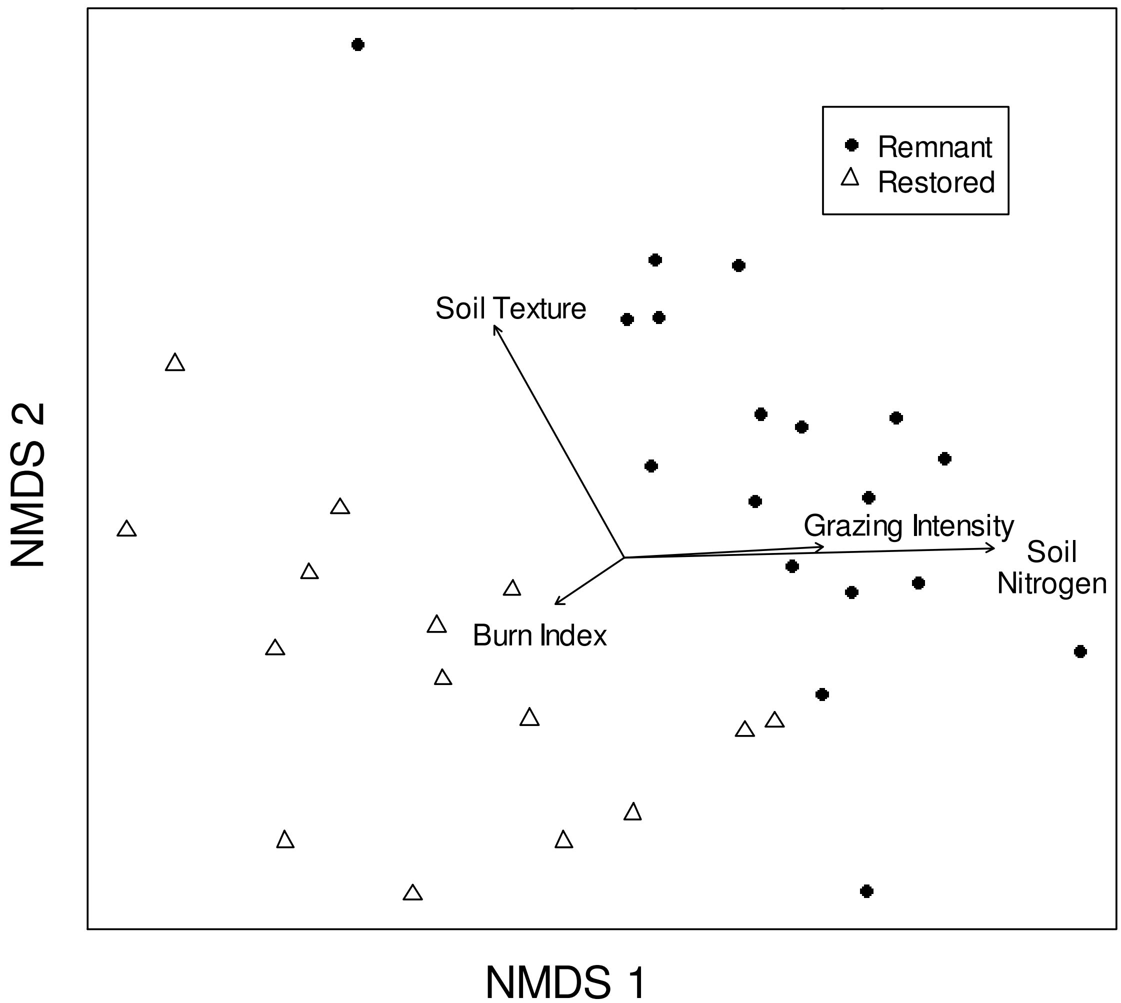

Figure 3. Nonmetric Multidimensional Scaling (NMDS) with linear vectors of environmental and management vectors. Data collected from 33 fields in 2010 at 21 plots/field and averaged for each field. Management records were collected at the plot-level and averaged to field level, management parameters shown are from 2006-2010. Direction and length of lines indicate species composition at with increasing values of predictor value.

Appendix

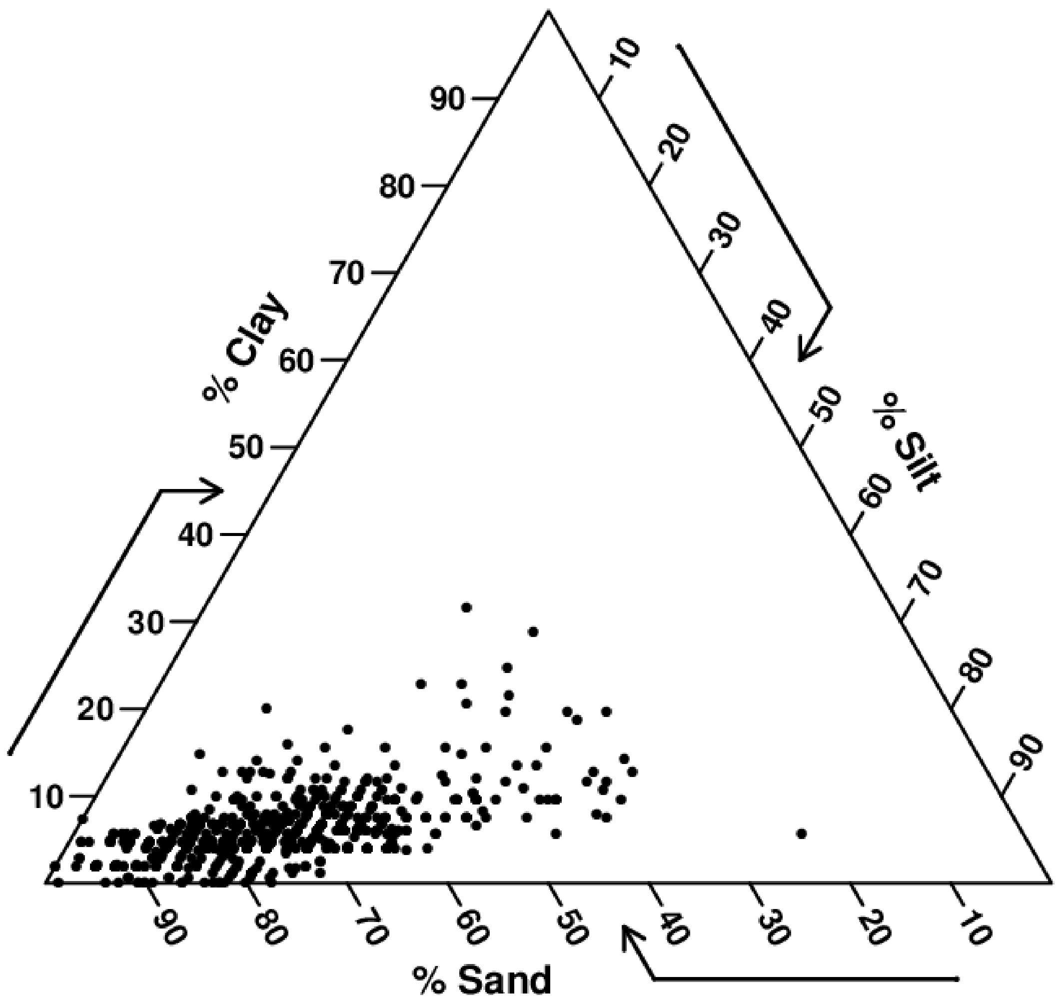

Figure A1. Soil texture of 33 restored and remnant prairies (0-10 cm for 694 plots, ~21 plots/field).

Table A1. Pearson correlations among predictor variables.

	Silt	Sand	Clay	Soil carbon	Soil nitrogen	C/N ratio	Restoration status	Soil texture	Burn frequency
Sand	-0.98								
Clay	0.57	-0.74							
Soil carbon	0.39	-0.33	0.04						
Soil nitrogen	0.37	-0.31	0.02	0.99					
C/N ratio	0.45	-0.41	0.19	0.55	0.46				
Restoration status	0.03	-0.09	0.24	-0.76	-0.78	-0.28			
Soil texture	-0.99	1	-0.69	-0.35	-0.33	-0.43	-0.07		
Burn frequency	-0.19	0.16	-0.04	-0.25	-0.23	-0.23	0.14	0.17	
Grazing intensity	0.18	-0.14	-0.04	0.26	0.27	0.15	-0.13	-0.15	0.09

Table A2.1. Richness. Shown are the ANOVA results for main factors and interactions on richness. .p<0.1, *p<0.05, **p<0.005, ***p<0.0005.

Richness	**Estimate**	**Sum Sq**	**F value**	
Restoration status	-2.72	7.71	9.96	**
Soil nitrogen	-0.92	7.59	9.81	**
CV nitrogen	-1.21	3.17	4.09	.
Soil texture	1.50	0.25	0.32	
Grazing intensity	2.23	1.30	1.68	
Burn frequency	1.02	0.22	0.29	
Restoration status:soil nitrogen	-0.28	0.02	0.03	
Restoration status:CV nitrogen	0.54	0.14	0.18	
Restoration status:soil texture	-0.96	0.45	0.58	
Restoration status:grazing intensity	-1.40	1.25	1.62	
Restoration status:burn frequency	-0.63	0.12	0.15	
Soil nitrogen:CV nitrogen	0.06	0.01	0.01	
Soil nitrogen:soil texture	-0.22	0.12	0.16	
Soil nitrogen:grazing intensity	-0.73	1.10	1.42	
Soil nitrogen:burn frequency	-0.13	0.02	0.02	
CV nitrogen:soil texture	-0.48	0.92	1.19	
CV nitrogen:grazing intensity	-0.32	0.99	1.27	
CV nitrogen:burn frequency	0.01	0.00	0.00	
Soil texture:grazing intensity	-0.19	0.13	0.17	
Soil texture:burn frequency	-0.24	0.31	0.40	
Grazing intensity:burn frequency	-0.07	0.03	0.03	
Residuals		8.51		
Adjusted R^2:	0.46			

Table A2.2. ANOVA results for main factors and interactions on evenness. .p<0.1, *p<0.05, **p<0.005, ***p<0.0005.

Evenness	**Estimate**	**Sum Sq**	**F value**
Restoration status	0.03	0.00	0.08
Soil nitrogen	-0.13	0.00	0.55
CV nitrogen	0.13	0.00	0.93
Soil texture	0.05	0.00	0.02
Grazing intensity	0.10	0.00	0.95
Burn frequency	-0.10	0.01	1.72
Restoration status:soil nitrogen	0.08	0.00	0.43
Restoration status:CV nitrogen	-0.11	0.01	1.23
Restoration status:soil texture	-0.04	0.00	0.16
Restoration status:grazing intensity	-0.06	0.00	0.45
Restoration status:burn frequency	0.08	0.00	0.44
Soil nitrogen:CV nitrogen	-0.06	0.01	1.40
Soil nitrogen:soil texture	-0.03	0.00	0.41
Soil nitrogen:grazing intensity	-0.01	0.00	0.01
Soil nitrogen:burn frequency	0.03	0.00	0.20
CV nitrogen:soil texture	0.01	0.00	0.09
CV nitrogen:grazing intensity	0.02	0.00	0.85
CV nitrogen:burn frequency	-0.01	0.00	0.18
Soil texture:grazing intensity	0.01	0.00	0.06
Soil texture:burn frequency	-0.01	0.00	0.16
Grazing intensity:burn frequency	-0.01	0.00	0.15
Residuals		0.05	
Adjusted R^2:	0.00		

Table A2.3. ANOVA results for main factors and interactions on FQI. .p<0.1, *p<0.05, **p<0.005, ***p<0.0005.

FQI	Estimate	Sum Sq	F value
Restoration status	-1.86	0.19	0.16
Soil nitrogen	0.92	2.11	1.75
CV nitrogen	-1.64	0.22	0.18
Soil texture	0.48	1.24	1.03
Grazing intensity	2.07	0.00	0.00
Burn frequency	1.99	1.51	1.25
Restoration status:soil nitrogen	-1.51	0.70	0.58
Restoration status:CV nitrogen	0.86	0.35	0.29
Restoration status:soil texture	-0.89	0.39	0.33
Restoration status:grazing intensity	-1.46	1.36	1.13
Restoration status:burn frequency	-1.09	0.35	0.29
Soil nitrogen:CV nitrogen	0.00	0.00	0.00
Soil nitrogen:soil texture	-0.06	0.01	0.01
Soil nitrogen:grazing intensity	-0.56	0.64	0.53
Soil nitrogen:burn frequency	-0.47	0.26	0.21
CV nitrogen:soil texture	0.08	0.02	0.02
CV nitrogen:grazing intensity	-0.17	0.28	0.23
CV nitrogen:burn frequency	-0.31	0.38	0.32
Soil texture:grazing intensity	-0.44	0.68	0.56
Soil texture:burn frequency	-0.23	0.27	0.23
Grazing intensity:burn frequency	0.48	1.35	1.12
Residuals		13.27	
Adjusted R^2:	0.00		

Table A3. PERMANOVA results with 2 way interactions included of environment and management impacts on plant composition from 33 grasslands. Environmental data and plant cover were collected at in 2010 at 21 plots/field and averaged for each field. Management records were collected at the plot-level and averaged to field level, management parameters shown are from 2006-2010. Restoration status is a 0/1 relationship where remnant fields=0 and restored fields=1. .p<0.1, *p<0.05, **p<0.005, ***p<0.0005.

	Df	Sum of squares	Mean squares	F model	R^2	
Restoration status	1	0.354	0.354	3.090	0.065	***
Soil nitrogen	1	0.670	0.670	5.842	0.123	***
Soil texture	1	0.227	0.227	1.977	0.042	*
Grazing intensity	1	0.365	0.365	3.183	0.067	**
Burn frequency	1	0.284	0.284	2.479	0.052	*
Soil texture:Restoration status	1	0.156	0.156	1.360	0.029	
Soil texture:Burn frequency	1	0.164	0.164	1.427	0.030	
Soil texture:Grazing intensity	1	0.215	0.215	1.879	0.040	*
Restoration status:Burn frequency	1	0.150	0.150	1.312	0.028	
Restoration status:Grazing intensity	1	0.185	0.185	1.615	0.034	.
Burn frequency:Grazing intensity	1	0.090	0.090	0.784	0.017	
Soil texture:Soil nitrogen	1	0.099	0.099	0.866	0.018	
Soil nitrogen:Restoration status	1	0.163	0.163	1.422	0.030	
Soil nitrogen:Burn frequency	1	0.173	0.173	1.508	0.032	
Soil nitrogen:Grazing intensity	1	0.182	0.182	1.587	0.034	
Residuals	17	1.949	0.115		0.359	
Total	32	5.426			1.000	

Table A4.1 Indicator species analysis results for soil nitrogen. Soil nitrogen values are 0.066-0.230 in cluster 1 and 0.230-0.394 in cluster 2.

	Cluster	Indicator value	Probability
Elymus canadensis	1	0.769	0.001
Solidago rigida	1	0.712	0.006
Solidago canadensis	1	0.709	0.007
Helianthus pauciflorus var. pauciflorus	1	0.703	0.001
Bromus tectorum	1	0.661	0.036
Desmanthus illinoensis	1	0.591	0.032
Conyza canadensis	1	0.588	0.041
Oxalis stricta	1	0.576	0.044
Achillea millefolium	1	0.529	0.002
Solidago gigantea	1	0.504	0.027
Lepidium densiflorum	1	0.471	0.01
Ratibida columnifera	1	0.441	0.046
Plantago patagonica var. patagonica	1	0.435	0.039
Rumex crispus	1	0.414	0.037
Calamovilfa longifolia	1	0.353	0.024
Equisetum laevigatum	2	0.888	0.001
Agrostis gigantea	2	0.748	0.001
Poa pratensis	2	0.720	0.002
Viola pratincola	2	0.678	0.003
Eleocharis palustris	2	0.667	0.003
Carex	2	0.638	0.028
Dicanthelium oligosanthes	2	0.629	0.006
Apocynum cannabinum	2	0.509	0.009
Trifolium pratense	2	0.367	0.009
Dicanthelium acuminatum	2	0.313	0.026

Table A4.2. Indicator species analysis results for soil texture. Cluster 1 corresponds to soils that are 58-72% sand and cluster 2 are 72-90% sand.

	Cluster	**Indicator value**	**Probability**
Physalis longifolia	1	0.6057	0.011
Conyza canadensis	2	0.6579	0.008
Sporobolus cryptandrus	2	0.6243	0.006
Plantago patagonica var. patagonica	2	0.5683	0.002
Ratibida columnifera	2	0.5238	0.013
Silene antirrhina	2	0.5	0.001
Cannabis sativa	2	0.4316	0.006
Paspalum setaceum var. stramineum	2	0.3968	0.036
Sphenopholis obtusata	2	0.3739	0.015
Astragalus canadensis	2	0.3125	0.022
Ambrosia	2	0.3125	0.02
Strophostyles helvola	2	0.2977	0.042

Table A4.3. Indicator species analysis results for burn frequency. Cluster 1 corresponds to fields which have not been burned in the last five years and have no indicator species. Cluster 2 has 0.095-0.418 burn frequency.

	Cluster	**Indicator value**	**Probability**
Symphyotrichum ericoides	2	0.7762	0.004
Solidago rigida	2	0.5918	0.041
Lotus purshianus	2	0.3122	0.027
Calamovilfa longifolia	2	0.3094	0.043
Oenothera biennis	2	0.25	0.038

Table A4.4. Indicator species analysis for grazing intensity. Grazing intensity is 0-0.591 for cluster 1 and 0.592-1.747 for cluster 2.

	Cluster	Indicator value	Probability
Bromus inermis	1	0.7097	0.037
Oxalis stricta	1	0.5899	0.044
Solidago gigantea	1	0.5684	0.011
Solidago maximiliani	1	0.542	0.011
Helianthus pauciflorus var. pauciflorus	1	0.4975	0.024
Silene antirrhina	1	0.3846	0.026
Ulmus pumila	1	0.348	0.044
Panicum virgatum	2	0.7239	0.002
Carex	2	0.7107	0.014
Spartina pectinata	2	0.6217	0.032
Agrostis gigantea	2	0.5571	0.018
Euphorbia maculata	2	0.5243	0.021
Festuca arundinacea ssp. arundinacea	2	0.437	0.008
Sphenopholis obtusata	2	0.3261	0.048
Sporobolus cryptandrus	2	0.25	0.044

Table A4.5. Indicator species analysis for restoration status. Cluster 1 are remnant fields, cluster 2 are restored fields.

	Cluster	Indicator value	Probability
Equisetum laevigatum	1	0.9283	0.001
Dicanthelium oligosanthes	1	0.8462	0.001
Eleocharis palustris	1	0.8302	0.001
Ambrosia psilostachya	1	0.7873	0.009
Agrostis gigantea	1	0.7778	0.001
Viola pratincola	1	0.7144	0.003
Carex	1	0.7122	0.006
Poa pratensis	1	0.6862	0.01
Callirhoe involucrata	1	0.6576	0.004
Apocynum cannabinum	1	0.5155	0.016
Eragrostis spectabilis	1	0.4444	0.004
Trifolium pratens	1	0.3889	0.018
Paspalum setaceum var. stramineum	1	0.3832	0.042
Sphenopholis obtusatum	1	0.3315	0.047
Lithospermum incisum	1	0.2778	0.046
Dicanthelium acuminatum	1	0.2778	0.046
Elymus canadensis	2	0.9975	0.001
Solidago canadensis	2	0.8412	0.001
Solidago rigida	2	0.8303	0.001
Taraxacum officinale	2	0.7784	0.007
Bromus tectorum	2	0.6962	0.019
Desmanthus illinoensis	2	0.6867	0.004
Solidago gigantea	2	0.6751	0.002
Helianthus pauciflorus var. pauciflorus	2	0.6347	0.002
Rumex crispus	2	0.6323	0.001
Achillea millefolium	2	0.5331	0.001
Helianthus maximiliana	2	0.5025	0.025
Lepidium densiflorum	2	0.4657	0.005
Vulpia octoflora	2	0.3333	0.015
Erigeron strigosus	2	0.3322	0.031
Oenothera biennis	2	0.2667	0.029
Chenopodium album	2	0.2667	0.032

Figure A2. Contour plots of grazing intensity, burn frequency, soil nitrogen and soil texture on 2010 plant composition. Lines on each plot represent intervals of each factor value, also denoted by shading of symbols, parallel lines represent linear relationships between factors shown and changes in species composition.