

ABSTRACT

EFFECTS OF MANAGEMENT ON FUNCTIONAL DIVERSITY IN RESTORED TALLGRASS PRAIRIE PLANT COMMUNITIES

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While recent studies have embraced evaluating ecosystems through functional diversity, the focus on interspecific trait changes may limit their usefulness and application. Functional traits (traits that explain species' responses to environmental conditions and their ecosystem roles) can provide a more nuanced understanding of how disturbances shape plant communities and the functions they perform. Further, the inclusion of intraspecific trait responses can explain a significant portion of these relationships. In ecosystem restorations, management strategies can act as environmental drivers and disturbances that affect community structure. This study examined how three environmental drivers (grazer presence, prescribed fire, and age) in restored grasslands influence plant functional trait diversity and values and if these influences differ when intraspecific trait variation is incorporated. Further, relationships between functional characteristics of communities and an ecosystem function, aboveground productivity, were measured. Functional diversity consistently decreased with age across multiple functional diversity metrics, both when using fixed trait values and intraspecific trait variation. Increased functional diversity, measured as functional evenness, promoted productivity, but both evenness and productivity declined with site age. This functional diversity and ecosystem function relationship was only observed when using intraspecific trait data, emphasizing the importance

of accounting for plasticity in functional ecology studies. These results of this study support the environment-trait-function framework and demonstrate the importance of intraspecific trait variation. In ecosystems with weaker environmental gradients, the inclusion of intraspecific changes may be more influential than species turnover in identifying functional diversity and ecosystem function responses. Accounting for this source of variation may improve predictive models and general community ecology rules. Additionally, testing ecology principles in the context of restoration and identifying community responses to disturbances is critical for improving the predictability and success of restoration outcomes.

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EFFECTS OF MANAGEMENT ON FUNCTIONAL DIVERSITY IN RESTORED
TALLGRASS PRAIRIE PLANT COMMUNITIES

BY

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CHAPTER 1

INTRODUCTION

1.1 Functional Diversity as an Evaluation Tool

A common goal of restoration ecology is to reinstate native flora and fauna, often with the endeavor to improve critical ecosystems functions, such as productivity, nutrient cycling, or decomposition (Jordan, Gilpen & Aber 1987; Benayas et al. 2009). However, little is known about how the species present in a restored community respond to changes in the ecosystem and affect these processes. Although communities are often studied (and restorations are often evaluated) based on the presence and abundance of individual species (i.e. taxonomic biodiversity) and their interactions, this approach does not fully describe general ecological patterns, or fully explain variations in ecosystem composition and functioning between communities or across environmental gradients (McGill et al. 2006; Niu et al. 2014). To better inform this gap in knowledge, ecologists have embraced the idea that communities can be studied as sets of traits that describe the ecological roles of species and define how they interact with environmental conditions (Lavorel & Garnier 2002; Kahmen & Poschlod 2004; McGill et al. 2006; Lebrija-Trejos et al. 2014; Jiang & Ma 2015). Functional traits are the biological characteristics of species that respond to and influence the dominant processes in an ecosystem (Gitay & Noble 1997; Lavorel et al. 1997). In plants, functional traits can include morphological characteristics like growth form, height, leaf area, and specific leaf area, chemical characteristics such leaf carbon, nitrogen, or phosphorus content, or physiological characteristics such as leaf phenology, photosynthetic pathway, and leaf lifespan (Cornelissen et al. 2003). Thus, these

functional traits can provide more information on species' roles in the ecosystem than species-based biodiversity alone offers, offering a more mechanistic approach to understanding the effects of environmental factors in diverse ecosystems (McGill et al. 2006). For example, measurements of leaf toughness can predict susceptibility to herbivore predation, and specific leaf area and leaf nitrogen content can determine photosynthetic rate and plant growth rate (Lambers & Poorter 1992; Wright & Vincent 1996; Cornelissen et al. 2003).

While the functional trait composition of a community often responds to changes in environmental conditions, these shifts can also affect changes in ecosystem functioning (Lavorel & Garnier 2002). Tilman et al. (1997), in one of the first studies of functional diversity and ecosystem function relationships, planted grassland communities varying in numbers of functional groups and species richness. Functional diversity was found to be a better predictor of ecosystem function (measured as productivity) than species diversity. More recently, Zirbel et al. (2017) found that another ecosystem function, decomposition rate, significantly increased with the functional trait of vegetation height in restored prairies, as well as increasing with site age and soil moisture. These functional diversity-ecosystem function patterns have been studied in many grassland systems, and have included ecosystem processes and characteristics like resistance to invasion, nitrogen retention, and soil microbial biomass (Diaz & Cabido 2001). These patterns are not limited to plant communities; studies of other taxa have yielded similar results. In dung beetle communities in tropical forests in Borneo, functional group richness was shown to increase ecosystem functions of dung decomposition and seed removal, especially when there was greater functional group complementarity (i.e., functional groups occupying divergent niches) (Slade et al. 2007). Functional diversity of grassland spiders (using functional

groups, measured as the ratio of active to passive predators) also drove ecosystem functions, in which an increase in the active:passive predator ratio led to decreases in nitrogen mineralization and plant productivity, and increase in litter quality (carbon:nitrogen content) (Schmitz 2009). Despite the importance of functional trait composition of plant communities for restoring biodiversity and ecosystem functions, knowledge of environment–trait–function relationships in most restored systems is still in its infancy.

1.2 Functional Traits and Intraspecific Trait Variation

Much of functional diversity research focuses on the interspecific differences in traits, assuming that the differences between species are greater than within species, or ignoring shifts in traits across environmental gradients. Functional diversity measured using “fixed trait values” assigns to each species an average value for each trait, so differences in community weighted mean values for each trait among sites are due to changes in the community taxonomic composition (i.e., species turnover and changes in abundances), and not due to variations in traits within species. Many studies have examined how functional traits within communities vary across environmental gradients using fixed trait values (e.g., Lavorel & Garnier 2002; Spasojevic et al. 2010; Jiang & Ma 2015); however, relatively few studies have investigated the contributions of intraspecific trait variation to these patterns, and there is a prominent call to address this gap in knowledge (e.g., Jung et al. 2010; Laureto & Cianciaruso 2015; Zuo et al. 2017). Trait values are known to vary within a species (i.e., individuals of a species are not all identical), and these differences may be the result of genetic diversity, phenotypic plasticity, or environmental gradients (Jung et al. 2010; Jiang & Ma 2015). On local scales where interspecific trait variations are relatively low, the intraspecific differences in functional traits

may play a significant role in determining where species persist and their interactions within communities (Hulshof & Swenson 2010; Albert et al. 2012).

Several studies have quantified the influences of intraspecific trait variation on community responses to environmental gradients and disturbances. When studying the effect of elevation near a riverbed on plant traits, Jung et al. (2010) found that in addition to interspecific variation, intraspecific variation of specific leaf area and height accounted for 44% and 32%, respectively, of trait-elevation patterns. Similarly, plant functional traits studied along an alpine elevation gradient in China were found to significantly correlate with minimum temperature and light availability, and patterns of correlation were driven by both species turnover and intraspecific variation (Jiang & Ma 2015). Their results show that as elevation increases, leaf mass per area, leaf thickness, and leaf hardness also increases, both when analyses only included variation from species turnover, and when analyses incorporated intraspecific trait values (Jiang & Ma 2015). When studying functional traits along subalpine gradients in New Zealand, Kichenin et al. (2013) also found that variation from intraspecific trait changes contributed to elevation patterns, yet for certain traits more than others; the contribution of intraspecific variation was greatest for specific leaf area, while leaf area and leaf dry matter content were less affected by differences within species as elevation increased. These results are consistent with other studies that quantified the contributions of intraspecific variation to environmental patterns, in that variations within species add non-negligible explanatory power and increase the probability of detection of environment-trait patterns, and thus should not be ignored (Albert et al. 2010; Kichenin et al. 2013; Niu, He & Lechowicz 2016). To accurately assess changes in community functional traits, and potential changes in ecosystem function, it is imperative to

include intraspecific variation, especially so for relatively smaller scales and short term effects (Kichenin et al. 2013).

1.3 Ecosystem Function

With an understanding of functional traits it is then necessary to determine the consequence of changes in functional diversity on ecosystem functions (Cadotte, Carscadden & Mirotchnick 2011). Functional traits can provide the mechanistic links between species composition and ecosystem functions through differences in values and ranges that determine how species respond to abiotic and biotic factors and species interactions, thus making environment-trait-function connections in ways that taxonomic approaches overlook (Diaz & Cabido 2001). Greater functional diversity may result from reduced niche overlap (i.e., improved resource partitioning and greater complementarity) between species, thus facilitating increases in ecosystem functions (Mason et al. 2005; Cadotte et al. 2011; Ebeling et al. 2017). Additionally, accurate assessments of biodiversity–ecosystem function relationships should require that the functional traits selected directly impact the function of interest (Cadotte et al. 2011). Thus, with careful *a priori* selection of traits, changes in functional trait diversity across environmental gradients and disturbances should correlate with ecosystem functions, providing a crucial insight to community and ecosystem dynamics and the factors that drive them.

1.4 Functional Diversity in Restored Ecosystems

In North America, the extent of tallgrass prairie has been severely reduced, making it a seriously threatened habitat. Starting in the mid-1800s, these highly valued areas with fertile soil, adequate precipitation, and flat topography made them ideal for homesteading and

agriculture (Samson & Knopf 1994). Today, less than 10% of intact original prairies remain; in the state of Illinois (where this study was performed), less than 1% remains (Samson & Knopf 1994). Existing prairie remnants experience different environmental conditions compared to pre-settlement times; absences of large herbivores and infrequent fires can have a large impact on the flora and fauna present (Samson, Knopf & Ostlie 2004). Fire served as an important ecological disturbance, aiding in the reduction of woody species, exclusion of invasive species, and maintenance of native grassland species, as well as altering nutrient cycles (Pauly 1997; Bond & Keeley 2005). Bison (*Bison bison*) were a keystone species on the landscape; large herds created spatial and temporal heterogeneity by preferentially grazing on graminoid species, depositing nutrients, altering soil structures, and wallowing as they moved across prairies (Knapp et al. 1999; Bond & Keeley 2005). Land managers have since recognized the need to protect and restore this vital ecosystem, and the importance of reinstating fire and grazing disturbance regimes as management tools.

Due to their extremely threatened status and increased focus in restoration, tallgrass prairies are an ideal ecosystem to study the relationship between functional diversity and ecosystem functioning, and how management practices affect these outcomes. Restored communities provide an environment for ecologists to observe and manipulate community assembly patterns in real time; management strategies can act as filters that constrain which species and functional trait ranges can persist within a restored site (Díaz, Cabido & Casanoves 1999; Zirbel et al. 2017). Through the intentional altering of environmental filters via management strategies, restored tallgrass prairies provide the opportunity to further examine

community assembly, focusing on how the functional trait makeup of plant communities responds to these patterns and influences ecosystem function.

Two common management practices in grasslands are prescribed fire and large herbivore reintroduction. Grazing has been shown to increase alpha and beta diversity, as well as influence nutrient cycling (Koerner & Collins 2014; Niu et al. 2016; Towne, Hartnett & Cochran 2016). Due to the spatial and temporal heterogeneity of grazing disturbances, as well as documented fire and grazing interactions, it is expected that reintroduction of grazers will increase functional diversity by creating more niche space within communities that may be filled by functionally diverse species (Coppedge & Shaw 1998). Fire has a more uniform effect on prairie landscapes and may alter specific functional traits within communities. For example, Zirbel et al. (2017) found that frequently burned restored prairie sites had lower specific leaf areas, likely due to reduced light competition and increased nutrient competition, and Johnson & Matchett (2001) found that frequent burning resulted in increased root growth and decreased root carbon to nitrogen ratio, due to nitrogen limitation in the soil. Such changes in community functional traits from management strategies can influence ecosystem functions, such as above and below ground productivity, decomposition rate, nutrient cycling, floral resources, and seed predation, yet have proven difficult to quantify (Johnson & Matchett 2001; Zirbel et al. 2017).

Although the re-establishment of ecosystem functioning is an implicit goal of restoration, there is little knowledge of how management activities affect this and site idiosyncrasies limit restoration predictability. An important first step is to expand on traditional measures of biodiversity through measuring functional diversity (including intraspecific trait variation) across disturbance gradients in grasslands (Brudvig 2017). Analyses of how community trait

composition emerges from these environmental conditions may reveal general patterns that can be applied across grasslands, allowing better predictions of the effects of management disturbances (McGill et al. 2006). This approach will also help link community patterns to ecosystem processes in ways that species-based approaches do not, and reveal how functional trait and environment relationships affect ecosystem functions (Díaz & Cabido 2001; McGill et al. 2006; Lebrija-Trejos et al. 2014; Laughlin et al. 2017). Understanding how plant functional traits affect ecosystem functions in response to disturbances will also allow restoration managers to determine how to reach desired ecosystem function goals in restorations using prescribed disturbances (Zirbel et al. 2017). The ability to better predict outcomes of management techniques is an increasingly necessary tool in the face of continuing global changes (Brudvig et al. 2017).

1.5 Objectives and Hypotheses

This project seeks to address three objectives: 1) determine how management strategies (fire and grazing) affect plant communities through variations in plant functional traits, 2) determine if the inclusion of intraspecific trait variation alters the relationships with management strategies or ecosystem function, 3) identify relationships between functional traits and net primary productivity, a critical ecosystem function.

Hypothesis 1a) Prescribed fire, acting as a less-selective disturbance, will reduce variation in functional traits and reduce functional diversity. *1b)* Grazing, acting as a more-selective disturbance, will increase variation in functional traits and increase functional diversity.

Hypothesis 2) Inclusion of intraspecific variation will alter the relationships between management practices (bison reintroduction, prescribed fire, and age since restoration

planting) and functional diversity as a result of more precise measurements of functional trait composition, and as communities compensate for variations in management practices.

Hypothesis 3) Functional diversity will positively correlate with net primary productivity, and the relationship will be stronger when intraspecific variation is included.

CHAPTER 2

METHODOLOGY AND STATISTICAL ANALYSES

2.1 Study Site

This study was conducted at Nachusa Grasslands, a tallgrass prairie consisting of remnant and restored plots in Franklin Grove, IL. Nachusa Grasslands is managed by The Nature Conservancy, who for over 30 years has purchased agricultural land and restored it to tallgrass prairie. The restoration plots at Nachusa vary in age, providing a chronosequence of restorations. Managers frequently use prescribed burns to manage the invasion of exotic species and limit woody encroachment, with most plots burned every 1-3 years. Prescribed burns either occur in late fall or early spring. Nachusa also reintroduced bison to the grasslands in October 2014. The bison herd, approximately 130 individuals during this study, has access to roughly half of the sites in Nachusa, potentially influencing the landscape through grazing, wallowing, and nutrient deposition. I studied sites, consisting of 13 restorations and two remnants. Bison had access to 7 restorations and 1 remnant, and approximately half of the bison sites and half of the non-bison sites were burned in spring 2017. Restored sites range from 4-30 years since planting (Figure 1, Table 1).

Figure 1: Map of Sites at Nachusa Grasslands. Areas shown in blue mark sites with reintroduced bison, and areas shown in yellow mark sites without bison present. Red areas show remnant prairie sites, and orange circles denote sites that were burned spring 2017. The shaded areas show the boundaries of Nachusa Grasslands.

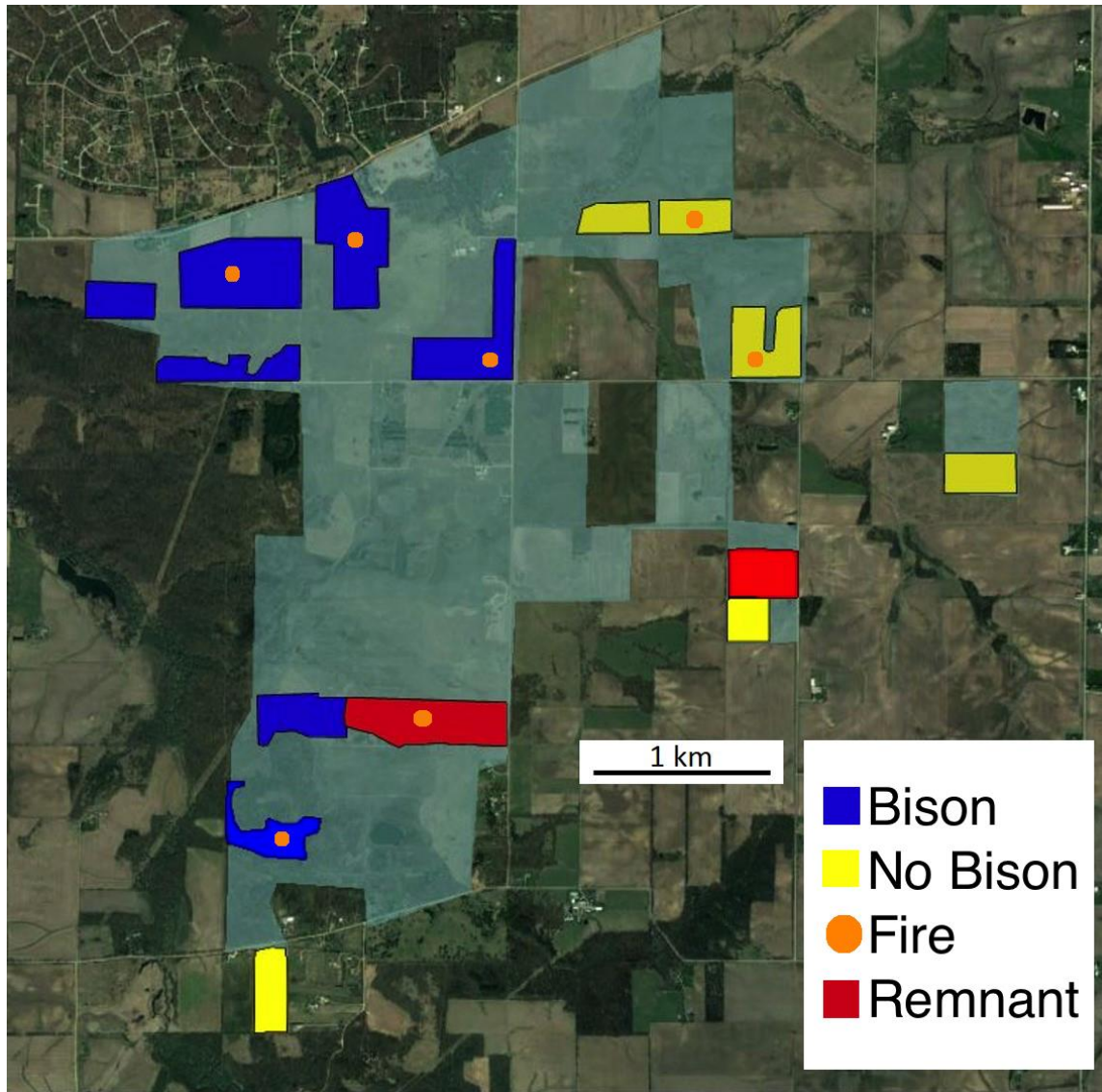


Table 1. Sampling Sites within Nachusa Grasslands. Sites are listed with age since restoration planting, bison presence, and year of most recent prescribed burn.

Name	Abbreviation	Age (Years)	Bison	Fire
Clear Creek East	CCE	10	N	Y
Clear Creek West	CCW	9	N	N
Franklin Creek	FC	11	N	N
Holland Farm	HF	4	Y	Y
Hook Larson	HL	16	Y	N
Holland North	HN	5	Y	Y
Holland Prairie West	HPW	9	Y	N
Lowden	L	6	Y	Y
Main Unit	MU	30	Y	N
Main Unit Remnant	MUR	Remnant	Y	Y
Thelma Carpenter	TC	15	N	N
Thelma Carpenter Remnant	TCR	Remnant	N	N
Stone Barn	SB	8	N	N
Sand Farm	SF	16	N	Y
West Heinkel	WH	25	Y	Y

2.2 Functional Traits

Functional traits were measured only for the 10 most abundant species at each site each year, allowing for species turnover from the first year to the second. Species abundances were determined by plant surveys, conducted early August in 2016, 2017, and 2018. In each sampling site, 10 vegetation survey plots were selected from a 60 m x 60 m, 5x5 point grid. To ensure accurate sampling of the same area each year, vegetation survey plots were marked by either a staked metal plate, or a staked circular metal tag with an identification number. Within 0.25 m² quadrats, plant species presence and relative abundance were recorded. Relative abundance was estimated as percent cover, which totaled to 100% within each plot, including area covered by bare ground and thatch (dead biomass); percent cover did not total greater than 100%, and therefore did not account for overlapping space shared by multiple species. Unidentifiable

seedlings made up a small portion of the plant communities, and did not affect the plant community composition (0.0-3.4% of cover, average=0.38%).

Using the previous year of survey data, the ten most abundant plant species at each site, determined by the summed percent cover per site, were sampled for functional traits in July each year. Sampling the ten most abundant species accounts for species turnover, as some species may be absent from different sites, and for yearly changes in the community composition. Plant functional traits measured for each species included plant height, leaf toughness, leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), growth form, and leaf C and N content, using standardized methods from Cornelissen et al. (2003) (Table 2, Table 3). These traits are commonly used in plant functional diversity studies because they respond to environmental conditions and can correlate with ecosystem function (particularly net primary productivity) (Cornelissen et al. 2003; Jung et al. 2010; Kichenin et al. 2013; Niu, He & Lechowics 2016; Zirbel et al. 2017). One individual from each species was selected at ten points within each site, totaling to 10 individuals per species, per site (100 samples per site, 1,500 samples total). Species individuals were selected within the 5x5 point sampling grid as the individual closest to 10 randomly selected points within the grid. Only mature individuals with little sign of damage were chosen, and leaf samples were taken from the highest, undamaged, mature leaf. Leaf samples were carefully wrapped in moist paper towel (avoiding folding or bending of the leaf when possible), placed in a plastic bag, and kept in a cooler of ice to avoid desiccation. Plant functional traits that require immediate assessment (leaf toughness and fresh mass for leaf dry matter content) were analyzed within 4 hours. Samples were then pressed and dried for subsequent trait measurements (specific leaf area, leaf dry matter content, and leaf C and N content). After plant surveys were conducted for the growing season in August, the 10

most abundant species were recalculated, and any species that significantly changed in abundance were sampled to ensure that at least 60% of the summed species cover at each site was assessed. When species were added to account for changes in abundance, the originally sampled species with the lowest abundance were excluded from analyses.

Table 2. Methodology of functional traits. Methods follow standardized protocols from Cornelissen et al. (2003).

Functional Trait	Categorical / Continuous	Methods
<i>Growth Form</i>	Categorical	Growth form was recorded for each species as woody, grass, or forb. Sedges were categorized as grasses (Poales).
<i>Plant Height</i>	Continuous	Plant height was measured from the base of the individual to the tip of its highest leaf. To avoid phenological variations in flowering time, plant height excluded reproductive structures. For grasses, the height was measured by elongating the longest leaf.
<i>Leaf Area</i>	Continuous	Leaf samples were pressed and dried at 60° C for three days. Dried samples were then scanned and uploaded to a computer, and area was measured using SigmaScan software. Area in pixels was converted to mm ² .
<i>Specific Leaf Area (SLA)</i>	Continuous	SLA was measured as the one-sided area of a leaf, divided by its oven dried mass, in mm ² /mg.
<i>Leaf Dry Matter Content (LDMC)</i>	Continuous	LDMC is measured as the oven dried mass of a leaf divided by its water saturated fresh mass (mg/g). On the day of collection, the leaf samples were patted dry and weighed for water saturated mass. Following leaf area protocol, pressed and dried leaves were weighed for oven dried mass.
<i>Leaf Carbon and Nitrogen Content</i>	Continuous	N and C content were measured at Northern Illinois University using a mass spectrometer (DELTAplus Advantage Mass Spectrometer, Thermo Scientific, Wilmington, DE, USA). Due to the cost of chemical analysis, only 3 leaf samples per species were used to measure N and C content.
<i>Leaf Toughness</i>	Continuous	Leaf toughness was measured with fresh leaf samples by a force penetrometer, measuring grams of force necessary to puncture the center of the leaf, avoiding leaf veins. The toughness of especially fragile leaves was estimated as 100 grams, as the force penetrometer cannot accurately measure forces less than 100 grams.

Table 3: Ecological Relevance of Functional Traits. The selected suite of functional traits for this study address a range of ecological roles, including resource competition (plant height, specific leaf area), growth and photosynthetic rate (specific leaf area, leaf nitrogen content, growth form), consumer interactions (leaf toughness, leaf nitrogen content), and nutrient cycling (leaf carbon content, leaf nitrogen content leaf dry matter content) (Cornelissen et al. 2003).

Functional Trait	Ecological Relevance
Plant Height	Competition
Leaf Toughness	Carbon investment, herbivory defense
Leaf Dry Matter Content (LDMC)	Density of leaf tissues, growth rate
Specific Leaf Area (SLA)	Growth rate, photosynthetic rate
Growth Form	Plant strategy, adaptation
Leaf Carbon Content (C)	Plant litter quality
Leaf Nitrogen Content (N)	Photosynthetic rate, nutritional quality to consumers

2.3 Ecosystem Function

To estimate net primary productivity (NPP), above ground biomass was collected at the end of the growing season, in Mid-August. Next to each of the ten quadrats used for vegetation surveys at each site, approximately 50 cm south, a 0.01 m² quadrat was placed. The above ground plant tissue within the quadrat was cut 2 cm above soil level and collected. Biomass was sorted by grasses, forbs, and thatch, dried to a constant mass, and weighed.

2.4 Functional Diversity

a. Fixed Value Functional Diversity: Functional diversity metrics were calculated first using fixed trait values, in which functional trait values for each species are averaged across all sampling sites. The use of fixed values assumes that all individuals within a species are identical, and ignores variation within species. Differences in functional diversity among sites,

therefore, are derived from changes in species composition and abundance (sampled species listed in Table 4). The dbFD function (FD package in R, Laliberté, Legendre & Shipley 2015) was used to calculate community weighted means (CWMs) of each trait for each site and four functional diversity metrics, standardizing continuous functional trait values, using relative abundances for calculations, and specifying the “cailliez” correction. Functional diversity metrics were functional richness (FRic, the range of values for plant functional traits), functional evenness (FEve, the distribution of values for plant functional traits), functional divergence (FDiv, the degree to which values for plant functional traits maximize extreme ends of the distribution), and functional dispersion (FDis, the mean distance in multidimensional trait space of individual species to the centroid of all species) (Mason et al. 2005, Laliberte & Legendre 2010).

b. *Site-Specific Trait Values*: To estimate the affects of intraspecific trait variation CWMs and functional diversity metrics were recalculated using site-specific functional trait values. Functional trait averages for each species were calculated using measurements from the individuals collected within each sampling site, as opposed to averaged across all sampling sites (fixed trait values).

2.5 Analyses

Functional diversity metrics and CWMs based on fixed trait values were examined using generalized linear models, with bison presence, prescribed fire, age, and two-way interactions as factors (H1a-b). Prior to calculations of functional diversity metrics, the following fixed value functional traits were log-transformed to fit normal distributions: toughness, specific leaf area, and percent nitrogen (Umaña et al. 2017). Fixed trait value and intraspecific trait value functional richness were also log-transformed prior to analysis. These analyses were repeated

with metrics and CWMs from site-specific trait values (H2). Generalized linear models were used to assess the effects of age, bison, and fire on NPP. To determine the relationship between functional diversity and ecosystem function, NPP was examined using linear models with functional diversity metrics and CWMs (derived from fixed trait values) as factors, analyzed individually. These analyses were repeated using functional diversity metrics and CWMs derived from site-specific trait values (H3).

Table 4: Sampled species across sites

Common Name	Species Name	Family	Type
Big Bluestem	<i>Andropogon gerardii</i>	Poaceae	Grass
Black Cherry	<i>Prunus serotina</i>	Rosaceae	Woody
Canada Bluegrass	<i>Poa compressa</i>	Poaceae	Grass
Canada Goldenrod	<i>Solidago canadensis</i>	Asteraceae	Forb
Canada Wild Rye	<i>Elymus canadensis</i>	Poaceae	Grass
Carex spp.	<i>Carex spp.</i>	Cyperaceae	Grass
Common Ragweed	<i>Ambrosia artemisiifolia</i>	Asteraceae	Forb
Dewberry	<i>Rubus flagellaris</i>	Rosaceae	Forb
Foxglove Beardstongue	<i>Penstemon digitalis</i>	Plantaginaceae	Grass
Golden Alexander	<i>Zizia aurea</i>	Apiaceae	Forb
Grassleaved Goldenrod	<i>Solidago graminifolia</i>	Asteraceae	Forb
Hairy Aster	<i>Symphyotrichum pilosum</i>	Asteraceae	Forb
Heath Aster	<i>Symphyotrichum ericoides</i>	Asteraceae	Forb
Indian Grass	<i>Sorghastrum nutans</i>	Poaceae	Grass
Kentucky Bluegrass	<i>Poa pratensis</i>	Poaceae	Grass
Little Bluestem	<i>Schizachyrium scoparium</i>	Poaceae	Grass
Missouri Goldenrod	<i>Solidago missouriensis</i>	Asteraceae	Forb
Mountain Mint	<i>Pycnanthemum virginianum</i>	Lamiaceae	Forb
Old Field Goldenrod	<i>Solidago nemoralis</i>	Asteraceae	Forb
Pale Purple Coneflower	<i>Echinacea pallida</i>	Asteraceae	Forb
Prairie Coreopsis	<i>Coreopsis palmata</i>	Asteraceae	Forb
Purple Prairie Clover	<i>Dalea purpurea</i>	Fabaceae	Forb
Pussy Toes	<i>Antennaria plantaginifolia</i>	Asteraceae	Forb
Queen Anne's Lace	<i>Daucus carota</i>	Apiaceae	Forb
Red Clover	<i>Trifolium pratense</i>	Fabaceae	Forb
Red Top	<i>Agrostis gigantea</i>	Poaceae	Grass
Rosinweed	<i>Silphium integrifolium</i>	Asteraceae	Forb
Roundheaded Bush Clover	<i>Lespedeza capitata</i>	Fabaceae	Forb
Sawtooth Sunflower	<i>Helianthus grosseserratus</i>	Asteraceae	Forb
Scribner's Panic Grass	<i>Panicum oligosanthos</i>	Poaceae	Grass
Showy Goldenrod	<i>Solidago speciosa</i>	Asteraceae	Forb
Showy Tick Trefoil	<i>Desmodium canadense</i>	Fabaceae	Forb
Side Oats Grama	<i>Bouteloua curtipendula</i>	Poaceae	Grass
Sky Blue Aster	<i>Symphyotrichum oolentangiense</i>	Asteraceae	Forb
Smooth Blue Aster	<i>Symphyotrichum laeve</i>	Asteraceae	Forb
Smooth Brome	<i>Bromus inermis</i>	Poaceae	Grass
Stiff Goldenrod	<i>Oligoneuron rigidum</i>	Asteraceae	Forb
Thimbleweed	<i>Anemone cylindrica</i>	Ranunculaceae	Forb

(continued on following page)

Table 4 (continued)

Western Sunflower	<i>Helianthus occidentalis</i>	Asteraceae	Forb
White Indigo	<i>Baptisia alba</i>	Fabaceae	Forb
White Prairie Clover	<i>Dalea candida</i>	Fabaceae	Forb
Wild Bergamot	<i>Monarda fistulosa</i>	Lamiaceae	Forb
Wild Quinine	<i>Parthenium integrifolium</i>	Asteraceae	Forb
Yarrow	<i>Achillia millefolium</i>	Asteraceae	Forb
Yellow Coneflower	<i>Ratibida pinnata</i>	Asteraceae	Forb

CHAPTER 3

RESULTS

3.1 Functional Diversity Metrics

I collected leaf samples from the 45 species that make up the ten most abundant species at each site (comprising >50% plant cover at each site), totaling 1,500 individual leaf samples. Bison, fire, and age of restoration significantly affected some, but not all, functional diversity metrics, and results varied between metrics using fixed trait values and intraspecific trait values (hereafter, FTV and ITV, respectively) (Table 5). Using FTV, functional richness (FRic) was significantly affected by a bison x fire interaction, in which non-bison sites increase in FRic in the presence of fire, but bison sites were unaffected (Figure 2A). Incorporating ITV in FRic (FRic_{ITV}) resulted in different environmental effects than FTV, with higher FRic_{ITV} in bison sites, and a fire x age interaction in which FRic_{ITV} increased with age for unburned sites but not burned sites (Figure 2B). There was a bison x age interaction on functional evenness (FEve), using FTV, in which FEve declined with age only in the presence of bison (Figure 2C). This interaction was not present for FEve_{ITV}, which decreased with age (Figure 2D). FDis_{ITV} decreased with age (Figure 2F), while FDis_{FTV} was not affected by bison, fire, or age (Figure 2E). Functional divergence (FDiv) was not affected by environmental variables, regardless of using FTV or ITV.

Table 5: Results of GLMs testing the effects of bison, fire, and restoration age on plant functional diversity metrics. Factors were analyzed using likelihood ratio tests that approximate χ^2 distribution. Bold text indicates $P < 0.05$, italic text indicates $P < 0.10$. Factors with $P < 0.05$ were retained in the model; factors with $P > 0.05$ were dropped from the model.

	Fixed Trait Values		Intraspecific Trait Values	
	χ^2	<i>P</i>	χ^2	<i>P</i>
<i>log(FRic)</i>				
Bison	-	-	22.00	0.042
Fire	-	-	-	-
Age	0.85	0.295	-	-
Bison x Fire	6.03	0.005	0.61	0.745
Bison x Age	2.18	<i>0.061</i>	6.15	0.303
Age x Fire	0.26	0.534	23.97	0.042
<i>F_{Eve}</i>				
Bison	-	-	1.07E-05	0.969
Fire	0.01	0.267	0.00	0.602
Age	-	-	0.04	0.015
Bison x Fire	0.01	0.236	0.00	0.857
Bison x Age	0.03	0.009	0.02	0.121
Age x Fire	0.00	0.804	0.00	0.428
<i>F_{Div}</i>				
Bison	0.01	0.131	0.00	0.463
Fire	0.01	0.167	0.01	0.175
Age	0.00	0.782	0.01	0.277
Bison x Fire	0.00	0.426	0.01	0.104
Bison x Age	0.00	0.511	0.00	0.944
Age x Fire	0.01	0.311	0.01	0.245
<i>F_{Dis}</i>				
Bison	0.00	0.310	0.00	0.156
Fire	0.00	0.608	0.00	0.590
Age	0.00	0.213	0.01	0.004
Bison x Fire	0.00	0.704	0.00	0.859
Bison x Age	0.00	<i>0.097</i>	0.00	0.382
Age x Fire	0.00	0.162	0.00	0.483

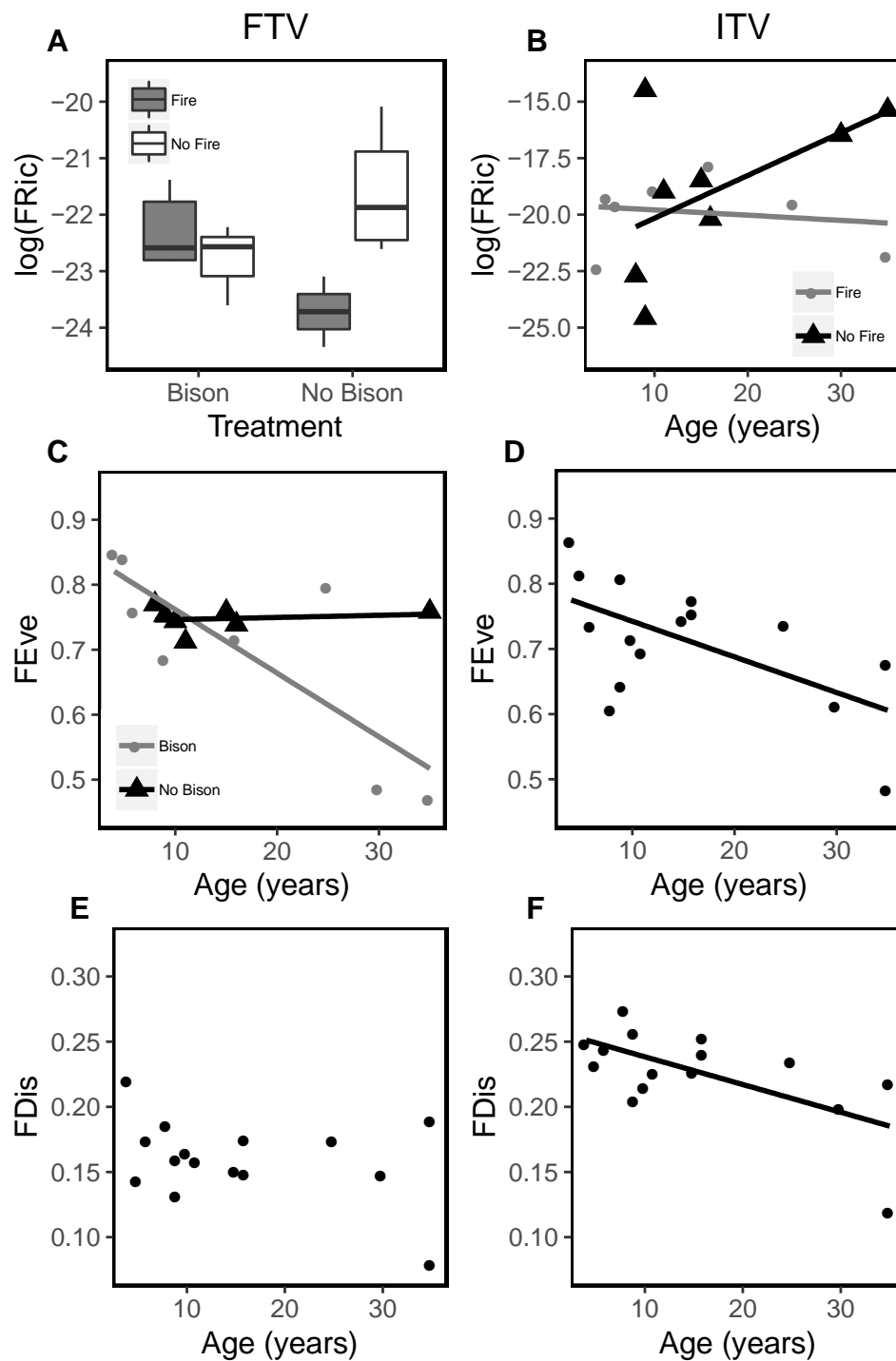


Figure 2: Functional Diversity Metrics Using Fixed and Intraspecific Trait Values. **A:** FRic_{FTV} bison x fire interaction; **B:** FRic_{ITV} fire x age interaction; **C:** FEve_{FTV} bison x age interaction; **D:** FEve_{ITV} age effect; **E:** FDis_{FTV} with no significant effects; **F:** FDis_{ITV} and age effect.

3.2 Ecosystem Function

NPP was influenced by an interaction between bison and fire, in which productivity was higher in burned non-bison sites (Figure 3A), and lower in older sites (Figure 3B, Table 6).

Among functional diversity metrics, FEve_{ITV} was the strongest predictor of NPP, with greater productivity where FEve_{ITV} was high ($R^2 = 0.277$, $P < 0.05$) (Figure 3B). FEve based on fixed trait values had a marginally significant positive effect on NPP ($R^2 = 0.145$, $P = 0.089$).

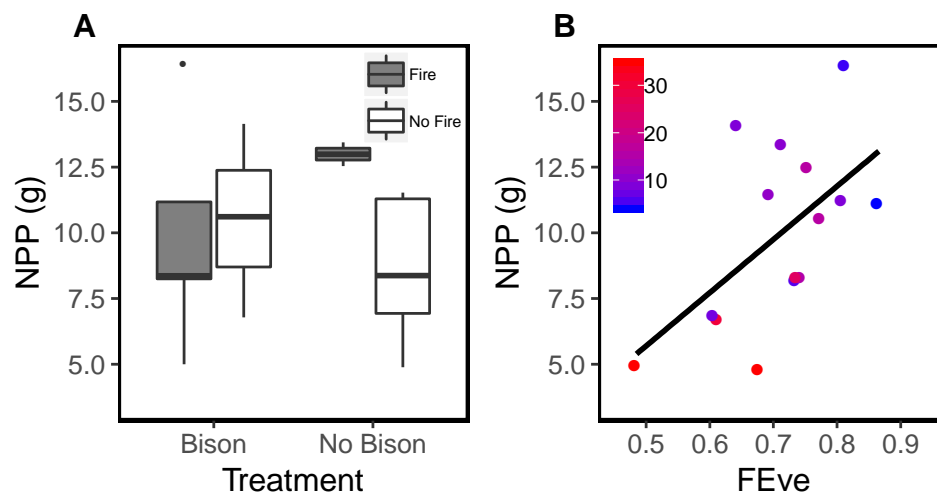


Figure 3: Effects of Management and Functional Evenness on Productivity. **A:** NPP and significant bison x fire interaction; **B:** NPP and significant FEve_{ITV} effect. Age of sites is shown by color, with the youngest sites in blue and the oldest sites in red. The effects of FEve_{ITV} and age on NPP were analyzed using separate models.

3.3 Functional Traits

For five of the seven functional traits measured, CWMs significantly varied with environmental factors, and four of these produced different results when CWMs were calculated from fixed trait values vs. values incorporating intraspecific variation (Table 7). Leaf toughness,

using FTV CWMs, showed a bison x age interaction in which grazed sites increased in leaf toughness with age, while ungrazed sites decreased (Figure 4A). Prescribed fire significantly decreased $LDMC_{FTV}$, leading to communities with leaves that are lower in tissue mass to water ratios (Figure 4C). Toughness and LDMC CWMs were unrelated to environmental factors when incorporating ITV (Figure 4B and Figure 4D, respectively). Specific leaf area was also significantly affected by management strategies, however, only for CWMs based on ITV, with significant interactions between each pair of factors. SLA_{ITV} was not affected by fire in sites with bison, but increased with fire in sites without bison (Figure 5B); as site age increased, SLA_{ITV} increased without the presence of bison and decreased with bison (Figure 5D). Both burned and unburned sites showed lower SLA_{ITV} in older sites, showing that older plant communities had thicker, denser leaves. Leaf chemistry was most strongly affected by the age of the site, with older sites increasing in leaf carbon content for FTV values only (Figure 6C). Leaf nitrogen content showed bison-age interactions. When analyzing both FTV and ITV nitrogen, older sites without bison increased nitrogen content, while sites with bison decreased (Figure 6B and Figure 6D, respectively).

Table 6: Results of GLMs testing the effects of restoration management and functional diversity metrics on net primary productivity. Factors were analyzed using likelihood ratio tests that approximate χ^2 distribution. Bold text indicates $P < 0.05$, italic text indicates $P < 0.10$. Factors with $P < 0.05$ were retained in the model; factors with $P > 0.05$ were dropped from the model.

	χ^2	<i>P</i>
<i>NPP</i>		
Bison	-	-
Fire	-	-
Age	78.58	<0.001
Bison x Fire	22.09	0.045
Bison x Age	1.59	0.605
Age x Fire	2.37	0.542

Table 7: Results of GLMs testing the effects of restoration management on community-weighted means. Factors were analyzed using likelihood ratio tests that approximate χ^2 distribution. Bold text indicates $P < 0.05$, italic text indicates $P < 0.10$. Factors with $P < 0.05$ were retained in the model; factors with $P > 0.05$ were dropped from the model.

	Fixed Trait Value		Intraspecific Trait Value	
	χ^2	<i>P</i>	χ^2	<i>P</i>
<i>Height</i>				
Bison	1.67	0.245	172.42	0.265
Fire	255.02	0.133	2.63	0.895
Age	1.92	0.901	167.55	0.288
Bison x Fire	113.55	0.338	333.97	0.109
Bison x Age	1.29	0.923	16.10	0.737
Age x Fire	310.99	0.101	0.01	0.995
<i>Toughness</i>				
Bison	-	-	2462.8	0.604
Fire	0.17	0.128	21832	0.101
Age	-	-	2883.4	0.562
Bison x Fire	0.01	0.351	19997	0.101
Bison x Age	0.03	0.038	256.41	0.860
Age x Fire	0.02	0.090	2819.9	0.574
<i>Leaf Area</i>				
Bison	23768	0.599	84596	0.521
Fire	52689	0.441	490620	0.100
Age	2798.6	0.865	33.51	0.990
Bison x Fire	185598	0.145	163591	0.367
Bison x Age	9229.4	0.757	97036	0.500
Age x Fire	245594	<i>0.075</i>	392380	0.151
<i>LDMC</i>				
Bison	53.91	0.676	78.26	0.759
Fire	1229.8	0.046	169.24	0.662
Age	427.31	0.231	759.13	0.358
Bison x Fire	77.64	0.623	337.93	0.551
Bison x Age	586.56	0.156	2799.3	<i>0.053</i>
Age x Fire	638.84	0.108	309.00	0.535
<i>SLA</i>				
Bison	0.00	0.795	-	-
Fire	0.02	<i>0.083</i>	-	-
Age	0.00	0.599	-	-
Bison x Fire	0.00	0.884	3.01	0.022

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Table 7 (continued)

Bison x Age	0.01	0.242	16.84	< 0.001
Age x Fire	0.07	<i>0.056</i>	7.89	< 0.001
<i>Percent N</i>				
Bison	-	-	-	-
Fire	0.00	0.576	0.04	0.577
Age	-	-	-	-
Bison x Fire	0.00	0.969	0.00	0.864
Bison x Age	0.09	0.042	0.53	0.040
Age x Fire	0.03	0.228	0.04	0.578
<i>Percent C</i>				
Bison	0.19	0.363	3.54	<i>0.068</i>
Fire	0.04	0.683	0.33	0.587
Age	1.22	0.026	0.95	0.357
Bison x Fire	0.00	0.926	0.10	0.782
Bison x Age	0.12	0.512	0.90	0.403
Age x Fire	0.44	0.200	2.01	0.193

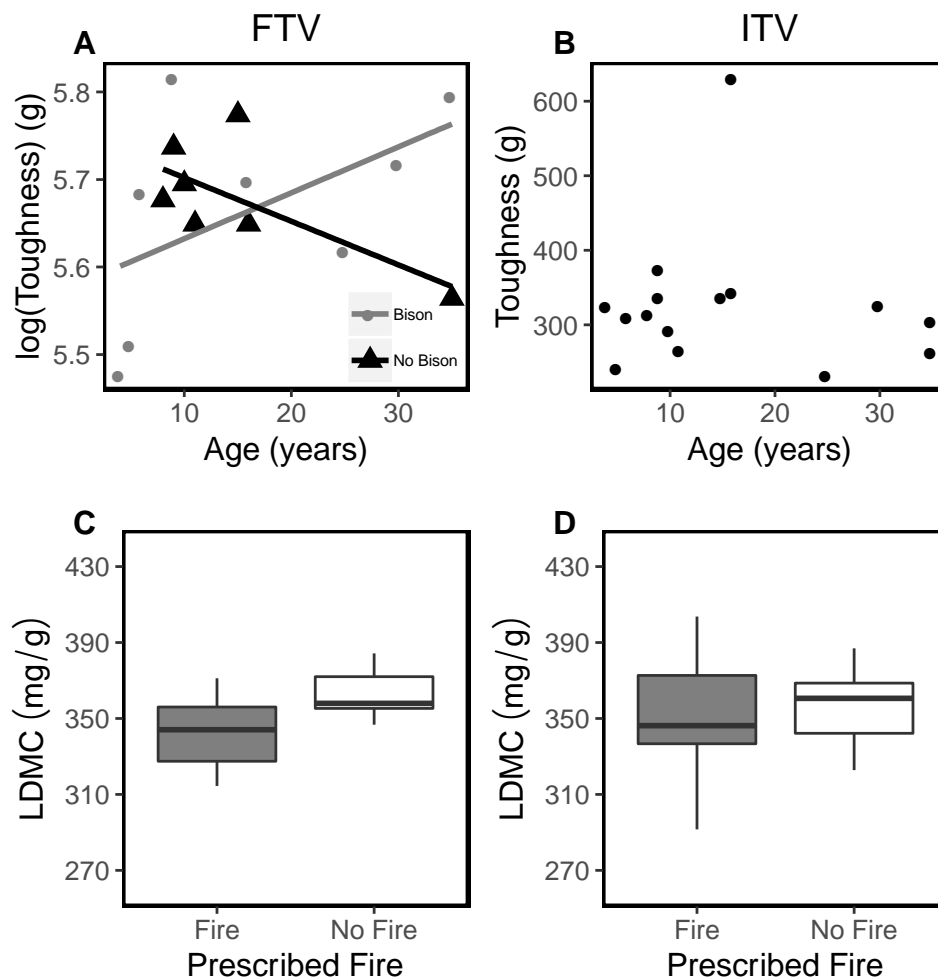


Figure 4: Effects of Management on Leaf Toughness and LDMC. **A:** FTV log(Toughness) and significant bison x age interaction; **B:** ITV Toughness with no significant effects; **C:** FTV LDMC and significant fire effect; **D:** ITV LDMC with no significant effects.

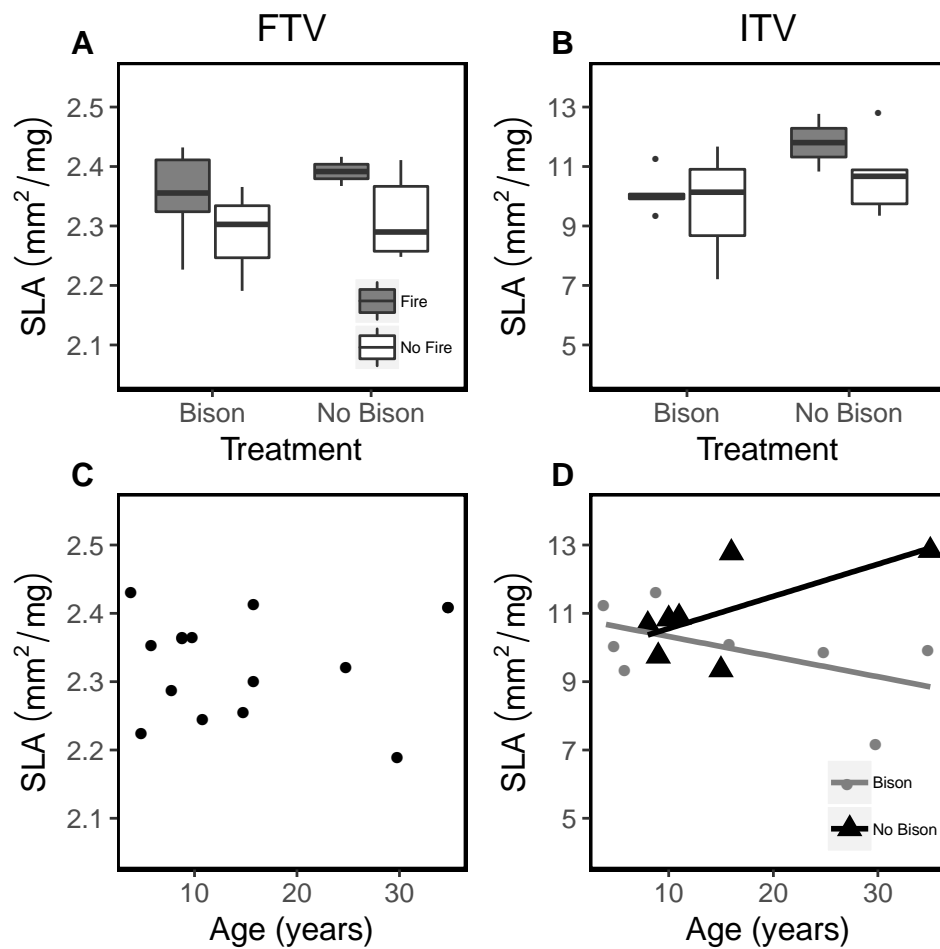


Figure 5: Effects of Management on SLA. **A:** FTV SLA and no significant effects; **B:** ITV SLA and significant bison x fire interaction; **C:** FTV SLA and no significant effects; **D:** ITV SLA and significant bison x age interaction.

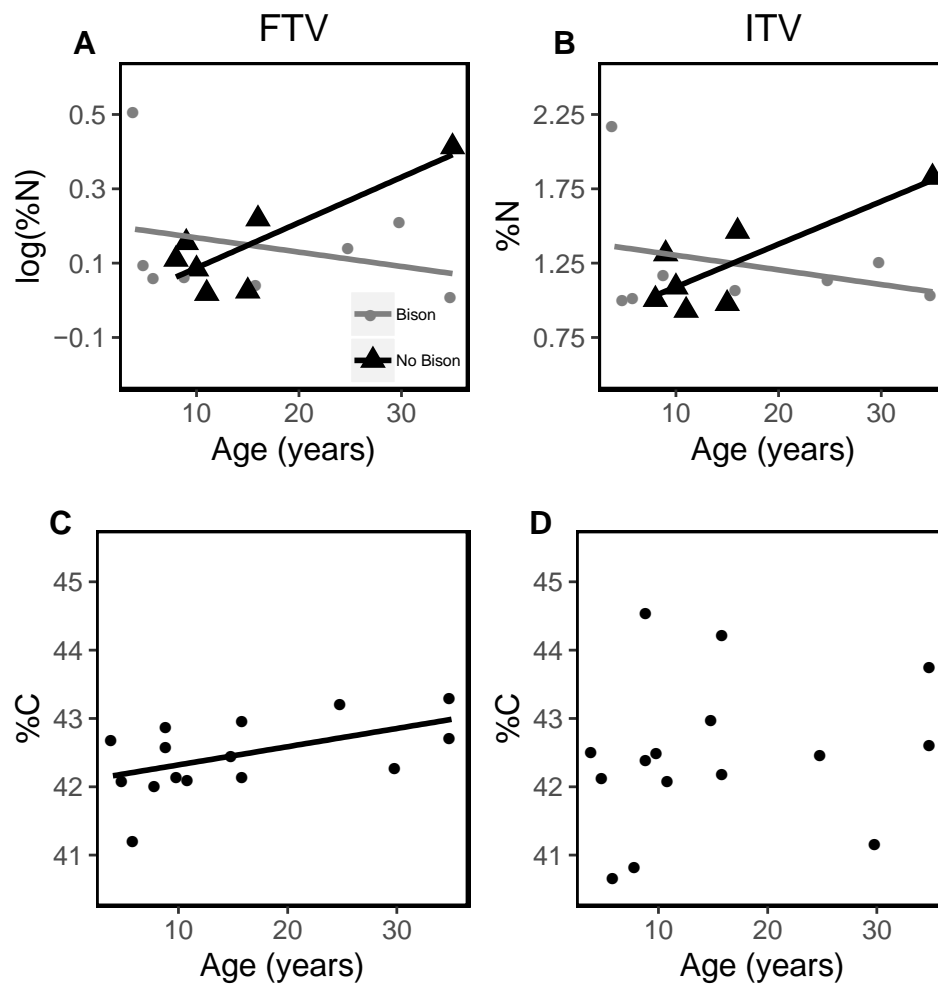


Figure 6: Effects of Management on Nitrogen and Carbon Content. **A:** FTV log(%N) and significant bison x age interaction; **B:** ITV %N and significant bison x age interaction; **C:** FTV %C and significant age effect; **D:** ITV %C with no significant effects.

CHAPTER 4

DISCUSSION

Despite recent attention to functional diversity as a method for evaluating communities, the influence of intraspecific trait variation and consequences for ecosystem function remains unclear. To address this gap, this study examined the plant functional diversity responses to altered environmental conditions in a restored tallgrass prairie, measures functional diversity using both fixed trait values and intraspecific trait values, and compares functional diversity to ecosystem function estimated as productivity. My results show that bison reintroduction and prescribed fire affect functional diversity, and that age since restoration planting has a consistent negative effect on functional diversity. Inclusion of ITV has significant impacts on environment-trait relationships, revealing patterns that are different from or obscured by fixed trait effects. Scaling from community level composition to ecosystem processes, these results outline a pathway from environmental conditions and functional diversity responses to subsequent influences on productivity.

4.1 Do restoration management practices affect functional diversity?

Prescribed fire and bison reintroduction impact plant communities and taxonomic diversity measures when they are used as management practices in restored habitats (Hartnett, Hickman & Walter 1996; Pauly 1997; Bond & Keeley 2005, Koerner & Collins 2014; Towne; Hartnett & Cochran 2016), yet few studies have focused on how these practices alter the functional diversity of restored communities, despite the many calls for functional ecology

research (Lavorel & Garnier 2002; McGill et al. 2006; Cadotte, Carscadden & Mirotchnick 2011; Brudvig 2017). My data show that bison reintroduction and prescribed fire greatly influence functional diversity metrics, with implications for primary productivity resulting from changes in trait composition. Across measures of FRic, FEve, and FDis, there is a strong pattern of site age as the most influential factor, with these measures generally reduced in older sites. This pattern is also maintained whether metrics were calculated using FTV or ITV, which shows the strength of the relationship across methodology. Reduced functional diversity in older sites and remnants compared to younger sites may be the result of species turnover, as the plant community composition shifts from early pioneer, weedy, or generalist species to later successional species of high conservation value (Swink & Wilhelm 1979, Hansen & Gibson 2014). The decrease in functional evenness with site age may be due to a reduction in forbs and increase in grass abundance, creating gaps in niche space. Older sites at Nachusa Grasslands tend to have lower species diversity and higher grass:forb ratios, showing that as sites age grasses become more dominant (Blackburn 2018). Grasses are functionally distinct from forbs, so decreases in the abundances of forbs in older sites create gaps in the distribution of species in trait space, thus decreasing FEve. This may be driven by environmental filtering in community assembly, in which environmental conditions favor specific trait values and drive the community towards the portion of niche space best suited for the conditions (Keddy 1992). As sites age, species that occupy portions of trait space not favored by environmental filters have lower abundances in the community, thus reducing the overall functional evenness. As FEve_{ITV} was not affected by prescribed fire and bison reintroduction, it may be influenced by other environmental conditions not measured in this study.

Although sometimes mediated by the affect of age since planting, bison reintroduction and prescribed fire were shown to affect functional diversity. Bison reduced $FRic_{ITV}$ (no age interaction) and $FEve_{FTV}$ (age interaction), which may be the result of preferential grazing. Despite many papers suggesting that bison reintroduction can reduce the dominance of competitive grasses and create new niche space for species functionally distinct from grasses (i.e., increase $FEve$ and increase $FRic$, respectively) (Knapp et al. 1999; Towne, Hartnett & Cochran 2005; Wilsey & Martin 2015; Elson & Hartnett 2017), our results show that bison reduce both $FEve$ and $FRic$. While increasing species diversity (Blackburn 2017), bison grazing may be negatively impacting $FRic$ by imposing a selective pressure for traits that respond well to grazing and reducing the variance of particular traits, such as SLA or nitrogen content. Additionally, the summed cover of the ten most common species, which were sampled for traits, does not differ in bison sites compared to non-bison sites, as might be expected if bison reduced the cover of dominant species and increased taxonomic evenness. Thus bison may not have as strong of an effect on controlling dominant species as expected. This effect on $FRic$ may result from sampling technique; following the mass ratio hypothesis (Aarssen 1997; Huston 1997; Grime 1998), we sampled the ten most common species at each site with the assumption that this subset would be an accurate sampling of the most influential species of the plant community, and thus disregarding rare species. However, bison grazing may indeed be reducing the competition with dominant grasses and providing niche space for functionally distinct species, but they may represent a small proportion of the plant community and were thus excluded from measurements in our study. Rare species can contribute disproportionately to functional richness and are often rare because of their functional uniqueness and specific niche requirements (Umaña et al. 2017).

While the results of FRic in this study have implications for the relationship between grazing and diversity in functional traits, the addition of rare species to FRic calculations in this system may alter the observed effect of bison reintroduction to restored grasslands.

The increase in FRic with age of unburned sites shows a broader range of functional trait values, possibly due to the lack of fire disturbance that year. Sites at Nachusa Grasslands are typically burned frequently, approximately every 1-3 years. Fire likely has a short-term effect with greater influence on traits of species rather than immediate changes in plant community composition due to the regular, frequent fire regime at Nachusa Grasslands. That is, because all sites are burned frequently, there is insufficient time during burn intervals for fire-intolerant species to establish. The species that make up these communities must be fire-adapted in order to persist, so fire impacts on FRic are the result of plasticity in functional traits and short-term changes in relative abundance. Other studies have also demonstrated the effects of disturbances on functional diversity, however with results that are sometimes incongruent with this study. In Brazilian forests, FRic of tree communities was unaffected by fragmentation disturbances (Biswas & Mallik 2010); however, canopy losses of Canadian riparian forests increased FRic for intermediate levels of disturbance (Magnago et al. 2014). In other restored grasslands, fire did not affect FRic, conflicting results here (Grman et al. 2018); however, that study had greater variation in fire intervals among sites, which might have obscured the patterns I detected. In grassland systems, land-use intensification and fertilizer inputs resulted in increased FEve and FRic, respectively, conflicting with the observed decrease in FEve with bison grazing disturbance (Pakeman 2011; and Niu et al. 2014). Similar to canopy loss and fertilizer input, prescribed fire may alter abiotic conditions in similar ways via changes in light penetration and

soil nutrients, which may play a role in increasing FRic. However, the responses of functional diversity metrics may depend on the type and intensity of disturbances.

Environmental conditions imposed by management strategies show clear effects on functional diversity metrics, indicating that plant communities respond to changes in their environment both through changes in community composition and functional composition. Inclusion of abiotic factors affected by management strategies in future investigations may further clarify functional responses to environmental conditions, as is common in other functional diversity studies (Jung et al. 2010; Kichenin et al. 2013; Schöb et al. 2013; Jiang & Ma 2015; Abgrall et al. 2017; Forrestel et al. 2017; Zirbel et al. 2017).

4.2 Does inclusion of intraspecific trait variation alter the relationships between management and functional diversity?

The observed relationships between bison reintroduction, prescribed fire, and site age on functional diversity measures were dependent on the method of calculating functional diversity. The inclusion of ITV altered the relationships between management strategies and functional diversity for three of four diversity metrics and four leaf traits. In the case of FRic, the results from the inclusion of ITV were incongruent with the FTV results; for FEve, inclusion of ITV led to age as the only significant effect, without a bison interaction that was seen from FTV results. When examining FDis, age was only seen to be significant when using ITV, revealing a relationship that had been masked by FTV. FDiv was not affected by management strategies, regardless of methodology. Thus, the hypothesis that the inclusion of ITV is important for measuring functional diversity is supported, as these relationships depend heavily on the trait values used for calculations. While it is difficult to quantify, many studies have also documented

the strength and direction of the effect of intraspecific variation on functional diversity and functional traits (Albert et al. 2010a; Jung et al. 2010; de Bello et al. 2011; Kichenin et al. 2013; Niu, He & Lechowicz 2016; Zuo et al. 2017).

The inconsistencies between FTV and ITV measures may be due the relative strength of environmental gradients from management practices and the resulting plasticity of individuals at each site (Albert et al. 2012, Laughlin & Joshi 2015). Species' realized niches can occupy a range of environmental conditions, and species can respond through plasticity to accommodate these ranges. As FTV functional diversity metrics can only reflect responses that arise from species turnover (i.e. changes in the species composition of the sampled community), this method of measurement cannot account for plastic responses to changes in environmental conditions. Considering that this study system comprises a relatively small gradient in environmental conditions (small range in prescribed fire frequency and limited time since bison grazing treatments began), the effect of species turnover is relatively small (many species occupy many sites) and cannot reliably explain the effects on functional diversity metrics. In systems with weaker environmental gradients that are within species' realized niches, plastic responses of individuals within a species are likely to have a greater influence on functional diversity patterns than species turnover (Albert et al. 2010a; Kichenin et al. 2013). Other studies that have examined the contributions of ITV to environment-trait patterns have depended on stronger environmental gradients that extend beyond some plant species' realized niches. Kichenin et al. (2013) found that changes in plant functional traits along a strong alpine elevational gradient (900 m) were more greatly affected by interspecific than intraspecific responses, while Niu, He & Lechowicz (2016) found that across comparatively weaker environmental gradients of grazing

and soil nutrient availability ITV had a significant effect on traits (see also: Albert et al. 2010a; Hulshof & Swenson 2010; Jung et al. 2010). Inconsistent findings on the relative importance of intraspecific variations may result from the types and severity of environmental gradients, in which gradients that extend beyond species' realized niches may favor FTV and gradients within realized niches may favor ITV (Albert et al. 2010b; Kichenin et al. 2013). This study is one of few to examine the importance of ITV in weaker environmental gradients and within a restoration context in which the gradients are manipulated by management plans. Studies examining functional trait composition of plant communities across relatively weak gradients likely will need to measure intraspecific variation in traits to detect any patterns in functional diversity.

In addition to the relative strength of environmental gradient conditions, the importance of ITV may depend on the plasticity of functional traits measured (Albert et al. 2010a). Traits vary in degrees of plasticity, and plasticity of the same trait may vary between species within an ecosystem, stemming from genetic variation, or the variation in phenotypes from gene responses to environmental stimuli (Rozendaal, Hurtado & Poorter 2006; Albert et al. 2010b; Burns & Strauss 2012; Funk et al. 2017). Traits that vary greatly along light gradients may be more responsive to changes in environmental conditions from prescribed fire (increase in dominant grasses, decreased canopy structure, increased light penetration), such as SLA (Poorter et al. 2009). SLA_{ITV} was significantly affected by each environmental factor, showing a strong intraspecific response over an FTV response from interspecific effects and species turnover, as seen in other studies as well (Poorter et al. 2009, Albert et al. 2010a, Jung et al. 2010).

Andropogon gerardii and *Sorghastrum nutans* (which comprised 32.2-49.9% of sampled plant

communities in burned, non-bison sites) showed higher SLA averages than CWM SLA_{FTV} in burned, non-bison sites, indicating that the intraspecific responses of these two dominant grasses may be the driver of this SLA_{ITV} pattern. LDMC, on the other hand, may be less plastic and resist changes across gradients, due to either limited genetic variation or limited gene response to environmental stimuli; the contribution of ITV may be weaker, and changes in LDMC CWMs may be more affected by species turnover (Roche, Díaz-Burlinson & Gachet 2004; Kichenin et al. 2013; although see also: de Bello et al. 2011); our data show significant effects of fire only from FTV and no effects from ITV, showing that decreasing LDMC in burned sites is due to changes in species composition. $LDMC_{ITV}$ was not significantly affected by management strategies, showing that with the effects of species turnover seen from $LDMC_{FTV}$ individuals may have compensated for disturbances by maintaining similar trait space. Therefore, the contributions of ITV to changes in CWMs and function diversity are highly dependent on the traits measured (Roche, Díaz-Burlinson & Gachet 2004; Hulshof & Swenson 2010; Kichenin et al. 2010; Jung et al. 2010; Messier, McGill & Lechowicz 2010; Auger & Shipley 2012). In addition to gradient strength relative to species' niches, ecologists must consider the level of plasticity in measured functional traits to decide *a priori* the methodology that best suits the system and objectives (Albert et al. 2012).

4.3 Do changes in functional diversity drive ecosystem function?

Despite the implicit restoration goal of reinstating ecosystem functions (Hobbs & Harris 2001; Thorpe & Stanley 2011), the factors that determine key processes still elude managers, and ecologists struggle to dissect individual site idiosyncrasies (Brudvig 2017). In an effort to resolve these questions for grassland restoration, I analyzed the effects of management and

functional diversity on NPP, as an estimate of ecosystem function. Prescribed fire, bison reintroduction, and site age affected productivity across sites, showing that management interventions themselves do have an effect on ecosystem function. Fire, in the absence of grazers, increased productivity, consistent with other grassland studies (Knapp & Seastedt 1986; Johnson & Matchett 2001). Increases in productivity post-fire may be due to increased light penetration and changes in soil temperatures and moisture, and nutrient cycling due to removal of dead plant material (Facelli & Pickett 1991; Chapin 1993; Anderson 2006; Garnier et al. 2007; Vogel et al. 2010). Consistent with proposed mechanisms of fire increasing dominant C₄ grasses that increase productivity (Anderson 2006; Vogel et al. 2010), *Andropogon gerardii* and *Sorghastrum nutans* still comprised a large portion of the plant community in burned, non-bison sites. The observed increase in NPP in burned non-bison sites may be the result of the reduction in build-up of dead material, allowing more light to reach the soil and promoting the growth of both dominant grasses and other subordinate species, rather than limiting either group. Within bison sites, the effect of fire potentially was ameliorated by bison grazing (fire reduced thatch by 50.0% and 23.9% in non-bison and bison sites, respectively). Removing dominant grass biomass may have reduced the volume and thus impacts of thatch on fire in unburned sites.

Functional traits and functional diversity are proposed as conceptual links to ecosystem functioning, in which community-level trait responses scale up to changes in ecosystem processes (Tilman et al. 1997; Diaz & Cabido 2001; Lavorel & Garnier 2002). Addressing the relationship between functional diversity and ecosystem function, I found that FE_{ITV} was significantly positively correlated with NPP; sites with greater functional evenness showed an increase in productivity. This result is supported by other studies that have found positive

diversity-function relationships, and supports the necessity of improved functional diversity for reinstating ecosystem functions (Tilman et al. 1997; Diaz & Cabido 2001; Zirbel et al. 2017; Grman et al. 2018). Increases in productivity with FEve may be due to improved resource partitioning, in which species are more evenly distributed across trait space, suggesting higher niche complementarity and decreased competition for resources, which has been shown to support ecosystem functions (Loreau & Hector 2001; Mason et al. 2005; Cardinale 2011; Turnbull et al. 2013). Site age also influenced this relationship, in which the youngest sites were the most functionally even and the most productive. The decreased FEve_{ITV} observed in older sites may be due to increased functional redundancy from the shift to grass dominated communities, which limits productivity. The demonstrated links between management strategies, FEve_{ITV} and ecosystem function show that alterations to environmental conditions affects responses that scale from community level diversity to ecosystem processes. Furthermore, the connection between functional diversity and ecosystem function is dependent on the intraspecific responses to management strategies, as this finding was not supported by fixed trait values.

4.4 Conclusions

As we face losses in biodiversity and ecosystem services, it has become imperative to evaluate the relationships between environmental conditions, functional diversity, and ecosystem functioning as measures of restoration success and ecosystem resilience. Many recent functional ecology studies have supported links between environmental conditions and functional trait responses (Tilman et al. 1997; Díaz & Cabido 2001; Garnier et al. 2007; Cadotte et al. 2009; Forrestel et al. 2017; Zirbel et al. 2017). However, this study addresses a gap in functional

research by incorporating intraspecific responses and subsequent impacts on ecosystem function. By examining community and ecosystem level responses, I show that individual responses to disturbances scale up to impact whole ecosystem processes, and that this connection is dependent on the inclusion of intraspecific trait variation. Future iterations of environment-trait-function studies should include deliberate selections of functional traits to fit the ecosystem functions in question, as well include multiple functions, or ecosystem multi-functionality measures (Cadotte, Carscadden & Mirotchnick 2011; Grman et al. 2018). Many other ecosystem functions important for ecological research and restoration management (e.g. decomposition, nutrient cycling, floral resources for pollinators, predation of other taxa, and seed predation) may be affected by changes in plant functional diversity, and warrant further investigation (Funk et al. 2017; Zirbel et al. 2017; Grman et al. 2018).

Additionally, these findings have significant implications for restoration ecology. While managers are successful at establishing communities with high functional diversity, the observed declines with age suggest that management plans should prioritize maintaining high functional diversity to improve ecosystem function, probably through ongoing efforts to limit the shift towards grass-dominated communities. Testing ecological principles in the context of restoration and identifying community responses to disturbances is critical for improving the predictability and success of restoration outcomes.

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APPENDIX A

Fixed Trait Value Means for Functional Traits

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Achillia millefolium</i>	40.3	100.15	1238.03	276.26	10.4	1.26	43.64
<i>Agrostis gigantea</i>	52.47	225.35	267.14	333	17.67	1.22	42.26
<i>Ambrosia artemisiifolia</i>	20.65	100.1	121.53	210.76	22.91	2.78	41.18
<i>Andropogon gerardii</i>	112.04	364.86	1804.24	373.55	9.57	1.18	43.26
<i>Anemone virginiana</i>	38.31	199.74	1512.82	372.86	9.46	0.89	42.69
<i>Antennaria plantaginifolia</i>	5.21	502.68	444.79	267.25	12.39	1.11	42.63
<i>Baptisia alba</i>	86.96	130.5	1142.31	234.98	10.89	3.88	44.97
<i>Bouteloua curtipendula</i>	53.92	220.4	301.4	574.98	7.16	1.6	42.52
<i>Bromus inermis</i>	67.3	436.43	956.21	386.16	13.19	1.42	42.88
<i>Carex</i>	47.99	321.64	496.89	421.55	14.47	1.2	42.56
<i>Coreopsis palmata</i>	62.33	154.43	262.99	479.9	7.38	1.21	44.16
<i>Dalea candida</i>	64.33	100.2	216.03	313.88	6.62	2.52	40.47
<i>Dalea purpurea</i>	54.74	102.3	67.37	310.81	6.71	2.36	41
<i>Daucus carota</i>	102.38	112.9	972.48	266.9	9.56	2.04	42.78
<i>Desmodium canadense</i>	64.21	127.6	2221.7	371.27	13.95	2.14	44.26
<i>Echinacea pallida</i>	52.15	278.09	2114	265.43	6.82	1.01	36.32
<i>Elymus canadensis</i>	101.41	607.96	852.95	437.48	9.26	1.41	43.96
<i>Helianthus grosseserratus</i>	84.96	272.2	302.92	216.02	13.96	2.68	46.5
<i>Helianthus occidentalis</i>	38.53	367.04	1912.61	266.12	7.46	0.87	37.42
<i>Lespedeza capitata</i>	80.19	183.6	538.57	383.25	11.83	2.32	45.69
<i>Monarda fistulosa</i>	65.19	116.18	538.33	367.31	12.22	1.29	43.48
<i>Oligoneuron rigidum</i>	89.19	287.82	1925.27	342.29	8.13	1.17	42.08
<i>Panicum oligosanthes</i>	31.82	288.8	317.68	325.58	10.07	0.9	42.46
<i>Parthenium integrifolium</i>	77.46	176.8	1480.91	264.14	10.84	1.53	43.09
<i>Penstemon digitalis</i>	70.77	222.61	1370.81	359.6	8.38	0.67	44.23
<i>Poa compressa</i>	35.64	392.5	203.55	361.17	13.6	1.03	42.01
<i>Poa pratensis</i>	31.33	359.19	210.64	387.37	10.38	0.95	41.83
<i>Prunus serotina</i>	123.25	192.6	2700.81	385.47	12.55	2.22	45.22

(continued on following page)

<i>Pycnanthemum virginianum</i>	57.04	358.9	42.23	442.43	9.11	0.77	43.44
<i>Ratibida pinnata</i>	95.21	130.16	1305.8	281.12	10.26	1.32	39.66
<i>Rubus flagellaris</i>	31.61	100	1883.45	332.8	17.17	1.89	46.16
<i>Schizachyrium scoparium</i>	45.97	353.68	508.28	369.72	10.5	0.96	42.72
<i>Silphium integrifolium</i>	82.03	358.6	1463.29	290.1	7.73	1.3	42.12
<i>Solidago canadensis</i>	88.63	162.27	592.41	344.4	9.81	1.25	43.74
<i>Solidago graminifolia</i>	54.23	178.58	85.28	389.05	8.39	1.55	46.09
<i>Solidago missouriensis</i>	75.8	145.67	503.71	371.63	7.6	1.09	42.87
<i>Solidago nemoralis</i>	41.43	100	203.07	329.02	10.58	0.76	39.5
<i>Solidago speciosa</i>	74.03	298.48	421.63	343.34	7.52	1.08	45.13
<i>Sorghastrum nutans</i>	91.6	398.58	1704.92	397.88	9.14	1.09	41.81
<i>Symphyotrichum ericoides</i>	52.57	102.35	29.73	337.6	9.58	1.2	41.78
<i>Symphyotrichum laeve</i>	74.2	220.83	985.64	282.99	11.61	1.16	41.11
<i>Symphyotrichum oolentangiense</i>	72.09	227.75	1259.24	346.86	8.48	0.96	40.66
<i>Symphyotrichum pilosum</i>	64.86	100	23	343.8	10.79	1.89	42.96
<i>Trifolium pratense</i>	48.04	144.86	1355.59	233.57	20.72	3.15	43.3
<i>Zizia aurea</i>	77.46	243.46	1314.26	334.24	11.37	1.07	41.4

APPENDIX B

Intraspecific Trait Value Means for Functional Traits by Site

Intraspecific Trait Value Means for Functional Traits: Clear Creek East

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Andropogon gerardii</i>	142.21	341.10	1579.70	380.05	8.97	1.04	44.74
<i>Echinacea pallida</i>	56.57	312.40	904.57	243.93	7.03	1.13	36.17
<i>Monarda fistulosa</i>	66.07	114.50	588.92	337.77	12.08	1.42	44.18
<i>Poa compressa</i>	22.46	285.20	193.98	339.91	14.21	0.97	42.38
<i>Poa pratensis</i>	21.67	286.10	150.07	337.07	11.56	0.81	41.56
<i>Ratibida pinnata</i>	93.97	148.30	1247.72	274.14	9.77	1.12	40.72
<i>Schizachyrium scoparium</i>	47.71	375.70	499.22	338.75	11.03	0.90	43.84
<i>Sorghastrum nutans</i>	103.79	451.20	1054.06	390.58	5.59	1.05	42.56
<i>Symphyotrichum ericoides</i>	50.27	100.00	24.42	180.35	11.55	1.17	42.53
<i>Trifolium repens</i>	59.68	215.80	1391.25	245.03	20.00	3.33	44.34

Intraspecific Trait Value Means for Functional Traits: Clear Creek West

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Carex spp.</i>	53.76	374.20	654.71	383.01	15.32	1.19	43.84
<i>Coreopsis palmata</i>	60.11	146.50	318.56	350.53	7.42	1.46	45.86
<i>Elymus canadensis</i>	105.51	661.50	586.02	428.70	7.91	1.93	45.90
<i>Parthenium integrifolium</i>	91.77	233.90	2231.63	279.75	9.69	1.47	42.95
<i>Poa compressa</i>	43.85	528.10	312.96	418.93	8.41	0.90	43.77
<i>Schizachyrium scoparium</i>	48.24	250.70	474.12	342.97	10.13	1.18	44.87
<i>Solidago canadensis</i>	106.19	168.60	615.32	332.63	9.99	1.48	46.43
<i>Sorghstrum nutans</i>	100.54	578.20	2660.39	347.99	8.76	1.14	44.31
<i>Symphyotrichum pilosum</i>	90.18	169.70	461.44	281.88	10.23	1.76	43.05
<i>Zizia aurea</i>	92.94	266.80	1691.62	334.19	10.80	1.21	42.41

Intraspecific Trait Value Means for Functional Traits: Franklin Creek

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Andropogon gerardii</i>	88.06	356.40	3849.93	384.05	13.27	0.91	42.94
<i>Solidago canadensis</i>	69.95	156.60	624.50	349.74	9.19	1.06	43.70
<i>Penstemon digitalis</i>	66.52	183.50	1314.62	372.55	8.95	0.59	44.41
<i>Symphyotrichum ericoides</i>	45.25	100.80	28.99	339.25	10.50	1.16	40.87
<i>Sorghastrum nutans</i>	79.05	392.40	2566.37	361.11	11.11	0.93	40.97
<i>Schizachyrium scoparium</i>	48.50	263.20	723.84	366.57	11.52	1.01	42.76
<i>Echinacea pallida</i>	47.46	278.20	3954.37	231.81	6.62	0.90	37.64
<i>Anemone cylindrica</i>	37.35	176.90	1247.33	442.28	8.58	1.02	42.01
<i>Monarda fistulosa</i>	60.98	127.20	501.52	662.14	11.18	1.76	43.10
<i>Ratibida pinnata</i>	72.44	154.60	5170.63	298.86	18.64	1.31	38.68

Intraspecific Trait Value Means for Functional Traits: Holland Farm

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Ambrosia flagellaris</i>	20.65	100.10	121.53	210.76	22.91	2.78	41.18
<i>Echinacea pallida</i>	62.60	227.90	2140.02	234.49	6.84	1.44	36.22
<i>Elymus canadensis</i>	108.08	684.20	983.02	446.75	8.19	1.97	43.81
<i>Oligoneuron rigidum</i>	119.84	251.90	959.87	351.00	8.52	1.89	42.05
<i>Solidago canadensis</i>	116.68	146.20	784.89	365.77	9.99	1.60	43.61
<i>Solidago graminifolia</i>	66.41	149.80	64.79	398.62	9.70	2.38	45.12
<i>Symphyotrichum ericoides</i>	71.58	100.00	8.25	666.67	5.98	1.65	41.08
<i>Symphyotrichum laeve</i>	74.51	200.30	1063.03	271.74	11.45	1.69	41.22
<i>Symphyotrichum pilosum</i>	64.86	100.00	23.00	343.80	10.79	1.89	42.96
<i>Trifolium pratense</i>	21.69	106.00	1023.10	183.56	22.31	3.91	42.86

Intraspecific Trait Value Means for Functional Traits: Hook Larsen

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Andropogon gerardii</i>	95.06	448.30	2114.61	328.53	8.23	1.16	43.54
<i>Anemone cylindrica</i>	43.36	182.20	1541.65	370.05	10.07	0.96	43.41
<i>Dalea purpurea</i>	54.74	102.30	67.37	310.81	6.71	2.36	41.00
<i>Echinacea pallida</i>	38.59	316.30	2944.72	258.74	7.84	0.81	39.05
<i>Helianthus occidentalis</i>	36.17	337.60	2107.47	257.58	8.46	0.94	39.96
<i>Monarda fistulosa</i>	68.67	114.20	613.83	285.34	12.66	1.08	43.34
<i>Ratibida pinnata</i>	90.15	137.60	838.83	291.12	8.44	1.49	39.87
<i>Schizachyrium scoparium</i>	44.62	1007.90	536.99	358.63	10.48	1.01	42.94
<i>Sorghastrum nutans</i>	72.50	425.60	2304.28	382.10	10.78	0.92	40.87
<i>Zizia aurea</i>	63.09	239.43	1355.87	332.21	11.82	1.12	42.27

Intraspecific Trait Value Means for Functional Traits: Holland North

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Antennaria plantaginifolia</i>	6.31	527.40	680.28	244.46	12.27	1.08	43.24
<i>Echinacea pallida</i>	61.01	216.90	1758.33	237.10	7.52	0.81	35.81
<i>Penstemon digitalis</i>	62.87	195.67	1469.69	359.53	8.74	0.65	43.95
<i>Schizachyrium scoparium</i>	50.58	273.10	531.07	339.69	13.32	0.69	42.45
<i>Solidago graminifolia</i>	54.31	171.80	63.74	334.75	8.52	1.62	46.61
<i>Solidago occidentalis</i>	52.99	405.30	1941.20	281.41	7.13	0.69	35.58
<i>Solidago speciosa</i>	79.14	239.90	449.51	320.88	7.54	1.09	45.12
<i>Symphyotrichum ericoides</i>	56.65	113.30	19.97	235.41	8.40	0.99	41.47
<i>Symphyotrichum laeve</i>	75.07	166.90	1170.26	261.70	13.10	0.99	41.55
<i>Symphyotrichum oolentangiense</i>	52.26	206.30	1253.72	342.19	9.45	0.77	39.44

Intraspecific Trait Value Means for Functional Traits: Holland Prairie West

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Andropogon gerardii</i>	117.60	347.40	2566.15	314.38	8.60	0.87	43.31
<i>Carex spp.</i>	92.77	236.10	552.56	361.10	18.38	1.53	42.75
<i>Coreopsis palmata</i>	67.64	155.20	200.71	400.74	7.65	1.21	44.68
<i>Elymus canadensis</i>	103.68	569.80	1327.92	405.26	13.29	1.28	43.28
<i>Parthenium integrifolium</i>	81.62	120.10	1022.68	227.27	13.60	1.90	43.83
<i>Poa compressa</i>	43.34	338.00	198.68	367.73	11.62	1.23	42.31
<i>Poa pratensis</i>	43.34	338.00	198.68	367.73	11.62	1.23	42.31
<i>Ratibida pinnata</i>	113.25	162.20	634.58	274.82	10.05	1.43	41.50
<i>Schizachyrium scoparium</i>	54.35	494.90	793.13	317.43	12.12	1.03	42.29
<i>Sorghastrum nutans</i>	121.51	328.67	1460.48	432.54	10.57	1.14	41.35
<i>Zizia aurea</i>	71.93	225.80	560.61	321.76	12.07	0.74	38.60

Intraspecific Trait Value Means for Functional Traits: Lowden

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Antennaria plantaginifolia</i>	6.22	559.13	525.79	288.36	11.12	1.11	42.02
<i>Carex spp.</i>	27.16	262.18	408.63	394.58	11.67	1.22	41.70
<i>Echinacea pallida</i>	50.23	218.60	1371.74	470.78	6.54	0.93	34.76
<i>Helianthus occidentalis</i>	26.44	349.40	1465.69	252.61	6.13	0.99	36.71
<i>Schizachyrium scoparium</i>	46.68	300.44	520.32	397.79	10.61	0.95	42.86
<i>Solidago missouriensis</i>	75.80	145.67	503.71	371.63	7.60	1.09	42.87
<i>Solidago nemoralis</i>	41.43	100.00	203.07	329.02	10.58	0.76	39.50
<i>Sorghastrum nutans</i>	113.29	336.10	737.08	410.88	10.02	1.14	41.17
<i>Symphyotrichum laeve</i>	71.94	174.20	599.05	313.22	8.44	0.92	40.41
<i>Symphyotrichum oolentangiense</i>	91.92	249.20	1264.77	351.52	7.51	1.15	41.88

Intraspecific Trait Value Means for Functional Traits: Main Unit

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Achillia millefolium</i>	29.14	100.00	1746.28	264.61	9.74	0.79	42.33
<i>Andropogon gerardii</i>	81.18	419.90	1109.92	395.12	7.20	1.17	40.69
<i>Baptisia alba</i>	75.51	139.10	1091.75	258.51	11.17	3.67	45.18
<i>Dalea candida</i>	64.33	100.20	216.03	313.88	6.62	2.52	40.47
<i>Echinacea pallida</i>	50.21	269.70	1076.30	257.82	6.80	1.14	34.92
<i>Lespedeza capitata</i>	80.19	183.60	538.57	383.25	11.83	2.32	45.69
<i>Oligoneurum rigidum</i>	45.71	235.60	8099.15	312.25	5.41	0.70	40.86
<i>Penstemon digitalis</i>	67.68	214.10	982.92	350.75	8.63	0.74	43.70
<i>Schizachyrium scoparium</i>	55.08	257.80	538.60	388.58	8.48	0.97	42.51
<i>Sorghstrum nutans</i>	78.00	374.90	1279.84	389.59	7.27	1.11	41.46

Intraspecific Trait Value Means for Functional Traits: Main Unit Remnant

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Agrostis gigantea</i>	45.50	262.40	172.95	351.15	15.84	1.24	41.42
<i>Anemone cylindrica</i>	35.87	194.60	1351.18	340.14	8.59	0.91	42.90
<i>Antennaria plantaginifolia</i>	3.09	432.80	144.51	273.16	13.53	1.15	42.64
<i>Baptisia alba</i>	98.41	121.90	1192.86	211.45	10.61	4.08	44.75
<i>Carex spp.</i>	30.90	360.10	464.06	349.29	12.56	0.94	41.14
<i>Panicum oligosanthos</i>	31.82	288.80	317.68	325.58	10.07	0.90	42.46
<i>Poa pratensis</i>	25.20	303.90	237.86	402.97	11.62	0.91	41.89
<i>Schizachyrium scoparium</i>	48.99	313.10	346.07	398.65	8.66	0.96	43.03
<i>Solidago graminifolia</i>	42.66	226.60	128.52	369.08	7.75	1.01	45.90
<i>Sorghastrum nutans</i>	64.01	400.00	848.23	383.35	6.07	1.12	41.82

Intraspecific Trait Value Means for Functional Traits: Stone Barn

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Echinacea pallida</i>	57.85	256.30	1341.87	233.77	6.34	1.00	35.24
<i>Elymus canadensis</i>	90.51	514.80	1102.80	414.83	13.18	1.26	41.88
<i>Oligoneuron rigidum</i>	93.72	266.20	676.94	332.44	8.35	1.02	42.51
<i>Penstemon digitalis</i>	77.19	259.60	1713.76	354.53	8.11	0.53	43.80
<i>Poa compressa</i>	25.80	471.80	209.21	412.50	9.32	0.78	41.78
<i>Poa pratensis</i>	25.80	471.80	209.21	412.50	9.32	0.78	41.78
<i>Ratibida pinnata</i>	93.36	101.40	811.93	263.99	10.09	1.16	37.60
<i>Schizachyrium scoparium</i>	42.12	191.40	493.41	313.72	11.00	0.87	40.46
<i>Solidago speciosa</i>	77.03	261.40	399.55	354.35	7.39	1.16	44.37
<i>Sorghastrum nutans</i>	82.63	312.40	1689.07	362.21	11.54	1.01	40.38
<i>Symphotrichum laeve</i>	71.86	243.10	1257.63	259.19	12.22	1.08	40.11

Intraspecific Trait Value Means for Functional Traits: Sand Farm

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Achillia millefolium</i>	50.02	100.60	690.32	277.62	12.04	1.28	43.79
<i>Agrostis gigantea</i>	59.43	188.30	361.33	314.85	19.50	1.19	43.10
<i>Andropogon gerardii</i>	143.27	431.60	1779.77	371.30	11.79	1.60	44.89
<i>Carex spp.</i>	42.36	258.33	435.58	712.45	17.64	1.17	42.72
<i>Poa compressa</i>	36.84	379.50	141.94	297.69	14.54	1.07	43.00
<i>Ratibida pinnata</i>	105.48	123.00	1177.51	259.01	9.45	1.61	41.31
<i>Schizachyrium scoparium</i>	46.32	479.78	542.49	383.27	10.92	1.01	44.76
<i>Solidago canadensis</i>	86.30	221.20	522.21	337.17	9.41	1.38	45.05
<i>Sorghastrum nutans</i>	91.38	394.22	1942.92	341.66	10.60	1.29	44.32
<i>Trifolium pratense</i>	33.80	122.00	1726.82	182.80	18.05	2.04	43.36

Intraspecific Trait Value Means for Functional Traits: Thelma Carpenter

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Anemone cylindrica</i>	34.67	228.30	1481.65	393.74	9.21	0.76	43.24
<i>Bromus inermis</i>	84.57	577.40	1097.55	452.55	8.91	0.87	42.64
<i>Echinacea pallida</i>	43.41	362.80	3501.07	247.16	5.58	0.93	37.72
<i>Monarda fistulosa</i>	59.01	108.70	495.14	340.85	11.79	1.07	43.86
<i>Pycnanthemum virginianum</i>	59.86	365.20	46.15	508.74	8.20	0.77	43.44
<i>Ratibida pinnata</i>	84.33	135.80	909.71	294.59	8.11	1.12	38.79
<i>Schizachyrium scoparium</i>	32.89	281.30	410.86	408.70	10.63	0.92	43.14
<i>Silphium integrifolium</i>	82.03	358.60	1463.29	290.10	7.73	1.30	42.12
<i>Solidago speciosa</i>	60.49	375.00	359.13	363.54	7.24	0.96	45.74
<i>Sorghastrum nutans</i>	88.04	467.80	1546.63	383.45	9.00	1.10	43.52

Intraspecific Trait Value Means for Functional Traits: Thelma Carpenter Remnant

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Achillia millefolium</i>	53.46	100.00	1135.13	283.11	9.42	1.67	45.96
<i>Bouteloua curtipendula</i>	53.92	220.40	301.40	574.98	7.16	1.60	42.52
<i>Bromus inermis</i>	54.37	327.10	879.18	335.54	14.88	1.85	43.61
<i>Daucus carota</i>	102.38	112.90	972.48	266.90	9.56	2.04	42.78
<i>Helianthus grosseserratus</i>	84.96	272.20	302.92	216.02	13.96	2.68	46.50
<i>Oligoneuron rigidum</i>	59.63	399.10	818.40	343.36	7.87	1.34	42.91
<i>Poa pratensis</i>	33.83	537.90	260.78	376.32	10.22	0.83	43.08
<i>Rubus flagellaris</i>	31.61	100.00	1883.45	332.80	17.17	1.89	46.16
<i>Symphyotrichum ericoides</i>	40.07	100.00	68.33	239.17	13.18	1.46	43.18

Intraspecific Trait Value Means for Functional Traits: West Heinkle

Species	Plant Height (cm)	Toughness (g)	Area (mm ²)	LDMC (mg/g)	SLA (mm ² /mg)	%N	%C
<i>Andropogon gerardii</i>	97.56	261.80	1802.16	370.72	8.32	0.90	42.90
<i>Coreopsis palmata</i>	59.23	161.60	269.70	688.44	7.07	0.97	41.96
<i>Desmodium canadense</i>	64.21	127.60	2221.70	371.27	13.95	2.14	44.26
<i>Oligoneuron rigidum</i>	85.61	156.10	1215.17	349.88	9.16	1.16	42.80
<i>Parthenium integrifolium</i>	58.99	176.40	1188.41	285.39	9.24	1.23	42.51
<i>Prunus serotina</i>	123.25	192.60	2700.81	385.47	12.55	2.22	45.22
<i>Schizachyrium scoparium</i>	39.92	315.90	477.63	387.79	9.08	0.75	42.10
<i>Solidago canadensis</i>	73.06	135.40	475.31	346.18	9.35	1.12	43.62
<i>Sorghastrum nutans</i>	104.99	204.00	1729.93	345.11	10.57	1.13	41.89
<i>Trifolium pratense</i>	53.05	105.67	1149.09	306.27	19.20	3.31	43.38