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Dynamics of community composition and ecological processes in Mesic and Semiarid Grasslands

Sydney K. Jones
University of New Mexico

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Sydney Jones
Candidate

Biology
Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

Dr. Scott Collins, Chairperson

Dr. Marcy Litvak

Dr. William Pockman

Dr. Bruce Hungate

DYNAMICS OF COMMUNITY COMPOSITION AND ECOLOGICAL PROCESSES IN MESIC AND SEMIARID GRASSLANDS

by

SYDNEY K. JONES

B.S., Biology, Northern Arizona University, 2011
Ph.D., Biology, University of New Mexico, 2017

DISSERTATION

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DEDICATION

By this merit,
May it be of benefit.

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Scott, may your happiness and success only increase!

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ABSTRACT

Grassland communities change in response to disturbance and chronic resource alterations. Temporal community dynamics were examined within mesic tallgrass prairie at Konza Prairie in northeastern Kansas, and semiarid desert grassland and shrubland in central New Mexico. In both grasslands, producer and consumer communities changed over time in response to fire frequency and shrub encroachment. Directional change was driven by changes in abundances of species already in the community, rather than turnover in species composition. Despite directional change, species richness was highly stable, making species abundance rather than richness a better indicator of future community change. Species reordering also occurred during a long-term precipitation manipulation experiment at Konza Prairie. Fewer larger rain events resulted in limited changes in plant community composition and structure, but instead caused reordering among forb species. Thus, mesic tallgrass prairie was resistant to long-term changes in precipitation variability and resilient to short-term extremes through species reordering. Further, community dynamics can influence ecological processes. In a shrub encroachment experiment in semiarid grassland, soil respiration was altered in plant-soil monoliths moved between creosotebush shrubland and desert grassland. Grassland respiration was less responsive than shrubland, and microbial activity in both grassland and shrubland soils responded like soils from which they originated. Thus, soil processes lag behind changes in vegetation composition under shrub encroachment. Alterations of species abundances and community composition are likely to continue under global environmental change. Understanding how grasslands respond to long-term changes in resource variability is important because changes in species composition can alter ecological processes.

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INTRODUCTION

Communities are characterized by variability and change. Community dynamics vary in space and time as a function of both stochastic and deterministic processes. Communities may exhibit stochastic variability in response to environmental variability (Bagchi et al. 2013, Matthews et al. 2013, Renner et al. 2014), such as mean annual temperature and interannual precipitation. Alternatively, community change could be directional in response to chronic ecological presses, such as increasing temperature, aridity or alterations in soil nutrients via nitrogen deposition (Sala et al. 2000, Avolio et al. 2014, Hoover et al. 2014). Community change can be gradual or abrupt depending on community resistance to environmental drivers or if drivers are pushing communities across ecological thresholds and tipping points (Scheffer et al. 2001, Bestelmeyer et al. 2011). Changes could be linear or non-linear (Magurran et al. 2010, Gravel et al. 2016). Communities are expected to respond to chronic changes in environmental drivers through a hierarchy of ecological processes, as proposed by the Hierarchical Response Framework (Smith et al. 2009). Phenotypic plasticity will occur relatively rapidly but limited in generating significant community change. This will be followed by a reordering of species dominance patterns and the rate of this change will depend on the turnover rate of the dominate species. Finally, there will be changes in species composition through colonization and local extinction.

Changes in environmental divers, such as disturbance regimes, have been increasing and altering communities (Pickett et al. 1989, Smith 2011a, Kröel-Dulay et al. 2015).

Grasslands are well studied ecosystems in how community composition responds to disturbance and regime shift (Collins and Smith 2006, Maestre and Reynolds 2007). In mesic systems, grasslands are disturbance dependent systems. For example, fire is a well-known regulator of vegetation dynamics in tallgrass prairie (Collins and Calabrese 2012), altering dominance, spatial heterogeneity and woody encroachment (Ratajczak et al. 2017a, 2017b). Communities also change in the absence of disturbance because of ecological presses. In arid systems, grasslands are changing in response to increasing aridity. Increased variability in growing-season precipitation, earlier snow melt, decreased winter precipitation, and later monsoon seasons along with increased mean annual temperatures are likely to increase aridity and alter arid grassland communities (Stewart et al. 2004, Seager et al. 2007, Gutzler and Robbins 2011). Nitrogen deposition is another ecological press leading to community change by increasing productivity and decreasing diversity (Tilman 1987, Baer et al. 2004, Suding et al. 2005). Community changes can take the form of altered species richness, community turnover in species entering and leaving the community or changes the relative species abundances. Changes in vegetation communities are likely to facilitate changes in co-occurring consumer communities that rely on vegetation for either food or habitat resources. For example, different fire frequencies results in changes in consumer community composition due to alterations in vegetation heterogeneity.

In Chapter 1, long-term, concurrent time series data for plants, grasshoppers, breeding birds and small mammals in mesic tallgrass prairie and arid grassland-shrubland ecosystems were analyzed to determine if communities of different taxa in the same ecosystem were undergoing directional change in response to common environmental drivers. These drivers included altered fire frequency in the mesic ecosystem shrub encroachment in the arid ecosystem.

Climate change is a deterministic process which can drive community change (Karl et al. 2009, Munson et al. 2012). Temperature and precipitation are the most influential abiotic factors shaping communities (Whittaker 1970), both of which are predicted to change across the globe within the current century (IPCC 2013). The rate and intensity of precipitation, for example, will likely have consequences on grassland community composition and productivity. Precipitation models predict that precipitation will become more variable with fewer but larger rain events (Huntington 2006, Min et al. 2011, Singh et al. 2013). Mesic grasslands of the US Great Plains in the past decade, have already experiencing a shift toward more extreme rainfall events (Kunkel and Others 2013, Wuebbles et al. 2014). This will have a significant impact on grassland structure and function due to altered soil moisture availability by increase the duration of soil water stress (Knapp et al. 2008a). Water availability and variability is known to have a consistent impact on grassland above net primary productivity as well as variable effects on community composition and structure (Knapp et al. 2001, Hsu et al. 2012, Cleland et al. 2013).

In Chapter 2, a 15-year precipitation manipulation experiment was used to determine if altering the timing and amount of growing season rainfall (fewer, larger events) will impact plant community structure in annually burned, native tallgrass prairie. Grass, forb and total cover and richness as well as community composition between ambient and altered treatment over time were assessed. Our predictions were based on the Hierarchical Response Framework prediction that community composition would be lagged in response under chronic alterations in precipitation.

Community dynamics can be a mechanism for ecosystem change. Shrub encroachment is an example of community change influencing ecological process by altering resource distribution and nutrient cycling via microbial mediated plant-soil feedbacks (Carney and Matson 2005, Bezemer et al. 2006, Harrison and Bardgett 2010). The replacement of grasslands with patches of woody vegetation is a form of land degradation and is occurring in many arid and semi-arid grasslands across the globe. Woody shrubs outcompete native grasses causing a loss in biodiversity and altered community stability (Báez and Collins 2008, Ratajczak 2012, Báez et al. 2013) and, biomass is transferred from mostly belowground to aboveground (Van Auken 2009). Nutrients are concentrated under shrub canopies that are interspersed between patches of unvegetated nutrient-poor soil that become sources of erosion (Schlesinger et al. 1996, Schlesinger and Pilmanis 2010). Increases in cover and nutrient heterogeneity cause changes in resource distribution and ultimately nutrient transfers out of the ecosystem (Turnbull et al. 2010a). How these changes may affect other ecosystem processes is unclear.

Given that aridlands constitute nearly one-third of the global land surface (Safriel 2005), they will greatly affect the global carbon budget. Aridland ecosystems are known to function differently from mesic systems (Huxman et al. 2004b, Austin 2011, Collins et al.

2014), and are driven by pulsed precipitation and subsequent effects on net primary productivity that tends to be decoupled from decomposition (Collins et al. 2008a, Maestre et al. 2012). Soil respiration, the total CO_2 produced from soils resulting from a combination of autotrophic respiration and microbial decomposition, is a globally important measurement. Respiration is used for estimating soil metabolic activity, rate of carbon flux and soil-atmospheric interactions (Raich and Schlesinger 1992, Ryan and Law 2005). However, little is known about the effects of shrub encroachment on soil respiration. Further, given that soil respiration is in part a microbial response, measuring changes in microbial nutrient demands via their extracellular enzymes could assess if encroachment will likely cause microbial facilitated alterations in soil carbon cycling.

In Chapter 3, transplanted plant-soil monoliths were used to determine how encroachment of creosote bush alters soil respiration and microbial enzyme activity in Chihuahuan Desert blue grama grassland. Plant-soil transplants have been used for understanding the impacts of global environmental change (Arnone et al. 2008, Blankinship et al. 2010, Bond-Lamberty et al. 2016) by simulate future abiotic conditions (Wu et al. 2011b) when moved along elevation gradients or between ecosystems. Our predictions were based on past findings that shrublands have higher temperatures, are less responsive to temperature fluctuations and have higher soil carbon compared to grasslands (Kieft et al. 1998, He et al. 2015b, Nuanez 2015).

The three studies mentioned above were conducted at Konza Prairie Biological Station in northeastern Kansas, USA (Chapters 1 and 2) and the Sevilleta National Wildlife Refuge in central New Mexico, USA (Chapters 1 and 3). Konza Prairie was the mesic grassland research site with native tallgrass prairie being the study system. This system is dominated by native C_4 perennial tall grasses and C_3 perennial forbs. The Sevilleta was the semiarid grassland research site with Chihuahuan Desert grassland and shrubland being the study systems. This desert grassland is dominated by perennial bunchgrasses and the shrubland by the C_3 shrub creosotebush. Both Konza Prairie and the Sevilleta are Long-Term Ecological Research sites which provide data for long-term research.

Chapter 1

Long-term dynamics in producer and consumer communities in tallgrass prairie and Chihuahuan Desert ecosystems

Sydney K. Jones[1], Julie Ripplinger[2], and Scott L. Collins[1]

[1]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM, 87131

[2]Department of Botany and Plant Sciences, University of California - Riverside, Riverside, CA, 92521

Abstract

Determining how ecological communities will change over time in response to global environmental change remains a challenging research problem. Recent metaanalyses have concluded that most communities are undergoing directional change despite no net change in local species richness. Here, we explore how species richness and composition of co-occurring plant, grasshopper, breeding bird, and small mammal communities in arid (Sevilleta LTER, New Mexico) and mesic (Konza Prairie LTER, Kansas) grasslands are changing over time in response to shrub encroachment and changes in fire frequency. We used annual data on community composition and abundance from 1982 to 2012, and 1989 to 2013 at Konza and Sevilleta, respectively, to determine if the composition and species richness of grassland vegetation and associated consumer communities were changing in concert under these different environmental drivers. At Sevilleta we found that grassland and shrubland plant and breeding bird communities were each undergoing different rates of directional change, while grasshopper and small mammal communities were stable. Most communities exhibited high interannual variability in composition. At Konza, vegetation, grasshopper, small mammal and breeding bird communities were all undergoing variable rates of directional change depending on fire frequency. Despite directional change in composition in some communities, species richness of all communities was highly stable. This occurred because directional change in composition was primarily a function of reordering of abundances of species already in the community, a less a function of turnover in species composition. Alterations of species abundances and community composition are likely to continue under global environmental change. Our results reconcile how directional change in composition can

occur without directional changes in species richness. Thus, changes in species richness alone are not a reliable metric for assessing the consequences of global environmental change.

Introduction

Ecologists now widely recognize that variability and change are fundamental characteristics of most ecological communities. Today, questions increasingly focus on the causes of variability, as well as the pattern of community change over time. In general, communities may exhibit stochastic variability around a loose equilibrium as a function of environmental variability (Bagchi et al. 2013, Matthews et al. 2013, Renner et al. 2014), such as interannual precipitation, or change directionally in response to chronic ecological presses, such as increasing aridity or nitrogen deposition (Sala et al. 2000, Avolio et al. 2014, Hoover et al. 2014). Furthermore, community change may be gradual and track environmental variability, or be abrupt as environmental drivers approach ecological thresholds and cross tipping points (Scheffer et al. 2001, Bestelmeyer et al. 2011).

Although disturbances are well known causes of ecological dynamics, many communities are changing in response to environmental drivers in the absence of disturbance. The Hierarchical Response Framework (Smith et al. 2009) proposes that communities will exhibit either linear or non-linear responses to chronic changes in environmental drivers through a hierarchy of ecological processes, beginning with phenotypic plasticity at the shortest time scale, followed by a reordering of species dominance patterns, and finally by changes in species composition through colonization and local extinction. Phenotypic change can be relatively rapid, but is unlikely to generate significant change over time. Turnover in species composition via dispersal and establishment could take years to decades to occur, especially in communities dominated by long-lived species. Thus, turnover creates directional change, often following time lags, and results in non-linear rates of temporal dynamics (Magurran et al. 2010, Gravel et al. 2016).

Change in species composition may or may not be accompanied by changes in species richness. For example, increased resource availability may increase dominance and reduce species richness in terrestrial and aquatic communities (Vitousek et al. 1997, Baer et al. 2004, Elahi et al. 2015). In other cases, richness fluctuates around a narrow equilibrium despite changes in composition and abundance (Goheen 2005, Dornelas et al. 2014). Such patterns emerge through strong coupling between local and regional species pools, resulting in what has been termed a “carrying capacity” for species richness (Goheen 2005, Ernest et al. 2008, Michalet et al. 2015). Thus, in some instances changes in community composition may be unrelated to changes in species richness leading some to suggest that richness is a relatively poor indicator of ecological response to environmental change (Hillebrand et al. 2007).

Two recent meta-analyses have evaluated changes in both species composition and richness over multiple time series data sets (Vellend et al. 2013, Dornelas et al. 2014). In both cases, the analyses found most communities were undergoing moderate to strong directional change, but despite these dynamics there was, on average, no net change in local species richness across all of the time series analyzed. Not surprisingly this conclusion has proven controversial (Gonzalez et al. 2016, Vellend et al. 2016). Indeed, it is difficult to draw strong inferences from time series data that differ among taxa (e.g., phytoplankton, fish, birds), habitats (e.g., tropical forest, open ocean), timeframes (e.g., 1950's vs 2000s), and lengths of time series (e.g., <6 to >50 years). Therefore, additional comparative analyses are needed to determine the link between changes in species richness and the dynamics of ecological communities.

To reduce some of these confounding contingencies, we analyzed long-term, concurrent time series data for plants, grasshoppers, breeding birds and small mammals in arid and mesic grassland-shrubland ecosystems to determine if communities of different taxa in the same ecosystem were undergoing directional change in both composition and richness in response to common environmental drivers. In this case, the drivers are shrub encroachment, which is the consequence of historical grazing pressure and increasing aridity in the arid ecosystem (van Auken 2000, Collins et al. unpublished data) and altered fire frequency in the mesic ecosystem (Briggs et al. 2005, Ratajczak et al. 2014). Previous work has shown that grassland vegetation at these sites was undergoing directional change (Collins 2000, Collins and Xia 2015). Given that vegetation provides structural habitat and resources for consumers (Ernest et al. 2000, Hovick et al. 2014, Duan et al. 2016), we hypothesized that the consumer communities would change in concert with vegetation in response to common environmental drivers in each ecosystem.

Methods

Arid grassland-shrubland

Study site. Our two aridland study sites are located at the Sevilleta National Wildlife Refuge (SNWR), a Long-Term Ecological Research (LTER) site in central New Mexico, USA. The climate is continental, with an average annual temperature of 13.9º C. Precipitation averages ~250 mm annually, with ~60% falling from July through September in highly localized storms during the summer monsoon, and the rest as winter frontal systems (Gosz et al. 1995, Pennington and Collins 2007, Notaro et al. 2010).

Sampling Methods. The desert grassland site is dominated by the perennial bunchgrasses black grama (*Bouteloua eriopoda*) and blue grama (*B. gracilis*) (Muldavin 2002, Collins and Xia 2015). The shrubland site is dominated by the long-lived C_3 shrub creosotebush (*Larrea tridentata*), with scattered grasses and forbs found primarily in open spaces between shrubs. Species composition of grassland vegetation was recorded in spring and fall along a 400 m long line-intercept transect established in 1989 and sampled annually through 2008 when the area was burned by a wildfire. Grasshopper and small mammal communities were sampled at the grassland and shrubland sites using a web design consisting of twelve 100-m transects radiating from a central point (Parmenter et al. 2003). Each site contains five replicate trapping webs (see Table S1 for data summary and sampling dimensions). Small mammal community composition was estimated starting in 1989 using 144 traps placed along each 100-m transect (Wolf et al. 2009) on three webs at each site for three nights twice per year. Grasshopper community composition was sampled in spring and fall starting in 1992 by walking along six 100 m long by 1-m wide strip transects per web (N=30 strip samples) and identifying all grasshoppers encountered to species. Starting in 1999, shrubland vegetation composition was estimated using four permanent 1-m^2 plots in the four cardinal directions of each web, for a total of 64 1 m^2 plots. (Muldavin et al. 2008). Bird species abundances were taken from Breeding Bird Survey data along the Escondida route located in the SNWR. This transect starts in black grama grassland and ends in creosotebush shrubland. We partitioned abundances on each half of the transect into grassland and shrubland habitat.

Mesic grassland

Study site. Our three mesic study sites are located at the Konza Prairie Biological Station (KPBS), a Long-term Ecological Research site located in the Flint Hills region of northeastern Kansas, USA. The site has a mid-continental climate, with a mean annual temperature of 12.6 C. Mean annual precipitation is ~840 mm $year^{-1}$, 76% of which falls during the growing season from April to September. KPBS is divided into 64 management units ranging in size from 16 to 133 hectares primarily along watershed boundaries. For this study we used long-term data from three ungrazed management units: annually burned, burned once every 4 years, and burned once every 20 years (Table S1). All sites were dominated by native C_4 perennial tall grasses (*Andropogon gerardii, Schizachirium scoparium*, *Panicum virgatum*, and *Sorghastrum nutans*, and perennial C_3 forbs (*Aster* spp., *Solidago* spp., *Salvia azurea* and *Vernonia baldwinii*). Over the past 15 years, shrub cover (*Cornus drummondii, Prunus americana,* and *Rhus glabra*) has increased rapidly primarily in lowland areas in infrequently burned management units (Briggs et al. 2005, Ratajczak et al. 2014).

Sampling methods. Vegetation, breeding bird, grasshopper and small mammal communities were all sampled on the same three management units. Vegetation has been sampled in spring and fall of each year since 1984 in five permanently marked 10-m^2 circular quadrats located along each of four 50-m transects (n=20 quadrats). Cover of each plant species in each quadrat was visually estimated with the Daubenmire cover scale and the abundance of each species at each site was determined by converting the Daubenmire scale to the midpoint of the cover range and averaging across the 20 quadrats (Collins and Calabrese 2012). Breeding birds were sampled by walking along ~1 km permanent transects during June of each year starting in 1981. At 15–20-m intervals along each transect, all individuals seen or heard were counted during a 3–5-min sampling period. Abundance of each species is the total number of individuals counted each year (Powell 2008). Wide-ranging species, such as the Red-tailed Hawk (*Buteo jamaicensis*), were not included in our analyses. Grasshopper populations were sampled each year starting in 1984 using 20 sets of 20 sweep-samples taken along parallel 10-m transects during the midsummer of each year. Abundance of each species is the total number of individuals collected at each site (Jonas and Joern 2007). Small mammals were sampled from1982 along permanently located trap lines in each management unit. Each trap line contained 20 stations at 15-m intervals consisting of two large Sherman live traps. Traps were baited with peanut butter and oatmeal on 4 consecutive nights in spring and fall of each year. Abundance was measured as the average of the spring and fall counts of total number of individuals of each species at each site (Kaufman et al. 1998).

Analysis

We used non-metric multidimensional scaling (NMDS) ordinations per taxa to visually assess differences in community composition of each taxonomic group among the two (Sevilleta) or three (Konza) sites in arid and mesic grassland, respectively. We then used permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarities to determine if communities of each taxon differed among habitats within a site. Bray–Curtis dissimilarity performs well with relative abundance data in multivariate analyses, such as NMDS and PERMANOVA (Clarke & Warwick 2001, Anderson and Braak 2003).

To determine whether or not communities are undergoing directional change under changing climate (aridity at Sevilleta) and disturbance (fire frequency at Konza) regimes, and to compare between producer and consumer communities, we calculated the temporal rate of change using time-lag analysis for each taxon in each habitat type at Sevilleta and Konza. Time-lag analysis uses Euclidean distance to measure similarity of community samples at increasing time lags and when regressed, yields an estimate of directional change over time (Collins 2000, Collins et al. 2000). Time-lag analysis was calculated and plotted using both abundance and presence-absence data to determine the relative influence of species reordering (abundance data) to species turnover (presence/absence data). If there is positive directional change with abundance data but no change with presence/absence data then change is driven by reordering among species already present rather than turnover in species composition. We used an analysis of variance (ANOVA) to determine if slopes were significantly different from zero and if slopes within each taxa in each grassland (e.g., grasshoppers between burn frequencies at Konza) were significantly different from each other. In addition, we plotted species richness and turnover through time, and calculated mean rank shifts to further quantify temporal variability. Species turnover is a temporal analog to species richness or the proportion of species that differ between sample intervals over time (Diamond 1969). Mean rank shift is a temporal analog calculated from species rank abundance distributions and serves as a measure of species reordering that occurs between sample intervals (Collins et al. 2008b). Statistical calculations were performed in R packages *vegan* (Oksanen et al. 2016) and *codyn* (Hallett et al. 2016).

Results

Based on the NMDS ordinations, Sevilleta vegetation and consumer communities showed distinct spatial separation between grassland and shrubland areas for all taxa (Fig. 1.1) and the PERMANOVA analysis (Fig. 1.1, inset) showed significant differences for site (r^2=0.35-0.49 and P=0.0001 for all taxa) and year (r^2=0.02-0.12 and P=0.0001-0.01) main effects. Only vegetation and grasshopper communities had significant site by year interactions. Konza Prairie vegetation communities also showed spatial separation in the NMDS ordination between fire frequencies. Although consumer communities did not separate visually in ordination space (Fig. 1.2), PERMANOVA analysis (Fig. 1.2, inset) showed significant differences for site (r^2=0.07-0.20 and P=0.0001-0.001) and year (r^2=0.03-0.11 and P=0.0001-0.01) main effects for all taxa.

At Sevilleta, most plant and consumer communities exhibited high interannual variability in composition. Despite that variability, time-lag analysis using abundance data (Fig. 1.3, Table 1.1) showed strong directional change in both black grama grassland (slope=2.1, P=0.014, see Table 1.2. for summary) and creosotebush shrubland (slope=1.3, P=0.002). Although the rate of change was higher in grassland than shrubland vegetation, differences in rates were not significant (F= 0.001, P=0.972; see Table 1.2 for summary). As for consumer communities, grassland (slope=16.3, P=<0.001) and shrubland (slope=21.9, P=<0.001) breeding bird communities at Sevilleta were undergoing strong directional change. Differences in rates were not significantly different (F= 0.043, P=0.836). As for grassland (slope=0.0, P=0.887) and shrubland (slope=-0.0, P=0.141) small mammal communities, they were relatively stable, especially in creosotebush shrubland where interannual variability was low. Again, sites were not significantly different (F=0.793, P=0.374). Finally, grasshopper communities in grassland are undergoing directional change (slope=0.9, P=0.017) whereas grasshoppers in shrubland (slope=0.1, P=0.142) have high interannual variability and exhibit little directional change. Sites were not significantly different (F=0.418, P=0.519).

At Konza, many plant and consumer communities exhibited high interannual variability in composition, as well. Vegetation (slope=0.2-0.8; F=2.607, P=0.074), grasshopper (slope=- 0.5-1.4; F=5.263, P=0.005) and small mammal (slope=0.1-1.2; F= 5.839, P=0.003) communities were undergoing variable rates of directional change under different fire frequencies (Fig. 1.4, Table 1.1) Unburned prairie communities are distinctly different from annually and 4-yr burned communities, significantly so in grasshoppers (P=0.005) and small mammals (P=0.003). Breeding birds (slope=0.1; F=0.161, P=0.851) have weak directional change but with varying amounts of interannual variability (see Table 1.2 for summary).

Despite weak to strong directional change in a number of taxa in both arid and mesic grassland, species richness for all taxa at all sites showed no directional change over time. This stability results from comparable levels of appearances and disappearances among taxa at each site. Not surprisingly, species turnover (Table 1.1) was highest in communities with higher overall species richness. Mean rank shift (Table 1.1), a measure of community reordering, was highest for breeding bird communities and lowest for small mammals. To assess the role of reordering vs. turnover we calculated time lag analyses for all sites and taxa using presence-absence data. In all cases slopes were lower than the analyses with abundance data, indicating no directional change in species occurrences over time (Fig. S1.1, S1.2).

Discussion

We used annual richness and composition data of co-occurring plant, grasshopper, small mammal, and breeding bird communities from arid and mesic grasslands to investigate if these communities were changing over time as a consequence of two ecological presses, increasing aridity at Sevilleta and differences in fire frequency at Konza Prairie. We found high interannual variability in composition in most communities. Despite this interannual variability, vegetation was undergoing variable rates of directional change at both sites, yet not all consumer communities were changing in concert with vegetation change. Despite directional change in several taxa at each site, species richness of all communities was highly stable and fluctuated within a narrow range of variation. This occurred because directional change was primarily driven by reordering of abundances of species already in the community, rather than turnover in species composition.

At Sevilleta, both grassland and shrubland plant communities were undergoing directional change, although the rate of change was greater in grassland than shrubland. Previous analyses have shown that this grassland vegetation is experiencing reordering as the abundance of the Chihuahuan Desert grass, *Bouteloua eriopoda*, has doubled while abundance of the co-dominant, *B. gracilis*, has remained relatively stable over time (Collins and Xia 2015). This reordering is a function of higher interannual climate variability under increasing aridity, which favors *B. eriopoda* over *B. gracilis* (Collins et al. in review). Forbs, on the other hand, tend to fluctuate from year to year in response to seasonal precipitation variability (Mulhouse et al. 2017).

Creosotebush shrubland has been encroaching on these grasslands over the past 150 years (Van Auken 2000) by invading areas dominated by *B. eriopoda* (Peters et al. 2004). Once established, grass and forb richness and cover decline as the abundance of creosotebush increases (Báez et al. 2007), especially following multiyear drought (Báez et al. 2013), reflecting the long-term but slow process of species turnover. In addition, shrub encroachment alters the local microclimate (D’Odorico et al. 2010) by creating warmer soil surface temperatures during winter and spring. As a consequence, these two vegetation types support significantly different consumer communities, yet temporal dynamics differs among taxa. There is no directional change in small mammal communities in either vegetation type, whereas breeding birds appear to be undergoing strong directional change in both grassland and shrubland which could be driven to some extent by stochastic processes (Rivers et al. 2010, Renner et al. 2014) or slow temporal changes occurring over decades (Kampichler et al. 2014). Grasshoppers, which include C_3 and C_4 specialists (Engel et al. 2009), as well as blue vs black grama specialists (Rominger et al. 2009), are likely tracking changes in food resources in grassland, whereas resource supply in shrubland may be more reliable from year to year resulting in no directional change and low interannual variability. If any cross-taxa congruence occurs between sites, abiotic factors are likely to exert a stronger influence than biotic ones (Duan et al. 2016).

Vegetation change was also occurring across the burning treatments at Konza, with the highest rate of change occurring in unburned grassland. Fire is a well-known regulator of vegetation dynamics in this tallgrass prairie, with frequent fire forcing reordering among dominant grasses (Collins and Calabrese 2012). Shrub encroachment occurs as fire frequency decreases resulting in higher spatial heterogeneity in grassland and shrubland vegetation (Ratajczak et al. 2017a, 2017b). Increasing spatial heterogeneity results in changes in consumer community composition among sites with different fire frequencies. Indeed, composition and dynamics of grasshopper (Jonas and Joern 2007), breeding bird (Powell 2008) and small mammal communities (Kaufman et al. 1998) in ungrazed grassland are mostly affected by fire return interval, in particular high fire frequencies primarily reduce the abundances of many grassland consumer species likely driving long-term change in annually burned grassland at Konza. In general, as disturbance events increase, the ability for communities to return to a former state becomes more difficult or will take longer to recover (Matthews et al. 2013, Ratajczak et al. 2017a).

Our findings shed light on previous studies (Vellend et al. 2013, Dornelas et al. 2014) that found strong directional change in communities from a large range of taxa across the globe despite no net change in local species richness. In many cases the directional changes they reported could be driven by local reordering of species abundances while species richness was maintained within a circumscribed range of variability. One potential mechanism driving this pattern is a tight coupling between local and regional species pools (Ricklefs 1987, Gravel et al. 2016). Most communities contain a subset of the regional species pool as a result of dispersal limitation, environmental filters and local species interactions (Ernest et al. 2008). This tight coupling drives non-random compensatory colonization and extinction dynamics at the local level. As a consequence, species richness may be saturated locally and thus exhibit limited temporal variability (Goheen 2005, Ernest et al. 2008, Gravel et al. 2016). Therefore, directional change can occur even when species richness remains constant.

In general, our results are consistent with predictions of the Hierarchical Response Framework (Smith et al. 2009). We observed strong directional change in aridland vegetation at Sevilleta in the absence of disturbance under increasing aridity and shrub encroachment. Dynamics of mesic grassland communities were strongly driven by fire return interval, with considerable shrub encroachment occurring under low and intermediate fire frequencies. These changes in plant community composition led to clear differences in consumer communities between grassland and shrubland at Sevilleta, and under different fire frequencies at Konza. Of note, several consumer communities were not undergoing directional change despite relatively strong changes in the vegetation underlying these consumer communities. Others have reported variable responses among taxa to common drivers of ecological change (Duan et al. 2016). Thus, temporal change in vegetation is not necessarily predictive of temporal change in co-occurring consumer communities.

Species richness, on the other hand, was remarkably stable for all taxonomic groups in arid and mesic grasslands. Because time-lag analyses of presence-absence data showed little directional change across all taxa, temporal dynamics in these communities primarily reflected reordering of species within the community, with only limited contribution from species turnover. Because directional change primarily results from reordering of abundances among species already present, our results reconcile how directional change can occur without concurrent directional changes in species richness (e.g. Vellend et al. 2013, Dornelas et al. 2014, Pärtel et al. 2016). Chronic drivers of global change are likely to affect species abundances and community composition in the future, and our study demonstrates that changes in species abundances and community reordering, rather than changes in species richness, will be a better indicator of the rate and pattern of community response to future global environmental change.

Table 1.1. Metrics of temporal dynamics for vegetation, grasshopper, small mammal and breeding bird communities among grassland and shrubland habitats at Sevilleta and fire frequency treatments at Konza Prairie. Time lag analysis measures rate of community change over time, species turnover is the average proportional change in species from one year to the next, and mean rank shift is a measure of how much species reordering of abundances occurs from one year to the next.

[redacted]

Table 2.2. Analysis of variance for time lag slopes between sites for Sevilleta and Konza producer and consumer communities. A significant positive slope indicates directional change over time. A significant size effect indicates that the slope was significantly different from zero. A significant interaction effect indicates that the slopes for a given taxon within a site (e.g., grasshoppers among fire frequencies at Konza) were significantly different from each other.

Sevilleta					**Konza**				
vegetation					**vegetation**				
	Sum Sq	DF	*F* value	*P* value		Sum Sq	DF	*F* value	*P* value
grassland	2.82	1	6.278	**0.014**	unburned	4.15	1	25.761	**<0.001**
shrubland	2.72	1	10.216	**0.002**	4-yr burned	0.32	1	1.45	0.229
					annually burned	0.85	1	2.889	0.090
interaction	0.00	1	0.001	0.972	interaction	1.18	2	2.607	0.074
grasshoppers					**grasshoppers**				
grassland	1.70	1	5.831	**0.017**	unburned	0.67	1	1.102	0.295
shrubland	0.65	1	2.167	0.142	4-yr burned	9.41	1	10.842	**0.001**
					annually burned	3.07	1	4.091	**0.044**
interaction	0.12	1	0.418	0.519	interaction	7.82	2	5.263	**0.005**
small mammals					**small mammals**				
grassland	0.01	1	0.020	0.887	unburned	14.17	1	67.973	**<0.001**
shrubland	0.58	1	2.176	0.141	4-yr burned	1.07	1	2.833	0.094
					annually burned	0.87	1	1.412	0.236
interaction	0.23	1	0.793	0.374	interaction	4.53	2	5.839	**0.003**
breeding birds					**breeding birds**				
grassland	1.10	1	19.098	**<0.001**	unburned	0.84	1	15.437	**<0.001**
shrubland	1.27	1	14.556	**<0.001**	4-yr burned	0.91	1	12.066	**<0.001**
					annually burned	1.16	1	7.237	**0.008**
interaction	0.00	1	0.043	0.836	interaction	0.03	2	0.161	0.851

Figure 1.1. Non-metric multidimensional scaling (NMDS) of vegetation, grasshopper, small mammal and breeding bird community composition between black grama grassland and creosotebush shrubland sites at the Sevilleta National Wildlife Refuge, New Mexico. Each point represents community composition for a given taxon at a site for each sample year (yr). Site is indicated by color. Inset presents results from PERMANOVA analysis.

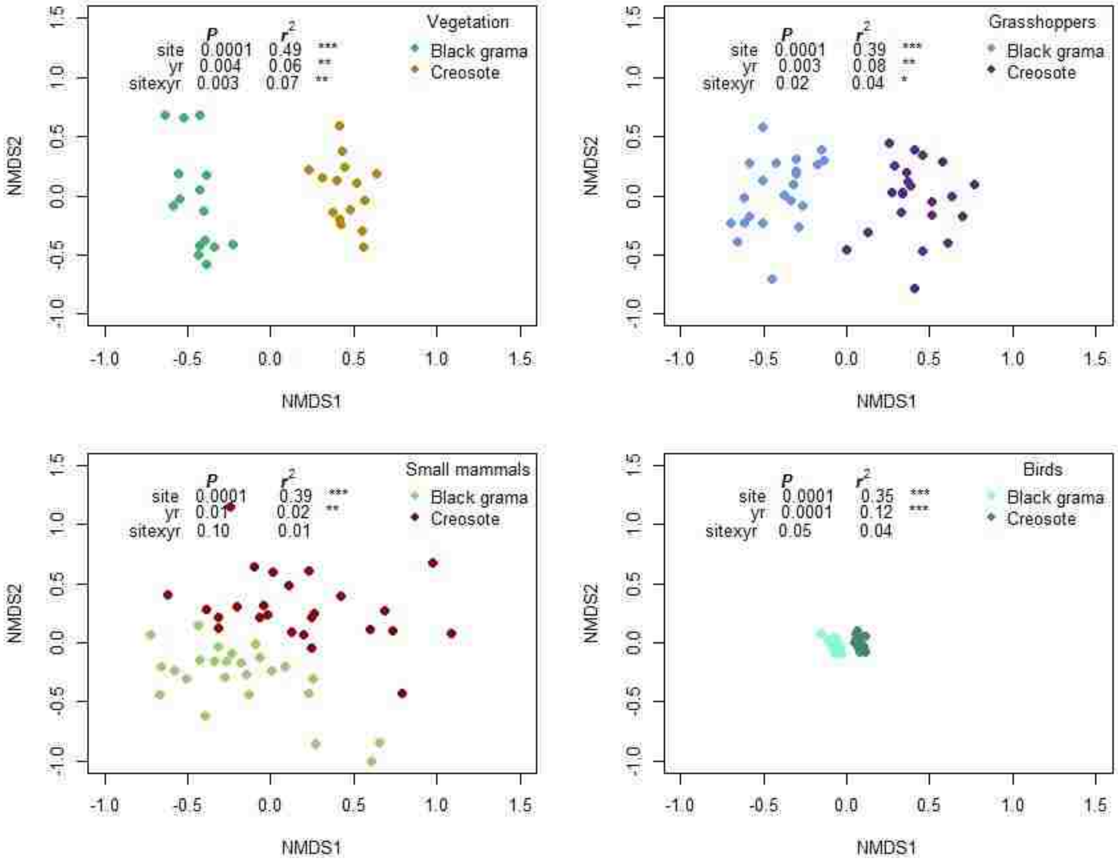


Figure 1.2. Non-metric multidimensional scaling (NMDS) of vegetation, grasshopper, small mammal and breeding bird community composition for grasslands that are annually burned, burned once every 4 years or unburned. Each point represents community composition for a given taxon at a site for each sample year (yr). Site is indicated by color. Inset presents results from PERMANOVA analysis.

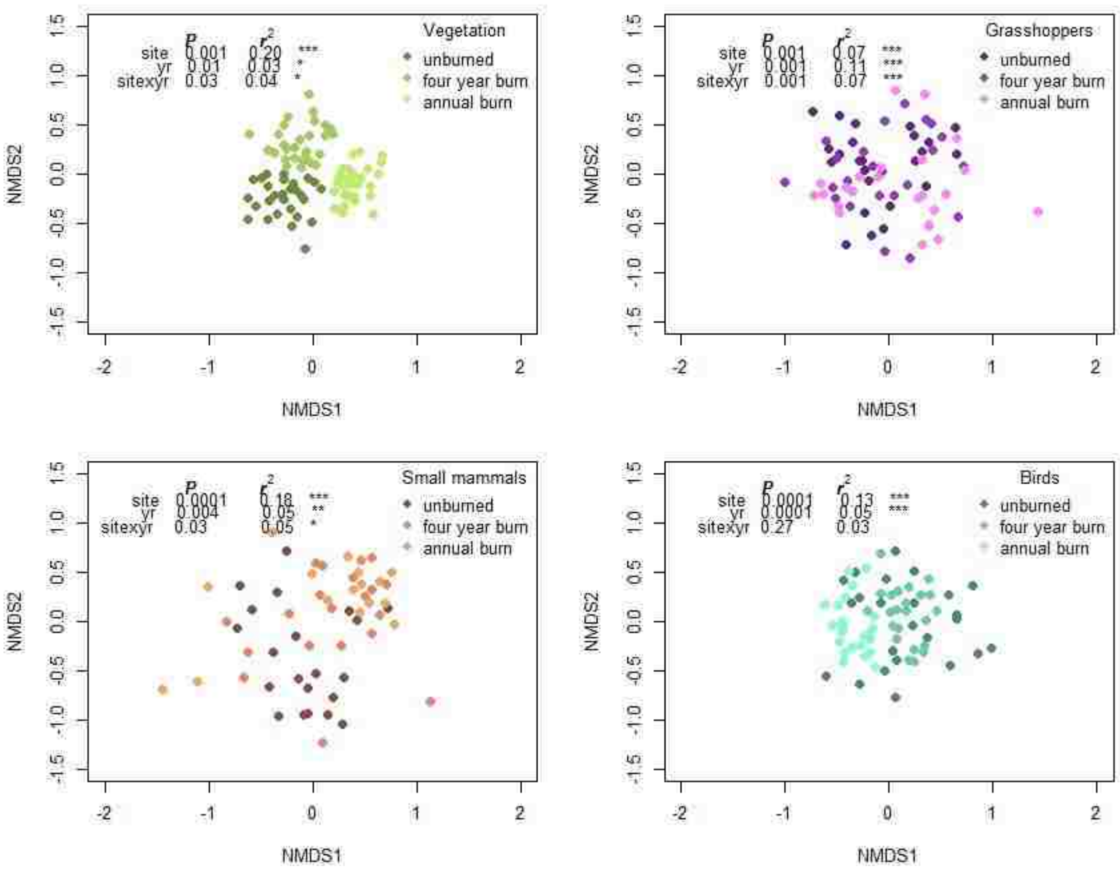


Figure 1.3. Community temporal dynamics of vegetation, grasshopper, small mammal and breeding bird communities for black grama grassland and creosotebush shrubland sites at the Sevilleta NWR. Time-lag analysis depicts the temporal rate of change in community composition by plotting similarity of community samples, using Euclidean distance, at increasing time lags. Insets include linear regression equation and significance values. Turnover plots depict total species richness (number of species) and cumulative year-to-year species appearance and disappearance over time. The dotted line is the species richness temporal mean.

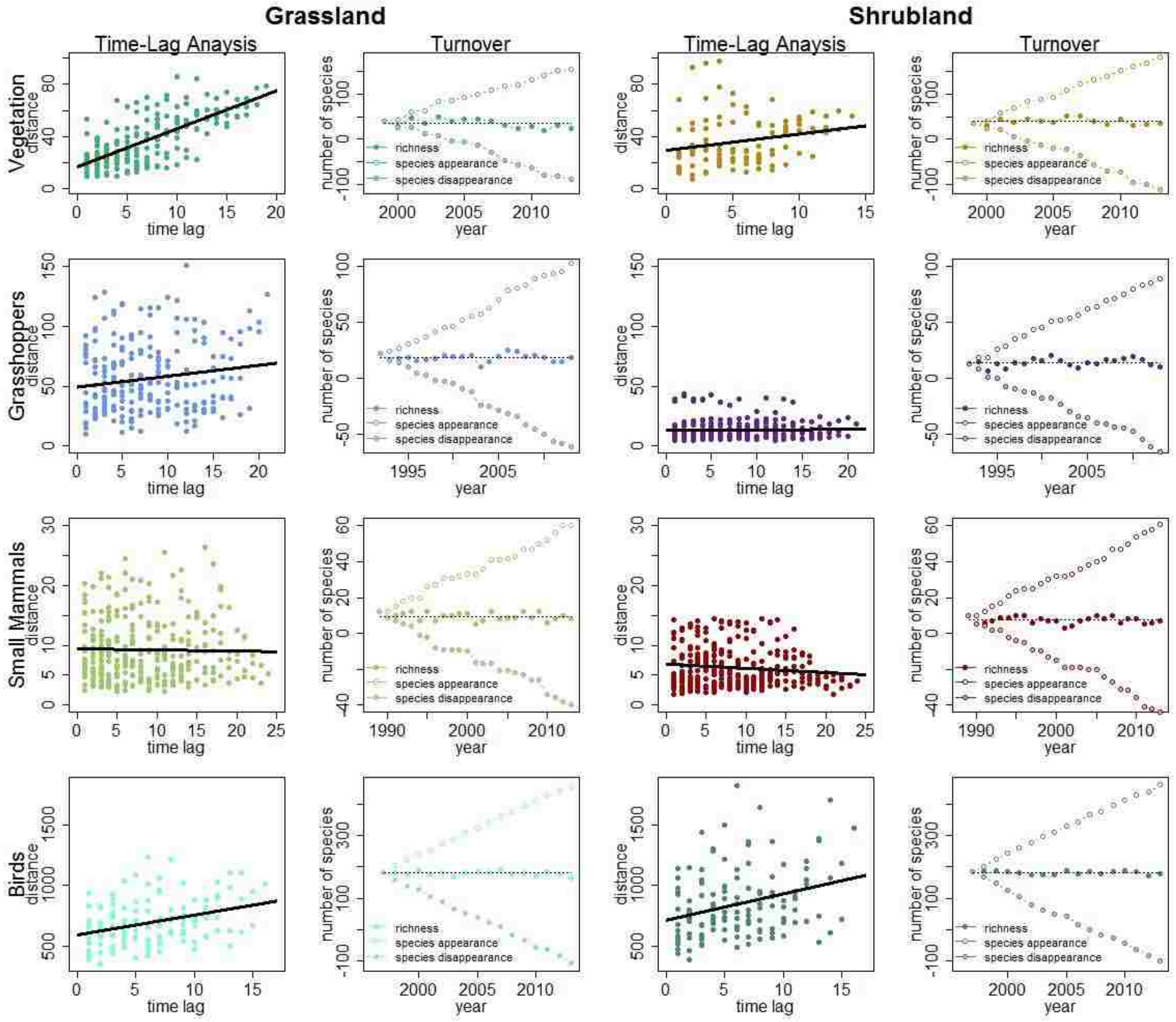
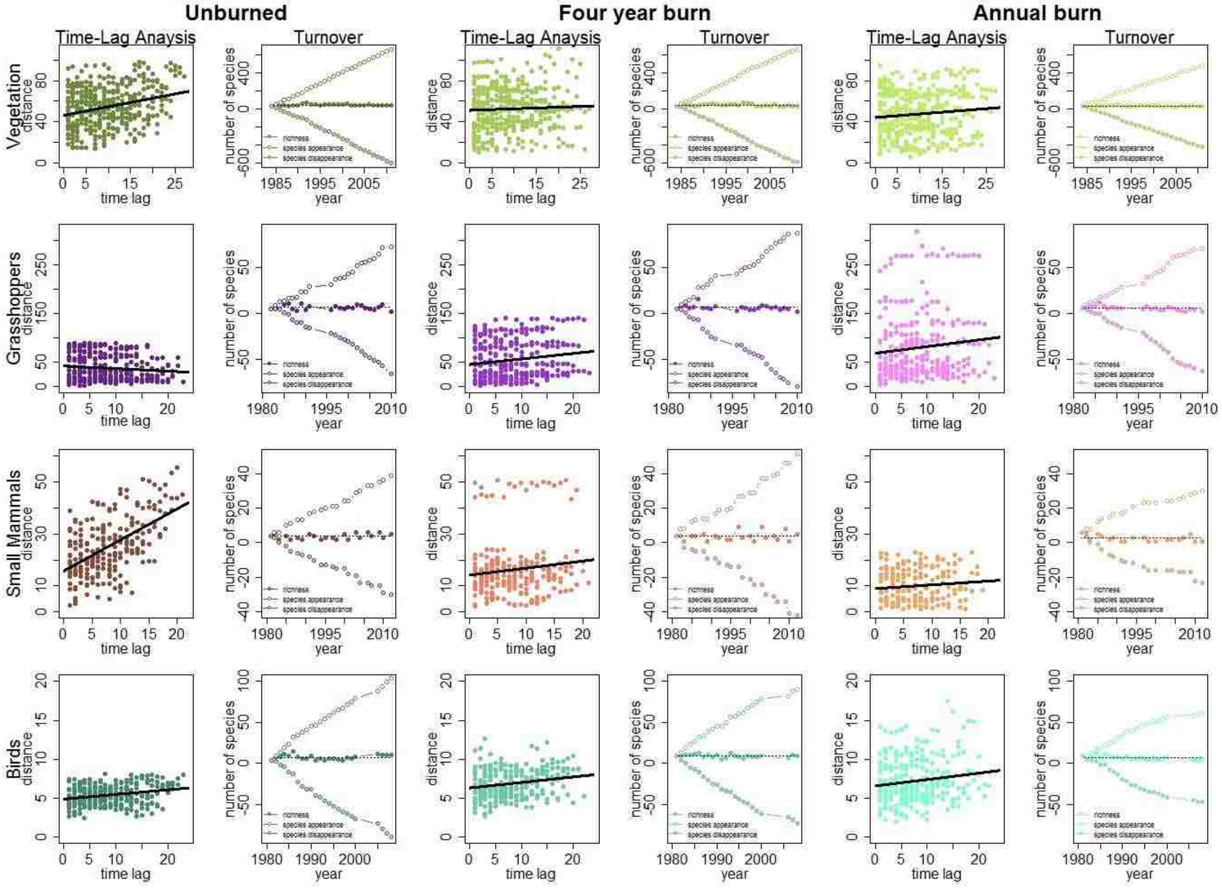


Figure 1.4. Community temporal dynamics of vegetation, grasshopper, small mammal and breeding bird communities for unburned, four-year burn and annually burned tallgrass prairie sites at Konza Prairie Biological Station. Time-lag analysis depicts the temporal rate of change in community composition by plotting similarity of community samples, using Euclidean distance, at increasing time lags. Insets include linear regression equation and significance values. Turnover plots depict total species richness (number of species) and accumulated year-to-year species appearance and disappearance over time. The dotted line is the species richness temporal mean.



Chapter 2

Altered rainfall patterns increase forb abundance and richness in native tallgrass prairie

Sydney K. Jones[1], Scott L. Collins[1], John M. Blair[2], Melinda D. Smith[3,4],
Alan K. Knapp[3,4]

[1]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM, 87131

[2]Division of Biology, Kansas State University, Manhattan, KS, 66506

[3]Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, 80523

[4]Department of Biology, Colorado State University, Fort Collins, CO, 80523

Abstract

Models predict that precipitation variability will increase with climate change. We used a 15-year precipitation manipulation experiment to determine if altering the timing and amount of growing season rainfall will impact plant community structure in annually burned, native tallgrass prairie. The altered precipitation treatment maintained the same total growing season precipitation as the ambient precipitation treatment, but received a rainfall regime of fewer, larger rain events, and longer intervals between events each growing season. Although this change in precipitation regime significantly lowered mean soil water content, overall this plant community was remarkably resistant to altered precipitation with species composition relatively stable over time. However, we found significantly higher forb cover and richness and slightly lower grass cover on average with altered precipitation, but the forb responses were manifest only after a ten-year lag period. Thus, although community structure in this grassland is relatively resistant to this type of altered precipitation regime, forb abundance in native tallgrass prairie may increase in a future characterized by increased growing season precipitation variability.

Keywords: climate change; precipitation variability; community structure; rainout shelters; grassland; Konza Prairie; tallgrass prairie; long-term research

Introduction

Changes in plant community structure and function are generally driven by multiple biotic and abiotic factors, such as resource competition, nutrient availability, precipitation patterns and disturbance regimes. The rate, pattern, and intensity of many of these drivers are rapidly changing under global environmental change, including increased climate variability, elevated levels of atmospheric N deposition, and changes in the type, frequency and intensity of disturbances (Knapp et al. 2002, Stevens et al. 2004, Collins and Smith 2006, Maestre and Reynolds 2007). As a consequence of altered biotic and abiotic drivers, plant communities are likely to undergo significant changes in ecological structure and function under global environmental change.

Plant community structure and ecosystem functioning of mesic grasslands, for example, are strongly driven by several factors, including grazing and fire (Collins 1992, Fuhlendorf and Engle 2004, Collins and Smith 2006), nutrient availability (Suding et al. 2005, Lebauer and Treseder 2008, Borer et al. 2014), and precipitation amount and variability (Sala et al. 1988, Lane et al. 2000, Huxman et al. 2004a, Hsu et al. 2012, Knapp et al. 2012, Cleland et al. 2013). Indeed, aboveground net primary production (ANPP) of mesic tallgrass prairie has been shown to be limited by both water and nitrogen availability (Gough et al. 2000, Knapp et al. 2001, Suding et al. 2005). Similarly, persistent drought reduced ANPP in mesic grasslands, but effects on plant species richness and community composition were variable and inconsistent (Wu et al. 2011a, Hoover et al. 2014, Koerner and Collins 2014). Thus, changes in water availability and variability may have relatively consistent impacts on grassland ANPP but more variable effects on community composition and structure.

In the US Great Plains, predicted changes in total annual precipitation are inconsistent under different future climate change scenarios although soils are predicted to become drier due to elevated temperatures (Cook et al. 2015). In addition, models consistently predict an intensification of the hydrological cycle with increased interannual variability in rainfall and, possibly of greater importance, altered within-season rainfall patterns such that rain events will be fewer but larger with longer intervals between rains (Huntington 2006, Min et al. 2011, Singh et al. 2013). Indeed, the number of extreme precipitation events in the US Great Plains has increased markedly during the past decade (Kunkel and Others 2013, Wuebbles et al. 2014). The ecological impacts of variation in total seasonal precipitation amount verses within-season patterns of rainfall remain a subject of considerable uncertainty and debate (Knapp et al. 2008a, Gerten et al. 2008).

Evidence suggests that changes in precipitation regimes during the growing season may have significant ecological consequences for grassland structure and function, and that these effects are mediated primarily by altered soil moisture availability and by increased duration and frequency of dry periods between rain events (Nippert et al. 2006, Swemmer et al. 2007, Knapp et al. 2008a, Fay et al. 2011). Indeed, increased rainfall variability in mesic grassland, independent of amount, has been shown to reduce ANPP, soil respiration, and leaf level photosynthesis over the short term, and to alter the genotypic diversity of the dominant grasses over longer time frames (Knapp et al. 2002, Fay et al.

2003, Maestre and Reynolds 2007, Heisler-White et al. 2009, Thomey et al. 2011, Cherwin and Knapp 2012, Avolio et al. 2013). Together these results support predictions that grassland ecosystems will be highly responsive to future changes in precipitation variability.

Mechanisms controlling ecosystem responses to altered resource availability vary among grasslands. For example, Hallett et al. 2014 (Hallett et al. 2014) found strong species asynchrony, where decreases in abundance of one species are compensated for by increases in others, in sites characterized by high precipitation variability, whereas species richness and dominance reduced temporal variability in sites with high mean annual precipitation. This is consistent with Fay et al. 2011 (Fay et al. 2011) who reported that dominant prairie grasses were generally buffered against more variable precipitation regimes. However, Hautier et al. 2014 (Hautier et al. 2014) found that increased soil nutrient availability (plant available nitrogen) decreased the effectiveness of these stabilizing mechanisms in grasslands. It is unclear, therefore, if changes in soil moisture availability will have similar effects on grassland community stability as altered soil nutrient availability.

The Hierarchical Response Framework (HRF) predicts that chronic changes in resource availability, such as soil moisture, will eventually lead to reordering of species abundances within communities, and ultimately species replacement over time, often but not always after some time lag has occurred (Smith et al. 2009). For example, mesic grassland communities responded rapidly to nitrogen addition, but slowly to increased soil moisture availability (Collins et al. 2012, Avolio et al. 2014, Kirkman et al. 2014). Because rate and pattern of response to long-term (chronic) alterations in resources varies considerably among ecosystems short-term outcomes may not accurately reflect long-term responses to chronic changes in resource availability. Yet, understanding how grassland communities respond to long-term changes in resource variability is important because changes in species composition can, in turn, feedback to alter ecosystem functions, such as ANPP (Isbell et al. 2009, Knapp et al. 2012, Avolio et al. 2014). Therefore, we investigated how long-term changes in *intra*-annual precipitation variability, which drive patterns of soil moisture availability, affected long-term dynamics of plant community composition and structure in native tallgrass prairie.

We used data from a unique 15-year long rainfall manipulation experiment at the Konza Prairie Biological Station in northeastern Kansas, USA, to determine how altered precipitation patterns (fewer, larger events) impacted plant species composition and structure in an annually burned, ungrazed, native tallgrass prairie. We tested two hypotheses. First, based on the HRF, we predicted that directional change in grass and forb cover and richness and community composition would eventually occur after a lag period under the altered precipitation treatment. Second, we predicted that change in cover and composition under altered precipitation would be driven by the response of forbs more so than grasses because the dominant grasses are reported to be buffered against precipitation variability (Fay et al. 2002, Knapp et al. 2002) and changes in the cover and richness of forbs contribute disproportionately to community responses to other drivers in this grassland (Collins 1992, Fuhlendorf and Engle 2004, Collins and Smith 2006).

Results

Rainfall Regime. Growing-season rainfall averaged 404.0 mm (± 2.0 se) from 1997 through 2012. From May through September an average of 29 ambient rainfall events occurred per year, with an average of 18 events >5 mm. The altered precipitation treatment resulted in an average of 12 rainfall events per year, with 10 events >5 mm (Fig. 2.1a). Mean length of dry periods between events averaged 8.7 (± 1.9 se) days for ambient and 16.2 (± 3.7 se) days for altered treatments (Fig. 2.1b). The nearly 100% increase in mean length of dry periods in altered compared to ambient treatments was due to the removal of multiple small rain events, which were most frequent on average during the months of May, June and August. Mean event size averaged 20.6 mm (± 3.3 se) and 38.8 mm (± 7.4 se) for ambient and altered precipitation treatments, respectively (Fig. 2.1c).

Soil Moisture Patterns. Seasonal mean soil water content (SWC) was significantly (5.3%) lower in the altered (23.0% ± 2.3 se) compared to ambient (24.3% ± 2.3 se) treatment during the growing season ($P < 0.0001$; Fig. S2.1a). This difference was greatest during the first six years of the experiment. In contrast, mean soil moisture was similar in the altered compared to the ambient treatment in the last three years of the experiment when below average precipitation occurred. The difference between ambient and altered SWC was marginally related to total ambient precipitation ($R^2 = 0.24$, $P =$

0.0787; Fig. S2.1b). The 15-year growing season mean SWC in the altered treatment was below that of ambient mainly during August and September. The 15-year mean growing season deviation from ambient was 1.5% (± 2.6 se), the mean maximum SWC was 3% lower and the duration of low SWC (20% or lower) was 19 days (38.7%) longer in the altered treatment compared to ambient. The 2005 growing season, a representative year showing a similar pattern, had a SWC mean deviation from ambient of 1.7%, a maximum value of about 6% lower and the duration of low SWC was longer by 14 days (78.8%) in the altered compared to ambient treatment (Fig. S2.2). Coefficient of variation (CV) of SWC was higher, on average, in the altered (44.3 ± 2.4 se) compared to ambient (37.4 ± 2.0 se) treatment over this 15-year period.

Plant Responses. Relative to the ambient treatment, 15 years of increased rainfall variability resulted in generally higher average total cover and species richness (Fig. 2.2), but these differences were driven more by changes in forbs than grasses. Total cover was higher on average by 5.5% under altered precipitation, primarily due to an overall 24% increase in forb cover, and slight decline in mean grass cover. Forb cover (30.5%, $P < 0.001$) and richness (8.9%, $P= 0.008$) were significantly higher under altered precipitation compared to the ambient. These changes were first observed around 2007, ten years after the start of the experiment (Fig. 2.2). Grass cover in the altered treatment was lower than ambient, but only by 3.4% ($P = 0.07$, Table 2.1) due to strong declines in 2002 and 2003 when precipitation was below average. Grass and total richness were also higher in the altered compared to the ambient treatment by 12.2% and 10.5% respectively (Table 2.1), but the difference in grass richness existed prior to the start of the experiment. Forb richness was positively correlated to average seasonal SWC in ambient treatments (r^2=0.42, P=0.013) and nearly so under altered precipitation (r^2=0.20, P=0.105). Total, grass and forb richness were unrelated to total seasonal rainfall, average days between rainfall events, and CV of SWC in both ambient and altered treatments (Table S2.1).

Based on time-lag analysis, directional change occurred at similar rates under ambient (mean slope = 2.84) and altered (mean slope = 2.96) treatments (Table 2.2). This is reflected in the lack of distinct spatial separation between treatments in the NMDS spanning the full experimental time (Fig 2.3a). Based on PERMANOVA, however, significant differences in community composition between ambient and altered treatments occurred in only two of 15 years (2007 and 2009) which resulted in an overall treatment effect on community composition across all years (Fig. 2.3a, inset). Indeed, this is seen in the NMDS for year 2007 where there is significant separation of ambient and altered treatments (Fig. 2.3b, inset). Population stability (averaged temporal variability of each species over time) and community stability (aggregated species abundance) were not significantly different between altered and ambient rainfall regimes (Table 2.2). Mean rank shift, relative changes in species rank abundances, also did not differ significantly among treatments (Table 2.2).

Three grasses (*Andropogon gerardii*, *Sorghastrum nutans*, and *Andropogon scoparius*) and two common forb species (*Solidago canadensis* and *S. missouriensis*) accounted for 64% of the difference in community composition between ambient and altered rainfall treatments over the 15 years based on the SIMPER analysis (Table 2.3). In particular, the dominant grasses *A. gerardii* and *S. nutans* had lower abundance, while *A. scoparius*, a perennial caespitose species more characteristic of drier sites, and *S. missouriensis*, a clonal understory forb, had higher abundance in altered relative to the ambient treatment. A similar pattern occurred in the 2007 SIMPER analysis. In 2009, *S. nutans* explained most of the community differences between rainfall treatments with *A. scoparius* second in importance, along with the perennial forb *Helianthus rigida* (Table 2.3).

Discussion

We found that increasing the size of rainfall events while reducing the number of events resulted in relatively limited changes in plant community composition and structure in this annually burned, ungrazed, tallgrass prairie. As we predicted, the altered precipitation regime eventually resulted in higher levels of forb cover and richness, while grass cover remained relatively stable over time. Richness of grasses and forbs was higher under altered precipitation by 1-2 species m^{-2} on average. Directional change in community composition occurred under both ambient and altered precipitation regimes, possibly in response to annual burning (Collins et al. 1995), as was observed in an adjacent annually burned, long-term irrigation experiment (Collins et al. 2012). Species richness is known to be negatively correlated with fire frequency in this system (Collins 1998). Thus, annual burning is likely driving the overall decline in species richness and explains why we found a strong year effect on both grass and total richness. Nevertheless, the greater increase in forb cover and richness under the altered precipitation regime in this experiment ultimately led to significantly different species assemblages; however, these differences resulted from changes in abundance of species already present in the altered treatment plots, rather than in new species establishing in the community.

Altering the amount and duration of rain events resulted in significantly lower and more variable soil water content than under ambient precipitation, and this was predicted to influence community composition and dynamics. Results from modeling studies and rainfall manipulation experiments in tallgrass prairie show that changes in the temporal patterns of soil water content have consequences for numerous ecosystem processes that can affect plant community composition (Fay et al. 2002, 2003, Gerten et al. 2008, Cherwin and Knapp 2012, Fry et al. 2013). Precipitation variability, expressed through soil moisture availability, is a well-documented driver of grassland community dynamics from one year to the next, but community sensitivity to precipitation variability may be contingent upon preexisting environmental contexts (Sala et al. 2012, Reichmann et al. 2013) and variable mechanisms of community stability (Hallett et al. 2014). For example, Cherwin and Knapp (Cherwin and Knapp 2012) found high variation in productivity responses of shortgrass steppe sites to experimentally imposed drought, despite consistent reductions in soil moisture. In a modeling study, Gerten et al. 2008 (Gerten et al. 2008) found productivity responses to precipitation change to be determined by current degree of water limitation. Overall, these generally short-term manipulations led to rapid initial responses that may not adequately represent community dynamics that may play out over a decade or more.

The “bucket” model predicts that increased precipitation variability resulting from fewer rain events and longer duration of dry periods will increase the duration of soil water stress in mesic grasslands (Knapp et al. 2008a). However, larger rain events will allow deeper infiltration of soil moisture to the benefit of deeper-rooted forbs compared to fibrous rooted grasses. Thus, although the bucket model predicts that productivity will be negatively affected by increased precipitation variability, such alterations in precipitation regimes may have different impacts on the plant community. In a short-term study, Heisler-White et al. 2009 (Heisler-White et al. 2009) found that fewer, larger rain events in a mesic grassland resulted in an 18% decrease in ANPP but no significant change in forb cover or richness. We also found lower grass cover under altered precipitation patterns in our study, but the increase in forb abundance and richness took nearly 10 years to develop illustrating how short-term responses may not reflect long-term dynamics, and highlighting the need for more long-term climate manipulation experiments (Beier et al. 2012).

The eventual rise in forb cover under the altered precipitation regime is likely linked to changes in soil water content at depth (Nippert and Knapp 2007, Knapp et al. 2008a) and can potentially be explained by the differential use of soil water between grasses and forbs, although evidence in support of this hypothesis is inconsistent. Nippert and Knapp (Nippert and Knapp 2007) found that C_4 grasses in tallgrass prairie consistently relied on shallow soil water (5 cm) across the growing season while C_3 forbs also utilized deeper soil layers when shallow layers were depleted, supporting the hypothesis of soil water partitioning between grasses and forbs when shallow soil moisture is depleted. Because fewer, larger rainfall events, such as those imposed here, promote deeper water infiltration and extended drying of surface soils, resource partitioning between shallow and deep soils may contribute to increased forb abundance in this system. Indeed, Hoover et al.2014 (Hoover et al. 2014) found that differences in rooting depth between *S. canadensis* and C_4 grasses caused *S. canadensis* to use deeper soil moisture during a 2-year drought experiment. Conversely, Fay et al.2002 (Fay et al. 2002) found that photosynthetic responses of *S. canadensis*, a species that accounted for 13% of variation in compositional differences between treatments in our study, were positively correlated with increased shallow soil moisture variability, suggesting that this species may at times also rely more on shallow than deep soil moisture. Furthermore, Koerner et al.2014 (Ollins et al. 2014) found a strong negative correlation between grasses and forbs in this system. When grass cover increased due to herbivore removal, forb richness decreased. The tall dominant grass *A. gerardii*, whose cover decreased substantially under the altered precipitation regime, most likely competes with forbs for light and nutrient resources as well as water. The reduction in cover of *A. gerardii* in combination with changes in temporal soil water content likely combined to increase forb cover.

The lagged response in forb cover is consistent with the temporal hierarchy of ecological responses to chronic changes in resource availability predicted by the Hierarchical Response Framework (Smith et al. 2009). For example, the persistence of dominant species could have a disproportionate influence on overall species turnover and community dynamics in grasslands (Hallett et al. 2014, Winfree et al. 2015). The dominant C_4 grasses in our study exhibited little change in abundance over the 15 years of precipitation treatments. However, these consistent measures of abundance could mask subtle changes in genotype diversity occurring within the dominant species. Specifically, long-term alteration of precipitation variability in this experiment has led to a shift in the genotypic composition of the dominant perennial grass, *A. gerardii* (Avolio et al. 2013), and the changes in these genotypes reflect adaptations to a more variable precipitation regime (Avolio and Smith 2013). Thus, overall stability in the dominant grasses regardless of the increase in forb abundance may result from genotypic divergence within the long-lived dominant C_4 grasses induced by chronic changes in soil moisture availability.

The overall low levels of community and population variability and lagged response of forbs found in this study suggest that the rate of species turnover in this tallgrass prairie may be mitigated, in part, by genetic diversity and functional traits of dominant grasses, at least until some threshold in resource availability is reached. The overall high level of community stability and low rate of temporal change in community composition may result from an increase in cover and richness of a few forb species along with a concomitant decrease in other species, resulting in no net change in abundance, and thus high community stability. Thus, stability is driven by compensatory dynamics (negative covariance) in which trade-offs among species populations stabilize the overall community (Hallett et al. 2014) as a consequence of differential responses to environmental variation. Moreover, the magnitude of precipitation variability we imposed may have crossed the resource limitation threshold of only a few species leading to overall community stability and lower demographic stochasticity (Andrew M. Cunliffe et al. 2016).

Although chronic changes in resource availability are predicted to significantly alter ecosystem structure and function (Smith et al. 2009), this long-term study suggests that mesic tallgrass prairie is relatively resistant to long-term increases in intra-annual precipitation variability. Our findings are in line with other recent studies showing relatively high resistance to climate manipulations (Tielbörger et al. 2014, Kröel-Dulay et al. 2015), such as heat waves and increased precipitation. For example, Hoover et al. 2014 (Hoover et al. 2014) imposed heat waves combined with extreme drought on mesic grassland during two consecutive growing seasons. Although ecosystem function was significantly impaired during the drought, ANPP was resistant to this combination of extremes. Collins et al. 2012 (Collins et al. 2012) found that nineteen years of irrigation led to few changes in grassland community structure and function despite a significant increase in net primary production (Knapp et al. 2012). In this study, our manipulation of rainfall variability, did not reduce total precipitation during the growing season, but resulted in an unprecedented change in the rainfall regime (Smith 2011b, Knapp et al. 2015). Thus, this mesic tallgrass prairie is an example of an ecosystem that is both resistant to long-term changes in precipitation variability and amount, as well as relatively resilient to short-term extremes, with community stability strongly influenced by high resistance of the dominant grass species to these forecast alterations in climate.

Methods

Study Site. This study was conducted in the Rainfall Manipulation Plots (RaMPs) experiment at the Konza Prairie Biological Station (KPBS), a 3487 ha native tallgrass prairie preserve and Long-Term Ecological Research (LTER) site located in the Flint

Hills region of northeastern Kansas, USA. Konza Prairie is characterized by a temperate mid-western continental climate with a mid-growing season mean temperature of 27°C and mean annual precipitation of 835 mm y^{-1}, of which 75% occurs during the growing season (May through September (Fay et al. 2003)). Growing season rainfall generally declines from June through September and is somewhat bimodal with high rainfall periods between May and June, and another smaller period in September. July through August has lower rainfall with high temperatures (Fay et al. 2000, Collins et al. 2012). Yearly and seasonal variation from these general precipitation patterns is common (Hayden 1998).

The RaMPs are located in typical lowland prairie on Irwin silty clay loam soils around 320 m above sea level. Vegetation is a matrix of perennial, warm season (C_4) tall grasses and primarily perennial C_3 forbs. The dominant grasses include *Andropogon gerardii A. scoparius*, *Panicum virgatum*, *Sorghastrum nutans*, and *Sporobolus asper*. Common forb species include *Aster* spp., *Ambrosia psilostachya*, *Helianthus rigida*, *Solidago* spp., *Kuhnia eupatoroides*, *Salvia azurea* and *Vernonia baldwinii* (Collins et al. 2012). The plots are burned annually each spring in late March, a burn regime characteristic of management practices throughout the region.

The RaMPs facility consists of 12 fixed rainout shelters located on 14x9 m experimental plots and three unsheltered control plots. Each plot includes a 6x6 m sampling area enclosed within a perimeter of sheet metal that extends 0.1 m above ground and 1.1 m deep. During the growing season, shelters are covered with polyethylene roofing, diverting natural rainfall into gutters that lead into storage tanks. Rainfall is then reapplied with an overhead irrigation system. Plots are instrumented with Campbell CSR-616 TDR probes to measure soil volume water content at one minute intervals averaged for each day. More details on the experimental design and instrumentation are provided in Fay et al. 2000 (Fay et al. 2000).

Rainfall Manipulation Treatments. RaMPs shelters allowed for (1) an ambient treatment (n = 6) that applied rain immediately (within 24 h) after natural rainfall events, replicating the natural precipitation regime and (2) an altered treatment (n = 6) that applied identical amounts of rainfall as ambient plots totaled across the growing season, but lengthened the time between rainfall events by 50%, resulting in fewer but larger events with longer dry intervals between events (Fay et al. 2011). Treatments were applied during every growing season from 1998 to 2012, with 1997 serving as a pretreatment year. Experimental rainfall applications each year were based on ambient rainfall measurements via on-site rain gauges. Unsheltered control plots (n = 3) were used to assess shelter effects, which have been reported previously (Fay et al. 2000) and are not analyzed here. Frequency and amount of rain events and soil moisture were measured throughout the duration of the experiment.

Measurements of Plant Community Structure. Each RaMP had four contiguous 1 m^2 permanent quadrats in a 2x2 m grid in which plant species composition was measured spring and fall every year by visually estimating percent cover for all plant species in each quadrat. Species richness (cumulative number of species m^{-2} appearing in spring and fall samples) was determined each year in each quadrat. Richness and cover in each quadrat were averaged across the four quadrats to get mean richness and cover per RaMP. Repeated measures analysis of variance (RM-ANOVA) was used on total, grass and forb cover and richness data to assess main and interactive effects of treatment and year, with year as a repeated factor. Cover data were arcsine square root transformed to improve normality. Cover data were used further to evaluate community composition dynamics. Non-metric multidimensional scaling (NMDS) was used to visually determine trajectories of change of community composition over time among replicates of each rainfall treatment. Permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarities was performed on community data to assess differences in community composition resulting from main effects (treatment and year) and their interactions. All analyses were performed on the mean values based on the average of the four 1m^2 quadrats in each RaMP.

To assess potential directional change in community composition under altered precipitation, we used time-lag analysis to quantify the rate of change in community composition in each RaMP over the 15 year study period. Time-lag analysis uses Euclidean distance to measure similarity of community samples at increasing time lags and when regressed, yields an estimate of rate of change over time (Collins et al. 2000, Collins and Xia 2015). To assess potential differences in temporal variability between treatments at the population and community level, population and community stability were calculated. *Population stability* is the average of the temporal variability (mean to variance ratio) of each species over time (Tilman 1999), and *community stability* is the temporal variability (mean to variance ratio) of total cover (aggregated species abundances) over time. Community stability was evaluated for the whole community, as well as for forb and grass functional groups separately. Larger values indicate greater temporal stability. Species mean rank shift was also calculated per treatment. This measure quantifies relative changes in species rank abundances by taking the sum difference of species ranks of consecutive pairs of years (Collins et al. 2008b). We used analysis of variance (ANOVA) and Tukey's HSD multiple comparisons test to assess treatment effects on population and community stability and mean rank shifts. Finally, to determine changes in the relative contribution of forb species to community composition under altered precipitation, similarity percentages (SIMPER) using Bray-Curtis dissimilarities were calculated between treatments. Again, all analyses were performed on the average of the four 1m^2 quadrats in each RaMP. Statistical calculations were conducted using R (R Core Team 2014) and the R package "vegan" (Oksanen et al. 2016).

Table 2.1. Repeated measures analysis of variance for total, grass, and forb cover and richness in ambient and altered precipitation treatments in mesic tallgrass prairie. Trt = treatment, Yr = year, se = standard error.

	Ambient	Altered	Effect	Num DF	*F* value	Pr > *F*
	mean ± se	mean ± se				
Total cover	143.7 ± 2.1	151.6 ± 2.8	**Trt**	1	13.2	**0.0009**
			Yr	15	20.8	**< 0.0001**
			Trt x Yr	15	1.7	0.06
Grass cover	105.9 ± 1.5	102.2 ± 1.2	Trt	1	5.0	0.07
			Yr	15	5.4	**< 0.0001**
			Trt x Yr	15	1.1	0.3
Forb cover	37.8 ± 1.7	49.4 ± 2.4	**Trt**	1	30.1	**< 0.0001**
			Yr	15	12.5	**< 0.0001**
			Trt x Yr	15	0.7	0.9
Total richness	11.2 ± 0.2	12.3 ± 0.2	**Trt**	1	21.2	**< 0.0001**
			Yr	15	1.8	**0.04**
			Trt x Yr	15	0.4	1
Grass richness	5.3 ± 0.1	5.9 ± 0.1	**Trt**	1	20.6	**< 0.0001**
			Yr	15	2.8	**0.0007**
			Trt x Yr	15	0.4	1.0
Forb richness	5.9 ± 0.1	6.4 ± 0.2	**Trt**	1	7.0	**0.009**
			Yr	15	1.6	0.1
			Trt x Yr	15	0.3	1.0

Table 2.2. Summary statistics describing treatment differences on community composition and stability of tallgrass prairie. Trt = treatment.

Population Stability		**Trt**	**mean**		
		ambient	0.66		
		altered	0.68		
			Num DF	*F* value	Pr > *F*
			1	0.0	0.876
Community Stability					
	forb	**Trt**			
		ambient	0.39		
		altered	0.48		
			Num DF	*F* value	Pr > *F*
			1	5.2	0.149
	grass	**Trt**			
		ambient	0.49		
		altered	0.53		
			Num DF	*F* value	Pr > *F*
			1	3.7	0.195
	total	**Trt**			
		ambient	0.31		
		altered	0.36		
			Num DF	*F* value	Pr > *F*
			1	5.5	0.145
Temporal Rate of Change		**Trt**	**mean slope**		
		ambient	2.84		
		altered	2.96		
			Num DF	*F* value	Pr > *F*
			1	0.0	0.87
Mean Rank Shift		**Trt**	**mean**	r^2	
		ambient	0.52	0.05	
		altered	0.73	0.13	
			Num DF	*F* value	Pr > *F*
			1	0.9	0.342

Table 2.3. Average abundance of dominant species over all years in ambient and altered rainfall treatments, and cumulative contribution of each species to differences in community structure between rainfall treatments based on SIMPER analysis.

Species	Ambient avg. abundance	Altered avg. abundance	Cumulative contribution
1997-2012			
Andropogon gerardii (grass)	72.3	66.8	0.21
Sorghastrum nutans (grass)	21.8	16.9	0.36
Solidago canadensis (forb)	17.2	15.0	0.49
Solidago missouriensi (forb)	1.0	12.2	0.59
Andropogon scoparius (grass)	1.8	6.9	0.64
2007			
Andropogon gerardii (grass)	77.9	70.4	0.16
Solidago canadensis (forb)	21.0	20.7	0.31
Sorghastrum nutans (grass)	27.6	19.5	0.41
Solidago missouriensi (forb)	0.8	14.1	0.52
Andropogon scoparius (grass)	3.1	11.7	0.60
2009			
Sorghastrum nutans (grass)	50.4	32.0	0.18
Andropogon gerardii (grass)	56.9	55.4	0.35
Solidago canadensis (forb)	32.8	25.8	0.50
Solidago missouriensi (forb)	2.7	22.1	0.64
Helianthus rigida (forb)	3.1	6.0	0.69

Figure 2.1. Growing season precipitation parameters between ambient and altered treatments (fewer, larger rain events) from 1997 (pretreatment year) through 2012. **a**, total number of rain events excluding events less than 5mm. **b**, mean number of days between rain events or the mean length of dry periods in days. **c**, mean size of rain events (mm). Differences between ambient and altered treatments were significant (*P* = < 0.0001) for all parameters. Error bars denote one standard error.

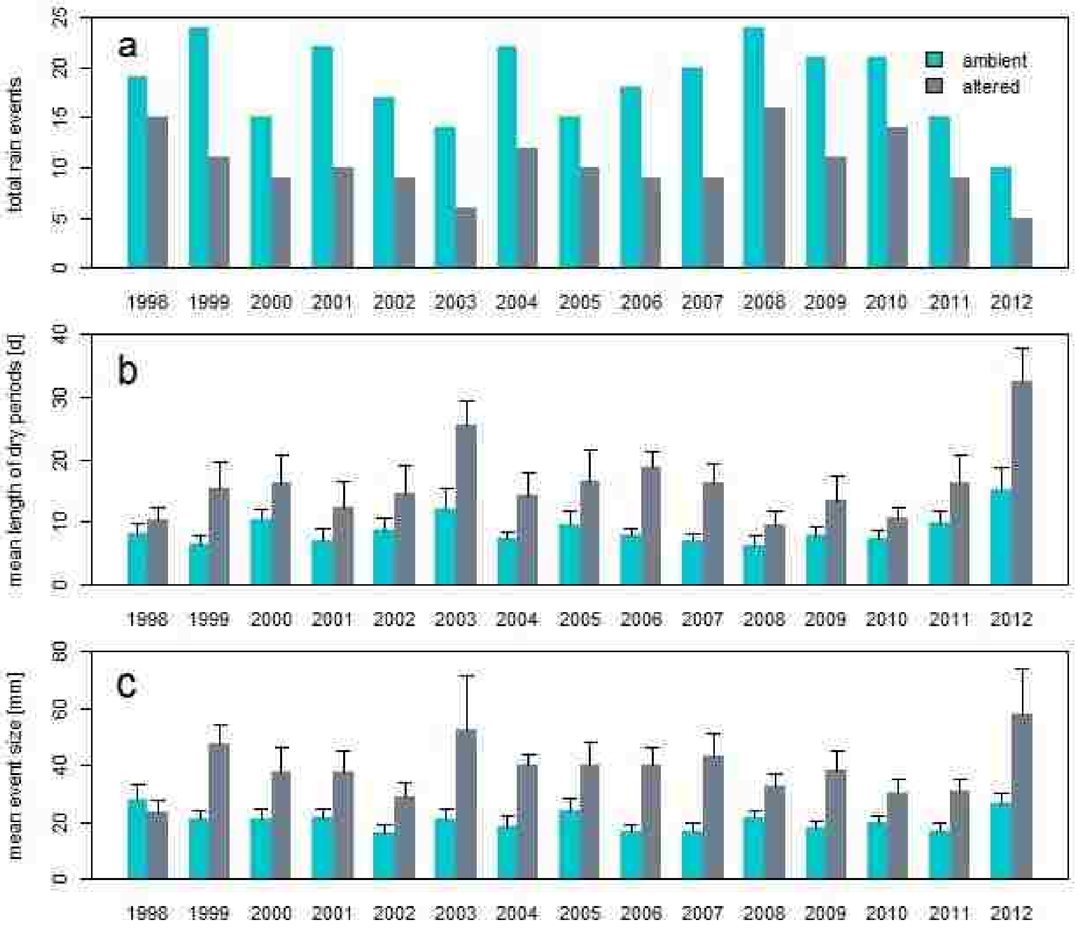


Figure 2.2. a, Forb, grass, and total cover by treatment from 1997 to 2012. Total cover was higher on average under the altered (fewer, larger rain events) treatment, primarily due to an increase in forb cover rather than grass cover. However, this effect did not emerge until after ten years of altered precipitation. **b**, Forb, grass, and total richness by treatment from 1997 to 2012. Total and grass richness were consistently higher on average in the altered treatment over the duration of the experiment. Higher altered forb richness occurred after a lag of ten years. Error bars denote one standard error.

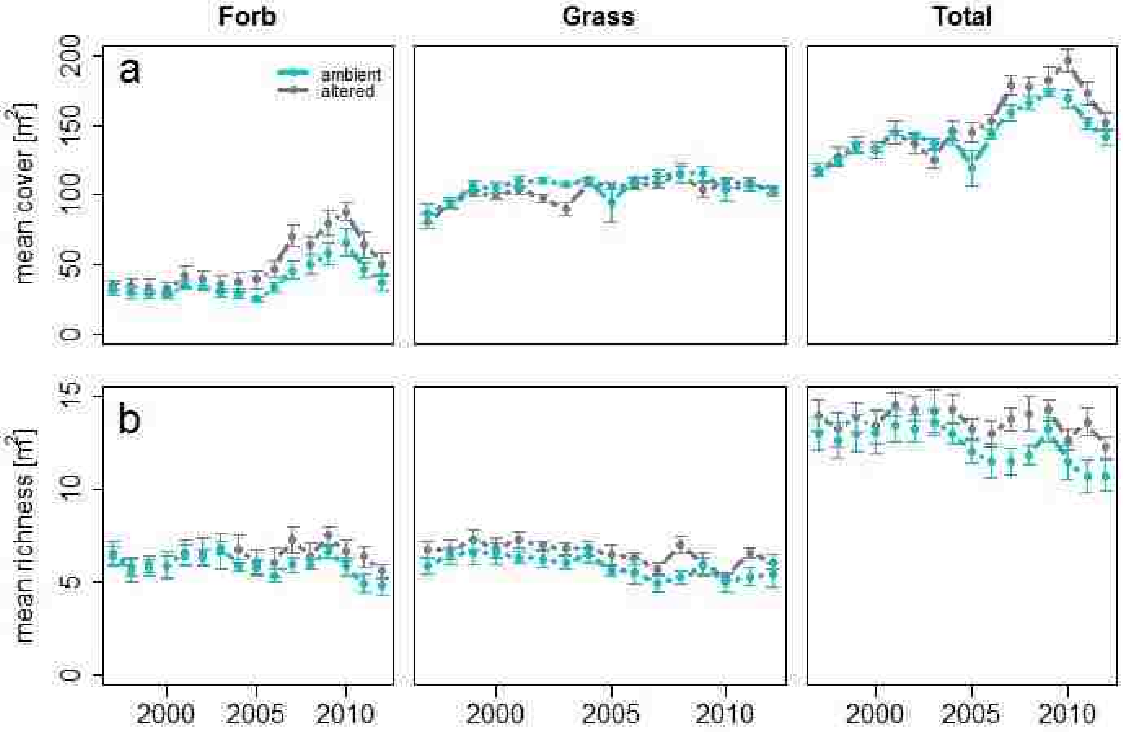
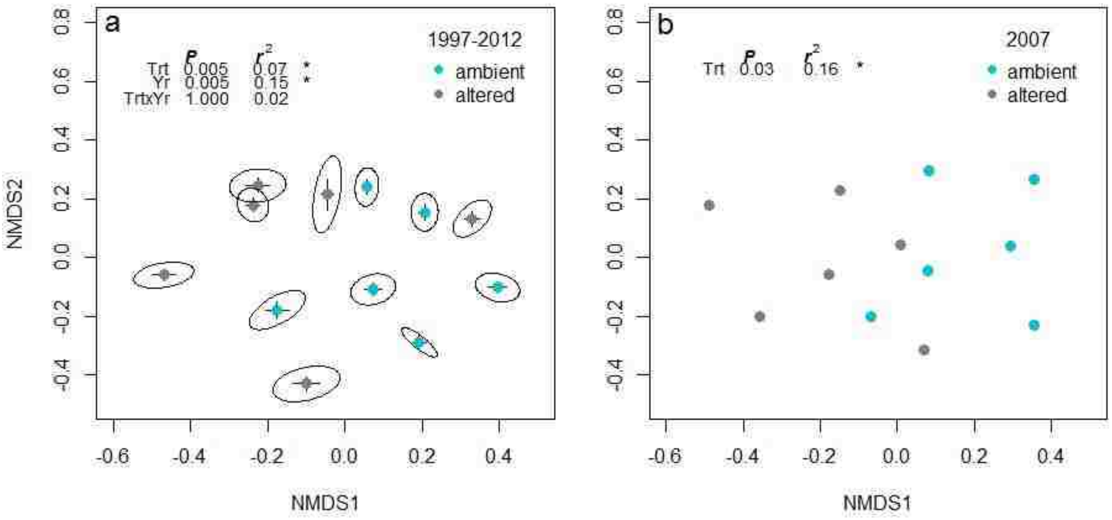


Figure 2.3. Non-metric multidimensional scaling (NMDS) of plant community composition for all plots **a**, between 1997 and 2012 and **b**, 2007 only, the year altered forb cover increased significantly from ambient. Each point is the temporal average of the NMDS coordinates for a given RaMP (plot) over the 15-year period. Error bars are one standard error. Ellipses are 95% confidence clouds based on standard error. Treatment is indicated by color. Ambient treatments are plots in which precipitation was added immediately after a natural rain event and altered treatments are plots with fewer, larger rain events. Annual treatment differences were only significant in 2007 and 2009 based on the PERMANOVA.



Chapter 3

Impacts of shrub encroachment on soil respiration and extracellular enzyme activities in Chihuahuan Desert grassland

Sydney K. Jones[1] and Scott Collins[1]

[1]Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, NM, 87131

Abstract

Encroachment of woody vegetation into grasslands can lead to land degradation and is a common phenomenon occurring across arid and semi-arid regions globally. Encroachment creates islands of fertility under shrub canopies interspersed between patches of unvegetated nutrient-poor soil. Subsequent changes in response to encroachment will likely alter soil carbon cycles. We used transplanted plant-soil monoliths to determine how encroachment of creosotebush (*Larrea tridentata*) alters carbon cycling in native Chihuahuan Desert grassland soils. We predicted that soil respiration and microbial extracellular enzyme activities (EEAs) would increase in grassland monoliths moved into creosotebush shrubland due to higher temperatures in shrubland compared to grassland. Further, respiration and EEAs of grassland monoliths moved into shrubland would be lower than shrubland controls because of lower soil carbon available for respiration in grassland soils. We measured soil respiration weekly, and microbial extracellular enzyme activities monthly over three growing seasons. Both soil respiration and microbial EEAs were highly correlated with soil moisture availability in grassland and shrubland. Soil respiration in monoliths moved from shrubland to grassland was greater than in monoliths moved from grassland to shrubland. Respiration was also higher in shrubland monoliths moved to grassland compared to shrubland controls. Respiration in grassland monoliths moved into shrubland was similar to controls. Microbial enzyme response by monoliths moved from grassland to shrubland was greater than monoliths moved from shrubland to grassland. Shrubland monoliths had higher LAP, BG and AP activities, and responded more like soils in vegetation from which they originated. The amount and ratio of enzymes remained relatively stable in both grassland and shrubland soil. The limited response from experimental shrub encroachment suggests that soil respiration and microbial activities are relatively resistant over the short term to changes in carbon cycling processes from future environmental presses such as shrub encroachment.

Keywords: Shrub encroachment, carbon dioxide efflux, soil respiration, monoliths, extracellular enzyme activity, desert grassland, *Larrea tridentata*

Introduction

Shrub encroachment or the replacement of continuous grass cover with patches of woody vegetation is occurring in arid and semiarid grasslands across the globe (Van Auken 2000, Eldridge et al. 2011). This shift in plant composition and dominance contributes to dramatic changes in vegetation composition, primary productivity and microclimate (Knapp et al. 2008b, D'Odorico et al. 2012, He et al. 2015a), as well as nutrient availability and heterogeneity (Schlesinger et al. 1996, Kieft et al. 1998). Following shrub encroachment, nutrients are concentrated under shrub canopies creating islands of fertility that are interspersed among patches of unvegetated nutrient-poor soil (Schlesinger et al. 1990). Once established, woody shrubs outcompete native grasses causing a loss in biodiversity and altered community stability (Báez and Collins 2008, Ratajczak 2012, Báez et al. 2013). Biomass is transferred from mostly belowground to aboveground (Van Auken 2009), overall vegetation cover is reduced in arid regions (Knapp et al. 2008b), and inter-shrub areas become a source of erosion (Schlesinger et al. 1996) with significant movement and losses of surface nutrients during rain events (Turnbull et al. 2010a, 2010b, Cunliffe et al. 2016). These changes in cover and nutrient heterogeneity facilitate localized transfers of soil resources and alter the carbon dynamics in ecosystems affected by shrub encroachment (Cable et al. 2012, Petrie et al. 2015).

Shrubs, such as creosotebush (*Larrea tridentata*) of the Southwestern U.S., can alter the local microclimate in ways that facilitate their own establishment, growth and persistence (He et al. 2010, D'Odorico et al. 2013). These microclimate factors include higher air and soil temperature, and more spatially heterogeneous nutrient and soil moisture availability, which alter soil carbon storage and fluxes either directly as with temperature and water (Wu et al. 2011b, Zhou et al. 2016) or indirectly by microbially facilitated nutrient cycling (Bardgett et al. 2008). For example, bare inter-shrub areas increase soil-heating during the daytime resulting in elevated nighttime air temperatures during winter, conditions that may promote further shrub encroachment (D’Odorico et al. 2010). Higher temperatures, as well as the transfer of nutrients by wind and runoff that accumulate under shrub canopies, increase nutrient availability and turnover under creosotebush canopies compared to inter-canopy areas. However, in arid regions, soil water content is the most critical factor controlling plant productivity (Noy-Meir 1973, Collins et al. 2014). Physiologically, C_3 shrubs such as creosotebush, have an advantage over C_4 grasses in that they have deeper roots (Ogle and Reynolds 2002), are able to transpire under drier conditions (Kurc and Small 2004) and growth is opportunistic, photosynthesizing and transpiring whenever conditions are favorable. C_4 grasses on the other hand, have higher maximum photosynthetic rates and water use efficiency compared to creosotebush (Pockman and Small 2010, Petrie et al. 2015). Soil respiration, the summation of below ground autotrophic respiration and microbial decomposition of soil organic carbon (Raich and Schlesinger 1992), can be a key diagnostic of water availability and acquisition, because soil moisture is highly correlated with soil and plant respiration (Huxman et al. 2004b, Ryan and Law 2005). Soil moisture increases autotrophic and heterotrophic access to substrates, triggering microbial activity and subsequently decomposition and carbon and nitrogen mineralization of recently produced organic material (Austin et al. 2004, Geisseler and Horwath 2009). Thus, the soil-water interface drives plant and microbial access to nutrients and is likely to be the most influential factor that shrub encroachment can have on ecosystem carbon dynamics, and respiration can be a measure for changes in carbon cycling under shrub encroachment.

In Chihuahuan Desert grassland and shrubland, soil respiration varies seasonally, with peak efflux occurring during the summer monsoon when high soil temperature and increased soil water availability, two main factors that drive soil respiration, co-occur. Basal soil respiration, the rate of soil respiration at extremely dry soil conditions (~2% water by volume), is similar between grassland and shrubland (Potts et al. 2008, Nuanez 2015). Soil respiration tends to track soil moisture and increases with warming until some optimum and then decreases. Temperature influences respiration either by modulating soil moisture or soil temperature (Carey et al. 2016). In arid systems, soil respiration is more sensitive to increases in soil moisture than decreases, and less sensitive at higher temperatures (Wu et al. 2011b, Carey et al. 2016, Liu et al. 2016). During shrub encroachment, however, shrubland soil respiration exhibits much lower sensitivity to both temperature and soil moisture availability than grassland (Nuanez 2015). In general, shrubland ecosystems are a carbon sink (there is more carbon stored than respired), while desert grassland appears to be carbon neutral over the long-term (Anderson-Teixeira et al. 2011). Even during periods of drought when respiration is high, shrublands are able to store carbon (Petrie et al. 2015). This occurs because ecosystem respiration is much greater in grassland than shrubland under increasing aridity (Petrie et al. 2015). However, changes in stored soil carbon alone have limited influence on soil respiration. The bulk of autotrophic respiration is derived from root and mycorrhizae growth (Ryan and Law 2005). As for heterotrophic respiration, particularly in arid systems, short-term changes in root exudates and labile carbon nutrient pools contribute heavily to soil respiration by stimulating carbon-limited microbial growth and decomposition of organic matter (Ryan and Law 2005, Bardgett et al. 2008).

Extracellular enzyme activities are proximate measures of microbial decomposition in soils and serve as indicators of the resource needs of soil microbial communities (Stursova et al. 2006). Because soil microbes use enzymes to break down organic compounds to access nutrients, and these enzymes can be stabilized through association with humic substances (Sardans et al. 2008), measuring potential enzyme activity provides insight into the availability of organic substrates in soils (Geisseler and Horwath 2009). Variability in potential enzyme activity can be due to differences in total microbial biomass and thus a larger enzyme pool of which some percentage may be antecedent (Bell et al. 2010). Comparing the ratios of different enzymes can indicate nutrient limitations (Sinsabaugh et al. 2008). For example, comparing potential enzyme activities for carbon and nitrogen indicates nitrogen limitation if the ratio is less than one. Enzyme activity, like respiration, tends to track soil moisture availability (Henry 2012) and changes seasonally, with increases following rainfall pulses early in the growing season and decreases late in the growing season (Ladwig et al. 2015). Increased microbial activity causes pulses of soil respiration fueled by labile carbon primarily from plant root exudates (Fierer and Schimel 2003, Vargas et al. 2012). Phenoloxidase and peroxidase activities, associated with lignin degradation and synthesis and carbon mineralization, are particularly high in desert grassland soils (Sinsabaugh et al. 2008) resulting in substantial organic matter decomposition and a low potential to accumulate soil organic matter

(Stursova and Sinsabaugh 2008). Further, because shrubland is less responsive (in terms of carbon uptake) to temperature and soil water content, reduced belowground root exudation and labile carbon substrates may limit the amount of carbon available for microbial respiration in these soils (Nuanez 2015).

Plant-soil transplants, also known as monoliths or mesocosms, serve as a potentially useful method for understanding the impacts of global environmental change (Arnone et al. 2008, Blankinship et al. 2010, Bond-Lamberty et al. 2016). Indeed, transplanting soil monoliths along elevation gradients or between ecosystems can be an effective means to simulate future abiotic conditions (Wu et al. 2011b). For example, Blankenship et al. (2010) transferred plant-soil monoliths from higher to lower elevations to expose soils to future conditions of warmer temperatures and lower precipitation. These soils can be monitored for changes in carbon fluxes and net ecosystem exchange (Arnone et al. 2008, 2011), soil respiration and carbon storage (Bond-Lamberty et al. 2016), microbial community structure (Bond-Lamberty et al. 2016), plant species composition (Breeuwer et al. 2010) and community dynamics (Saccone and Virtanen 2016). Thus, moving soil monoliths from one environment to another can provide a powerful mechanism to assess how ecosystem processes will change under global environmental change.

We determined experimentally how encroachment of creosotebush (*Larrea tridentata*) alters soil carbon dynamics, specifically carbon dioxide efflux (soil respiration), and potential microbial extracellular enzyme activity in Chihuahuan Desert vegetation. To do so, we transplanted plant-soil monoliths containing blue grama (*Bouteloua gracilis*) and intact soil microbial communities into substrate adjacent to creosotebush in nearby creosotebush shrubland. Because the Chihuahuan Desert grass black grama (*Bouteloua eriopoda*) is currently replacing blue grama (Collins and Xia 2015), reciprocal transplants containing black grama from creosotebush shrubland were moved into the desert grassland to determine how this reordering of dominance affects soil processes. Also, at each site control monoliths were excavated and reinstalled to determine the impact of disturbance on response variables. We then measured pretreatment total carbon and nitrogen, and microbial extracellular enzyme activities (EEA). For three growing seasons (May-Oct.), weekly soil respiration and monthly microbial EEA measurements were taken. We predicted that soil respiration in grassland monoliths moved to shrubland would be higher compared to control grassland monoliths because temperatures are higher in shrubland (He et al. 2015b) and respiration is higher in grassland compared to shrubland as temperature increases (Petrie et al. 2015). Also, shrubland soils are less responsive to temperature fluctuations than grassland (Nuanez 2015). Further, we predicted that soil respiration of grassland monoliths moved into shrubland would be lower than shrubland controls because of lower soil carbon available for respiration in grassland soils. Finally, we predicted that enzyme activities would be lower in grassland soils because of higher N and C content in shrubland soils. Overall, these effects would be strongest following precipitation events because microbial activity increases with soil moisture (Fierer and Schimel 2003, Austin et al. 2004, Collins et al. 2008a).

Methods

Study Site. Our study sites are located at the Sevilleta National Wildlife Refuge (SNWR; latitude 34°20'N, longitude 106°43'W), a Long Term Ecological Research (LTER) site along the Los Pinos Mountains, central New Mexico, USA. The grassland site is dominated primarily by the Chihuahuan Desert grass, black grama (*Bouteloua eriopoda*), and the Great Plain grass, blue grama (*Bouteloua gracilis*). Other common grasses include *Sporobolis spp*., *Muhlenbergia spp*., and *Pleurophis jamesii* (Muldavin 2002, Kröel-dulay et al. 2004). Common forbs and sub-shrubs include *Cryptantha crassicarpa*, *Macraentherium* spp., *Melampodium leucanthum*, *Sphaeralcea* spp., *Yucca elata* and *Ephedra torreyana* (Mulhouse et al. 2017). The shrubland site is dominated by the Chihuahuan Desert C_3 shrub creosotebush with scattered patches of black grama. In general, black grama is replacing blue grama in this grassland (Collins and Xia 2015) and historical photographs show that creosotebush primarily replaced black grama during the last century. Invaded areas have 20-30% fewer vascular plant species per m^2 compared to adjacent non-invaded areas (Báez and Collins 2008). Soils are Typic Haplargids derived from piedmont alluvium. The water holding capacity and nutrient reserves of these soils are very low (Zak et al. 1994, Stursova et al. 2006). Average annual temperature is 13.2°C, with average daily temperature being 1.6°C in January and 25.1 °C in July. Average annual precipitation is ~250 mm, 60% delivered during the summer monsoons that occur from July through early September each year (Notaro et al. 2010, Petrie et al. 2014). Growth is driven primarily by soil moisture rather than precipitation (Muldavin et al. 2008, Xia et al. 2010), because precipitation is lost through evaporation and surface runoff. Precipitation is spatially and temporally variable in this system, and the relative contribution of winter and monsoon rainfall varies considerably from year to year (Pennington and Collins 2007).

Experimental Design. In spring of 2014, soil monoliths were constructed using PVC cores, 50-cm deep by 30-cm diameter, capped off at the bottom with a small opening for drainage. Plant-soil cores were excavated using a custom-built soil core and a backhoe. Monoliths used to simulate encroachment (*n*=10) containing blue grama and associated soil microbial communities were transplanted into substrate adjacent to creosotebush (grassland to shrubland, G->S) at the encroached shrubland site. Reciprocal transplants (*n*=10) containing black grama from creosotebush shrubland were moved into the desert grassland (shrubland to grassland (S->G). Control monoliths (*n*=10 per site) were excavated and reinstalled at both the grassland (G->G) and shrubland (S->S) sites.

Pretreatment Total Soil Carbon and Nitrogen. At the start of the experiment in 2014 prior to transplanting, soils in each monolith (*n*=40, 20 per site) were sampled from 0- to 20-cm depth with a 2.5-cm diameter soil core. Soils were homogenized using a 2-mm sieve, oven dried and ground using a pestle and mortar. Percentage of soil carbon and nitrogen in each sample was determined using a Costech elemental analyzer (Costech, Valencia, CA) by running three analytical subsamples and averaging them for a single measure of carbon and nitrogen content for each monolith.

Carbon Dioxide Efflux. For three growing seasons (May-Oct.) from 2014 to 2016, weekly carbon dioxide efflux, soil respiration, was measured using a LI-COR 6200. A soil collar was placed inside the monolith with a cap cycling air from the Li-COR sealed on top. Soil temperature was taken and sample air volume calculated with each measurement. Efflux was calculated in units of µmol m^{-2} s^{-1}. Because respiration measurements occurred over several hours (10:00-14:00 hours) each sample period, regression equations were developed for predicting respiration rates at a given soil temperature for each site. Respiration values were then normalized to the average soil temperature by using the derived regression equation.

Extracellular Enzyme Activity. For three growing seasons (May-Oct.) from 2014 to 2016, monthly extracellular enzyme activity (EEA) of soil (0- to 10-cm depth) from each monolith was assayed from 1 g subsamples. Potential hydrolase enzyme activities analyzed were β-glucosidase (BG), alkaline phosphatase (AP) and leucyl aminopeptidase (LAP). These are proxies for carbon, phosphorus and nitrogen acquisition, respectively. BG catalyzes the terminal step in cellulolysis, AP removes phosphate groups and LAP is an aminopeptidase that removes amino acids from proteins. These hydrolytic enzymes were measured fluorometrically and potential activities calculated in units of nmol h^{-1} g^{-1}. In addition, phenol oxidase (POX) and peroxidase (PER) potential activities were measured to estimate lignin synthesis and degradation, and usually are uncorrelated with hydrolase activities (Sinsabaugh 2010), are less stable and more spatiotemporally variable (Stursova and Sinsabaugh 2008). POX oxidizes phenolic compounds in recalcitrant organic matter. PER is similar but uses H_2O_2 as an electron acceptor. These oxidative enzymes were assayed chlorometrically using L-3,4-dihydroxyphenylalanine (DOPA). Phenol oxidase analysis used DOPA only and peroxidase analysis used both

DOPA and H_2O_2 as substrate. Activities were calculated in units of umol h^{-1} g^{-1}. Because these soils are alkaline, assays were conducted at a pH 8.0 using 50 mM sodium bicarbonate buffer. Alkaline soils increase oxidative enzyme potentials which lead to the breakdown of recalcitrant organic compounds such as lignin, limiting the accumulation of organic matter in aridland soils (Stursova and Sinsabaugh 2008). For both hydrolase and peroxidase activities, sample fresh weights were corrected for moisture content using hourly volumetric water content taken from nearby meteorological towers at each site for each day soil samples were taken. This method does not account for monolith-scale microclimate variability in moisture content. Also, the composition and quality of organic matter are known to influence enzyme activities, however these measurements are unknown for our samples.

Statistical Analysis. An analysis of variance (ANOVA) for each month was used to test the significance of treatment on soil respiration. Linear mixed effects models were used to test the association of site, treatment, year, month and their interaction with soil volumetric water content (vwc) against changes in soil respiration and potential EEA activities (‘lmer’ R package). The ratios between enzyme activities were also compared to the above main effects and interactions to estimate nutrient limitations (Sinsabaugh et al. 2008). A BG:AP ratio <1 indicates phosphorus limitation, whereas a BG:LAP ratio <1 indicates nitrogen limitation. A BG:POX ratio estimates relative differences between degradation of cellulose and lignin. The models account for random effects from measurements taken from the same site and plot. Soil respiration and EEA activities were analyzed separately due to high co-variability between site and EEAs. The ‘glht’ function (‘multcomp’ R package) was used to test pairwise contrasts between treatments on soil respiration and EEA. Total daily volumetric water content was taken from nearby meteorological towers for each day soil respiration was measured.

Results

Pretreatment analysis. Pretreatment total soil carbon and nitrogen were significantly higher (P = <0.0001) in creosotebush shrubland compared to desert grassland (Figure 3.1.). Pretreatment extracellular enzyme activity was significantly higher in creosotebush shrubland compared to desert grassland for alkaline phosphatase (AP; mean = 76.5 and 52.0 nmol h^{-1} g^{-1}, respectively, P = 0.024) and marginally higher for beta-D-glucosidase (BG; mean = 114.3 and 84.2 nmol h^{-1} g^{-1}, respectively, P = 0.087) proxies for potential microbial phosphorous and labile carbon activity, respectively.

Soil respiration significantly correlated with soil volumetric water content across all measurements in both grassland and shrubland (P=<0.001; Figure S3.1). The slopes for grassland monoliths moved into shrubland (G->S) and grassland control (G->G) monoliths were not significantly different. All other combinations were significantly different.

In 2014, grassland precipitation in July, August and September was higher than the long-term monthly averages by 38, 16 and 116%. May, June and October were moderately lower than the long-term monthly averages by 36, 61 and 38%. Shrubland precipitation in June and August was higher than the long-term averages by 299 and 27%. July was similar to the moderately long-term average. May, September and October were lower by 36, 38 and 62%. In general, 2014 had higher than average total precipitation. Grassland and shrubland sites received similar total growing season precipitation (202 and 200 mm, respectively) from a similar number of events (45 and 51).

In 2015, grassland precipitation in May and October was much higher than the long-term monthly averages by 222 and 136%. June through September were lower, particularly September by 96%. Shrubland precipitation in May, June and October was much higher than the long-term average by 117, 147 and 104%. July through September were moderately lower. This year in general had higher than average late season precipitation. Grassland and shrubland sites received similar total growing season precipitation (169 and 161 mm, respectively) from a similar number of events (54 and 58).

In 2016, grassland precipitation was moderately higher than the long-term monthly average in July by 63%. All other months received lower than average precipitation, particularly September by 88%. Shrubland precipitation in June, July and October was higher than average, particularly June by 94%. May and August were moderately lower than average, September was much lower by 93%. In general, 2016 received lower than average precipitation with the grassland site receiving 17 mm less during the growing season than the shrubland site from slightly fewer rain events (34 and 40, respectively).

Soil Respiration. We found high within- and between-season variability in soil respiration in response to treatment affects (Figure 3.3). In general, responses by monoliths moved from shrubland to grassland (S->G; i.e. reciprocal effect) were greater than monoliths moved from grassland to shrubland (G->S; Table 3.4). Respiration was higher in shrubland monoliths moved to grassland (S->G) compared to control monoliths (S->S). In 2014, soil respiration was significantly lower in monoliths moved from grassland to shrubland (G->S) compared to grassland controls (G->G; Table 3.1, Figure 3.3) in April. Also, soil respiration was significantly lower in soils moved from shrubland to grassland (S->G) in April, and significantly higher in August and September compared to shrubland controls (S->S). In 2015, there was both an encroachment effect (i.e, G->S) and reciprocal encroachment effect (i.e. S->G). In this case, soil respiration was significantly higher in grassland monoliths moved to shrubland (G->S) compared to grassland controls (G->G) in July, August and October. Respiration was lower in shrubland monoliths moved to grassland (S->G) compared to control monoliths (S->S) in August and higher in September. In 2016, Shrubland monoliths moved to grassland (S->G) were significantly lower from grassland controls (G->G) in October. Respiration was significantly higher throughout the growing season in monoliths moved from shrubland to grassland (S->G) compared to shrubland controls (S->S; see Table 3.1 for summary). In all cases, significant treatment effects occurred primarily during months with high soil vwc (Figure 3.2.). Regressions of soil respiration versus vwc showed that slopes between grassland treatment and shrubland control (i.e. reciprocal encroachment effect) and between grassland and shrubland controls were significantly different (*P*=<0.000). Slopes between shrubland treatment and grassland control (i.e. encroachment effect) were not significantly different (*P*=0.146; Figure S3.1).

Extracellular Enzyme Activity. After the monoliths were transplanted, enzyme activity showed considerable variability between years and between enzymes in response to treatment affects (Figure 3.4). In general, shrubland monoliths had higher LAP, BG and AP activities. Soils responded more like soils from which they originated, significantly so for BG, AP and POX activities in shrubland soil and AP activity in grassland soil (Table 3.4). LAP, BG and AP activities were higher in shrubland monoliths moved to grassland (S->G) compared to grassland controls (G->G) and lower in grassland monoliths moved to shrubland (G->S) compared to shrubland controls (S->S). Response by monoliths moved from grassland to shrubland (G->S, i.e. encroachment effect) was greater than monoliths moved from shrubland to grassland (S->G; Figure 3.4). Response was higher in grassland monoliths moved to shrubland (G->S) compared to control monoliths (G->G; Figure S3.2, S3.3, S3.4).

In 2014, no enzymes showed a significant effect for either treatment. However, LAP and to some extent BG had progressively decreasing reciprocal treatment effects (S->G) and progressively increasing encroachment effects (G->S), converging on similar values at the end of the growing season (Figure S3.2). In 2015, EEA values were markedly lower for all enzymes (Figure S3.3) with significant reciprocal effect (S->G) in LAP activities (Figure 3.4). LAP had the opposite trend from the year before with a progressively decreasing encroachment effect and increasing reciprocal effect over the growing season.

There was not a clear trend for the other enzymes in 2015. In 2016, activity levels were much higher than prior years, and all EEAs showed a unimodal response, peaking around late August (Figure S3.4). There was a significant reciprocal effect for LAP most of the growing season. BG and AP had both significant encroachment (G->S) and reciprocal effects (S->G) early in the growing season and later in the season for POX. May had significant peaks in BG, AP and PER for both grassland (G->S) and shrubland (S->G) treatments (Figure 3.4).

Linear Mixed-effects Model. In the soil respiration linear mixed-effects model, all main effects were significant predictor variables except volumetric water content (vwc; Table 3.2). The site and treatment interaction, along with the pairwise comparison, indicates a significant reciprocal encroachment (S->G) effect. The site, treatment and vwc interaction was also significant. As for the EEA activity models, all main effects were significant predictor variables, except vwc for PER (Table 3.2). The site and treatment interaction, which indicates an encroachment (G->S) or reciprocal encroachment (S->G) effect, was significant for all EEAs. A site and vwc interaction occurred for LAP and POX indicating that the soil moisture differences between grassland and shrubland sites drove variation in these enzyme activities. Year and month interactions with vwc were significant in all of the enzymes except for year in LAP.

As for enzyme activity ratios, BG and AP ratios were very similar across all treatments and lme models showed only significant year and month main effects and their interaction with vwc (Table 3.2). This indicates that there was little change in soil phosphorous and what change there was, was significantly driven by soil moisture. BG and LAP ratios were lower in shrubland soils than grassland soils and consistently lower than one. This indicates that shrubland soils were more limited in nitrogen, or there was more energy expended, via carbon, per unit of nitrogen acquired. All main effects and interactions were significant. Soils responded like soils from which they originated for this enzyme ratio (Table 3.3). In 2015 and 2016, BG and POX ratios were higher in shrubland soils, indicating that there is less potential for lignin breakdown in shrubland soil compared to grassland soil. Site, treatment and year main effects were significant, as well as the site and treatment interaction indicating a significant encroachment effect (G->S; Table 3.2, 3.3). There was also a significant site, treatment and vwc interaction for this enzyme ratio.

Discussion

We experimentally determined how encroachment of creosotebush altered soil respiration and potential enzyme activities in Chihuahuan Desert grassland and shrubland ecosystems. We predicted that soil respiration, our measure for carbon cycling, in grassland monoliths moved to shrubland would be higher compared to control grassland monoliths. We also predicted that respiration in monoliths moved from shrubland to grassland would be higher than grassland respiration because of (1) higher soil carbon content in shrubland, (2) higher ecosystem respiration in grassland compared to shrubland as temperature increases, and (3) shrubland soils are less responsive to temperature fluctuations than grassland. Further, we predicted that soil respiration of grassland monoliths moved into shrubland would be lower than shrubland controls because of lower soil carbon available for respiration in grassland soils. We predicted that these effects would be strongest following precipitation events due to increased microbial activity following precipitation pulses. We found that weekly soil respiration was highly variable within and among years and positively correlated with soil volume water content in both grassland and shrubland. Consistent with our predictions, soil respiration response by monoliths moved from shrubland to grassland was greater than monoliths moved from grassland to shrubland. Respiration was higher in shrubland monoliths moved to grassland compared to control monoliths. Microbial enzyme activities were also highly correlated with soil moisture. Response by monoliths moved from grassland to shrubland was greater than monoliths moved from shrubland to grassland. Shrubland monoliths had higher LAP, BG and AP activities, lower BG:LAP and BG:POX ratios and responded more like soils from which they originated.

Our results support our former predictions in that responses by soil respiration would be driven by soil moisture. Soil respiration is highly correlated with soil moisture availability in aridland ecosystems (Vargas et al. 2010, 2012). Carbon fixation in these shrubs and grasses is tightly coupled to soil moisture availability (Pockman and Small 2010) and soil respiration lags behind carbon uptake by only 24 hours suggesting that respiration is dependent on plant root exudates (Vargas et al. 2012). At the site level, soil moisture also drove differences in soil respiration. In 2015, the year flux was relatively low yet had a significant encroachment effect (monoliths moved from shrubland to grassland), the peak in monsoon rainfall came late in the season and could be driving the encroachment effect not seen in the other two years. Drier conditions with only small rain events and warmer temperatures in shrubland could have caused higher respiration rates in grassland monoliths in shrubland compared to grassland controls. In 2014 and 2016, years characterized by a significant reciprocal encroachment effect (monoliths moved from shrubland to grassland), the timing and amounts of soil water content were more similar. Indeed, the soil respiration mixed effects model showed significant interaction between soil water content and treatment effects, particularly the reciprocal effect on creosote monoliths moved into grassland. Further, monoliths moved from shrubland to grassland had significantly higher sensitivity to soil moisture compared to shrubland control monoliths, supporting the idea that shrubland soil is less sensitive to moisture fluctuations.

Our pre-treatment analysis of total carbon and nitrogen established that nutrient levels are indeed higher under creosotebush canopies compared to grass canopies, results consistent with Kieft et al. (1998). Jackson et al. (2002) also found gains in soil organic carbon and nitrogen in arid grasslands invaded by woody vegetation and Cunliffe et al. (2016) reported a six fold increase in organic carbon across a grassland-to-shubland ecotone due to erosion-induced redistribution of organic carbon. Therefore, inherent differences in soil nutrient availability likely influences treatment differences between monoliths moved into grassland and shrubland habitats. In our study, soil respiration of grassland monoliths was not always greater when transplanted under shrub canopies. Instead, in two out of three years, shrubland monoliths tended to have higher soil respiration when moved into the grassland environment. This could be the result of shrubland soils having more soil carbon to begin with and likely reflects use of shrubland-derived carbon that will not be replenished in the grassland environment. This does not support the findings from

Nuanez (2015) that soil respiration in creosotebush shrubland is limited in carbon substrates. However, we did find shrubland soils to be less responsive to soil water availability as mentioned above but not due to a lack in substrate availability. However, this nutrient difference does not explain why shrubland soil when moved into grassland, has higher respiration than shrubland controls. Scott et al.(2006) found shrubland soil respiration to decrease through the growing season. This effect could have been mitigated in the grassland environment. Soil respiration can be sensitive to microclimates created by differences in vegetation structure (Cable et al. 2012). Subtle changes in canopy shading in shrubland verses grassland, as well as decreases in evaporation could also drive treatment differences in respiration. As for the grassland soils, they were less responsive to treatment effects and when moved into shrubland, continued to respond like control monoliths. Again, this could be the result of grassland soils having less soil carbon than shrubland soil as predicted.

EEAs for nitrogen, carbon and phosphorous substrates in monoliths originating from the shrubland site were consistently higher than monoliths originating in the grassland site. Site and treatment effect (site and treatment interaction) were a significant predictor of all potential EEAs. This suggests that site differences in microbial activity were major drivers of soil respiration and that shrubland soils have higher microbial biomass (Bell et al. 2010) or higher nutrient availability (Geisseler and Horwath 2009) than grassland soils. Indeed, shrub encroachment can increase phosphatase activities (Maestre et al. 2011). Shrublands are also associated with higher soil microbial biomass due to higher plant productivity and organic carbon inputs (Liao and Boutton 2008). However, Liao and Boutton (2008) also found more respiration was required per unit of soil microbial biomass carbon compared to grassland, making this microbial biomass expensive in terms of carbon. Thus, higher microbial biomass may not lead to higher nutrient availability.

BG and LAP ratios were lower in shrubland soils and consistently lower than one, indicating that shrubland soils were limited in nitrogen, or there was more carbon expended per unit of nitrogen acquired. This suggests that higher LAP activities in shrubland soil were not due to higher nitrogen availability, but that the demand for nitrogen could be outstripping availability. Hibbard et al. (2001) found woody encroachment increased nitrogen accumulation but also increased nitrogen turnover even more, creating nitrogen limitation regardless of increases in nitrogen inputs. Similarly, McKinley and Blair (2008) found encroachment to significantly increase nitrogen, as well as carbon, accrual in soils without changes in labile soil nitrogen pools. Also, increases in soil microbial biomass carbon following encroachment have been correlated with concurrent increases in stored carbon and nitrogen pools in soils, as well as in roots and litter (Liao and Boutton 2008). These studies are consistent with our results of higher nitrogen limitation regardless of higher total carbon and nitrogen and microbial activities for carbon and nitrogen in shrubland soil. Further, the ratio of BG to LAP, as well as BG to AP, was maintained in both grassland and shrubland soils even when moved into the new environments. Thus both the amount and ratio of enzymes remained relatively stable. The maintenance of these enzyme ratios could indicate a relative stability in the uniqueness of the microbial communities of each soil type (Yannarell et al. 2014) that may not change until nutrient availability is altered such as the addition of C_3 leaf litter, with relatively higher nitrogen concentrations, under shrub canopies (Lett et al. 2004, Cable et al. 2012) or from belowground organic matter inputs from increasing woody root biomass (Hibbard et al. 2001). This is consistent with findings that soil EEA stoichiometry is maintained by soil nutrient stoichiometry (Peng and Wang 2016).

In 2015 and 2016, BG and POX ratios were higher in shrubland soils, indicating that there is less carbon being used for lignin breakdown in shrubland soil compared to grassland soil. The potential for concurrent increases in stored soil carbon and nitrogen pools during encroachment may make woody litter relatively resistant to decay and less suitable for microbial enzyme breakdown compared to grassland litter (Liao and Boutton 2008). Grass lignins are also more soluble under alkaline conditions compared to lignins from woody plants, increasing the likelihood for enzymatic breakdown in grasslands (Stursova and Sinsabaugh 2008). Further, grassland control monoliths had consistently high POX activities, indicating a limitation in the accumulation of organic matter (Sinsabaugh 2010) which could also contribute to lower nutrient availability in grassland.

Taking into account the influence of soil moisture on microbial activity, almost all enzymes measured had significant interaction effects with soil volume water content. PER was the only enzyme that did not have significant interaction with VWC. Thus, microbial activity was strongly influenced by soil moisture, which is in line with the general pattern from other studies that found nutrient cycling to be highly influenced by microbial activity triggered by precipitation pulses (Fierer and Schimel 2003, Austin et al. 2004, Bardgett et al. 2008, Collins et al. 2008). For example, drying-rewetting or pulse events can significantly increase the activity of autotrophic nitrifier populations in the microbial community (Fierer and Schimel 2003) and decrease microbial carbon-use-efficiency (Tiemann and Billings 2011). Our results also support the finding from Lagwig et al. (2015) that microbial activity changes seasonally in response to rainfall pulses early in the growing season and decreases late in the growing season. In 2016, EEAs followed this pattern of response, as well as in 2015 when enzyme activity continued to increase with the lagged peak in monsoon rainfall. Indeed, responses of microbial communities to precipitation amounts are highly dependent on seasonal precipitation dynamics (Cregger et al. 2012), alter the relative contribution of bacteria and fungi to decomposition and nitrogen mineralization (Bell et al. 2008) and soil type (Borowik and Wyszkowska 2016). For many EEAs, shrubland soils responded like the soils from which they originated, rather than the soils in their new environment, making these soils potentially resistant to the impacts of shrub encroachment. However, the fact that our soils were physically separated from the soil and vegetation outside the monolith could have buffered the monolith soils from influences such as horizontal redistribution of nutrients that influence plant-microbe interactions and soil -carbon dynamics as a consequence of shrub encroachment.

Shifts in community composition from relatively uniform and homogenous grassland cover to a more heterogeneous and open shrubland could significantly alter how ecosystems will respond to future abiotic changes such as the timing and size of precipitation events leading to subsequent changes in microbial dynamics and feedback effects on plant productivity and composition (Bezemer et al. 2006, Bardgett et al. 2008). However, we found much resistance in soil respiration and microbial activity from the effects of shrub encroachment. We found a greater response in soil respiration in plant-soil monoliths moved from under creosotebush canopies into desert grassland, with transplanted monoliths having higher respiration compared to control monoliths. This effect was driven directly by water availability and indirectly by microbial activity. A lack of response in soil respiration from grassland soils suggests that these ecosystem processes in grassland soils will lag behind vegetation composition during shrub encroachment. Potential microbial enzyme activity in grassland and shrubland soils responded like the soils from which they originated, rather than the soils in their new environment. This also suggests that, at least in the short term, these soils are resistant to abiotic changes and potentially resilient to future environmental presses such as shrub encroachment.

Table 3.1. Carbon dioxide efflux control and treatment monthly averages for months with significant encroachment and reciprocal effects from 2014 - 2016. Variance is in standard error.

	Encroachment effect				Reciprocal effect		
	control	**treatment**	***P***		**control**	**treatment**	***P***
2014	GC	ST		**2014**	SC	GT	
Apr	1.6±0.2	0.5±0.3	<0.0001	Apr	0.03±0.1	1.1±0.2	<0.0001
				Aug	7.8±0.7	11.1±1.3	0.03
				Sep	3.4±0.6	7.1±1.1	0.002
2015				**2015**			
July	5.0±0.4	7.8±0.4	<0.0001				
Aug	4.2±0.4	7.9±0.3	<0.0001	Aug	6.1±0.3	4.5±0.4	<0.0001
				Sep	1.4±0.1	2.2±0.1	0.0004
Oct	2.0±0.2	3.3±0.3	0.002				
2016				**2016**			
				Jun	1.5±0.1	4.7±0.7	<0.0001
				Jul	1.6±0.1	5.1±1.6	0.01
				Aug	6.9±0.6	10.2±0.7	0.001
				Sep	3.5±0.5	5.9±0.5	0.003
Oct	2.3±0.2	1.4±0.1	0.01	Oct	1.4±0.2	2.4±0.2	0.0003

Table 3.2. Linear mixed-effect models comparing CO2 efflux and each potential extracellular enzyme activity with main effects and interactions of site (grassland verses shrubland), treatment (control verses treatment), year (2014-2016), month (May-Oct), volumetric water content (vwc). BG, AP and LAP estimate carbon, phosphorous and nitrogen availability respectively. POX and PER estimate lignin synthesis and degradation. The ratio of BG to AP indicates a change in phosphorous. The ratio of BG to LAP indicates nitorgen limitation. The ratio of BG to POX indicates relative amounts of cellulose to lignin.

		Efflux		**BG**		**AP**	
	Df	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)
site	1	5.760	**0.016**	143.587	**0.000**	83.599	**0.000**
treatment	1	29.881	**0.000**	350.732	**0.000**	414.660	**0.000**
year	2	21.964	**0.000**	962.175	**0.000**	553.994	**0.000**
month	5	465.615	**0.000**	68.032	**0.000**	155.619	**0.000**
vwc	1	0.157	0.692	29.710	**0.000**	16.923	**0.000**
site:treatment	1	6.270	**0.012**	663.494	**0.000**	593.374	**0.000**
site:vwc	1	8.704	**0.003**	1.956	0.162	0.490	0.484
year:vwc	2	5.779	0.056	68.867	**0.000**	86.955	**0.000**
month:vwc	5	167.151	**0.000**	98.803	**0.000**	49.535	**0.000**
site:treatment:vwc	2	26.509	**0.000**	1.258	0.533	4.405	0.111

		LAP		**POX**		**PER**	
	Df	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)
site	1	406.558	**0.000**	30.954	**0.000**	59.586	**0.000**
treatment	1	506.633	**0.000**	25.831	**0.000**	26.710	**0.000**
year	2	1754.275	**0.000**	408.146	**0.000**	98.742	**0.000**
month	5	154.866	**0.000**	272.840	**0.000**	68.796	**0.000**
vwc	1	6.633	**0.010**	64.118	**0.000**	0.692	0.406
site:treatment	1	1239.118	**0.000**	32.928	**0.000**	45.738	**0.000**
site:vwc	1	3.954	**0.047**	4.230	**0.040**	3.248	0.071
year:vwc	2	5.210	0.074	131.118	**0.000**	9.682	**0.008**
month:vwc	5	56.340	**0.000**	114.907	**0.000**	90.776	**0.000**
site:treatment:vwc	2	0.979	0.613	0.054	0.973	0.310	0.856

		BG:AP		**BG:LAP**		**BG:POX**	
	Df	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)	Chisq	Pr(>Chisq)
site	1	2.283	0.131	66.506	**0.000**	16.474	**0.000**
treatment	1	1.088	0.297	60.807	**0.000**	25.719	**0.000**
year	2	163.077	**0.000**	341.382	**0.000**	57.174	**0.000**
month	5	33.691	**0.000**	82.412	**0.000**	10.295	0.067
vwc	1	3.062	0.080	17.831	**0.000**	0.189	0.664
site:treatment	1	1.375	0.241	146.801	**0.000**	28.317	**0.000**
site:vwc	1	1.416	0.234	10.296	**0.001**	3.548	0.060
year:vwc	2	7.111	**0.029**	10.583	**0.005**	0.269	0.874
month:vwc	5	139.650	**0.000**	51.102	**0.000**	1.975	0.853
site:treatment:vwc	2	1.766	0.413	12.961	**0.002**	12.159	**0.002**

Table 3.3. Pairwise comparisons of treatments on CO_2 efflux and potential extracellular enzyme activity. Controls are grass-soil monoliths excavated and reinstalled at respective sites (GC, GC). Grassland treatments (GT) are shrubland monoliths installed in blue grama grassland. Shrubland treatments (ST) are grassland monoliths installed in creosote shrubland. BG, AP and LAP estimate carbon, phosphorous and nitrogen availability respectively. POX and PER estimate lignin synthesis and degradation. The ratio of BG to AP indicates a change in phosphorous. The ratio of BG to LAP indicates nitorgen limitation. The ratio of BG to POX indicates relative amounts of cellulose to lignin.Shaded rows indicate treatment comparisons for an encroachment effect (ST - GC) and reciprocal treatment effect (SC - GT).

	Flux				**BG**				**AP**			
	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)	Estimate	Std. Error	z value	Pr(>|z|)
GT - GC	0.261	0.058	4.510	**0.000**	1.032	0.054	19.136	**0.000**	1.153	0.057	20.354	**0.000**
SC - GC	-0.262	0.099	-2.635	**0.037**	1.280	0.105	12.228	**0.000**	0.906	0.100	9.074	**0.000**
ST - GC	-0.141	0.099	-1.423	0.461	0.282	0.105	2.694	**0.030**	0.093	0.100	0.937	0.769
SC - GT	-0.523	0.099	-5.266	**0.000**	0.247	0.105	2.362	0.074	-0.247	0.100	-2.474	0.057
ST - GT	-0.402	0.099	-4.054	**0.000**	-0.750	0.105	-7.172	**0.000**	-1.059	0.100	-10.612	**0.000**
ST - SC	0.120	0.058	2.078	0.146	-0.998	0.054	-18.491	**0.000**	-0.812	0.057	-14.342	**0.000**
	LAP				**POX**				**PER**			
GT - GC	0.989	0.043	22.846	**0.000**	-0.317	0.061	-5.199	**0.000**	-0.379	0.071	-5.376	**0.000**
SC - GC	1.516	0.076	20.042	**0.000**	-0.465	0.087	-5.356	**0.000**	-0.889	0.116	-7.636	**0.000**
ST - GC	0.311	0.076	4.112	**0.000**	-0.270	0.087	-3.105	**0.010**	-0.569	0.116	-4.884	**0.000**
SC - GT	0.527	0.076	6.964	**0.000**	-0.148	0.087	-1.703	0.310	-0.510	0.116	-4.379	**0.000**
ST - GT	-0.678	0.076	-8.967	**0.000**	0.048	0.087	0.548	0.944	-0.190	0.116	-1.628	0.342
ST - SC	-1.205	0.043	-27.830	**0.000**	0.196	0.061	3.204	**0.007**	0.320	0.071	4.542	**0.000**
	BG:AP				**BG:LAP**				**BG:POX**			
GT - GC	-0.077	0.078	-0.980	0.753	-0.413	0.048	-8.568	**0.000**	4.752	0.912	5.209	**0.001**
SC - GC	0.192	0.108	1.788	0.269	-0.520	0.064	-8.138	**0.000**	4.719	1.247	3.786	**0.001**
ST - GC	0.215	0.108	2.004	0.179	-0.084	0.064	-1.320	0.541	3.246	1.247	2.604	**0.043**
SC - GT	0.269	0.108	2.501	0.057	-0.107	0.064	-1.673	0.329	-0.033	1.247	-0.027	1.000
ST - GT	0.292	0.108	2.717	**0.032**	0.329	0.064	5.145	**0.000**	-1.506	1.247	-1.208	0.611
ST - SC	0.023	0.078	0.296	0.991	0.435	0.048	9.036	**0.000**	-1.472	0.912	-1.614	0.360

Figure 3.1. Pretreatment analysis of total soil carbon and nitrogen in creosotebush shrubland and desert grassland (P = <0.0001 for both C and N).

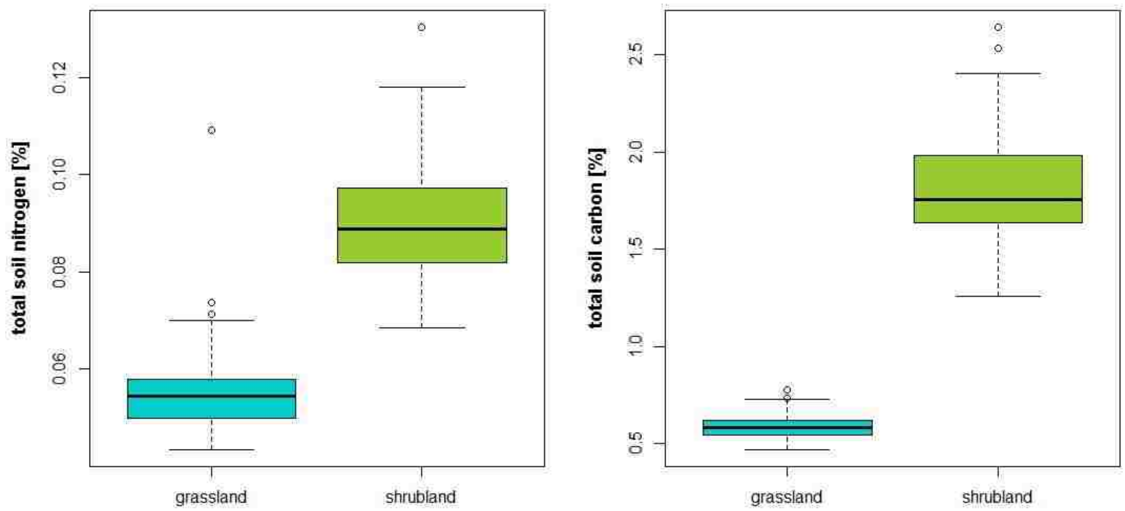


Figure 3.2. Daily volumetric water content (VWC) and monthly precipitation in desert grassland and creosotebush shrubland from 2014-2016.

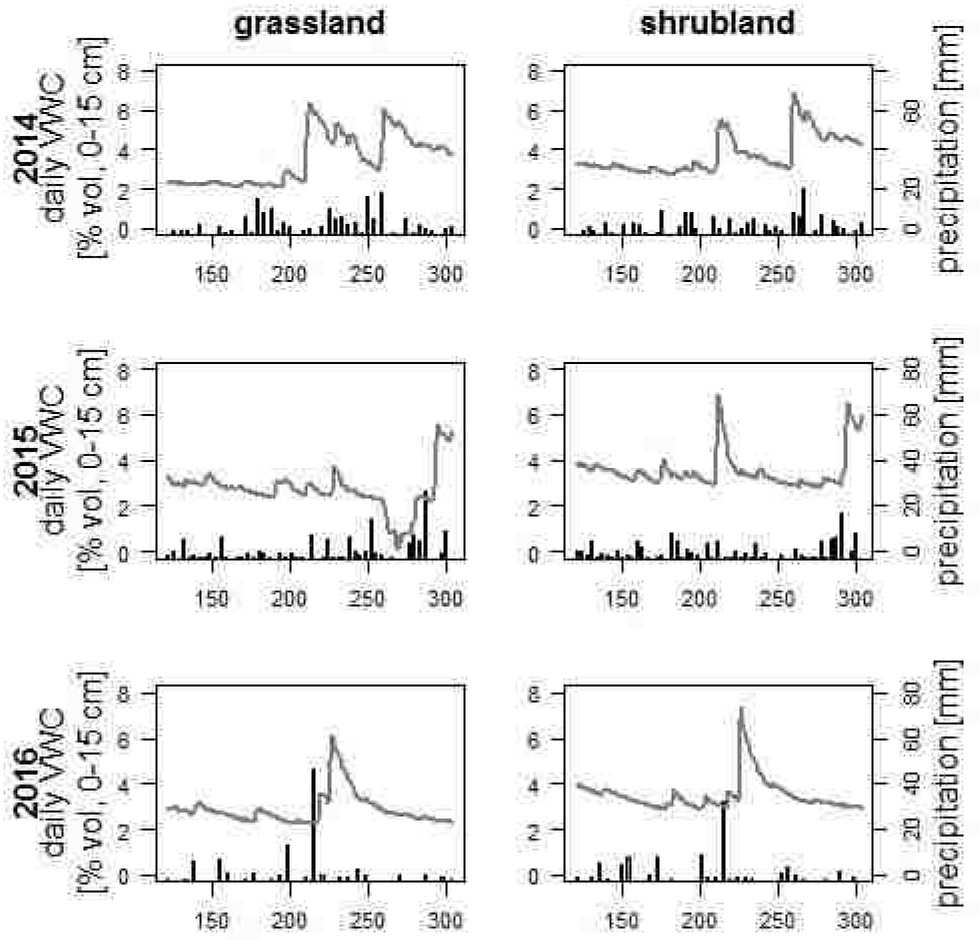


Figure 3.3. Carbon dioxide efflux control and treatment monthly averages for encroachment and reciprocal monoliths from 2014-2016. Variance is in standard error. Asterisks indicate significance for that month.

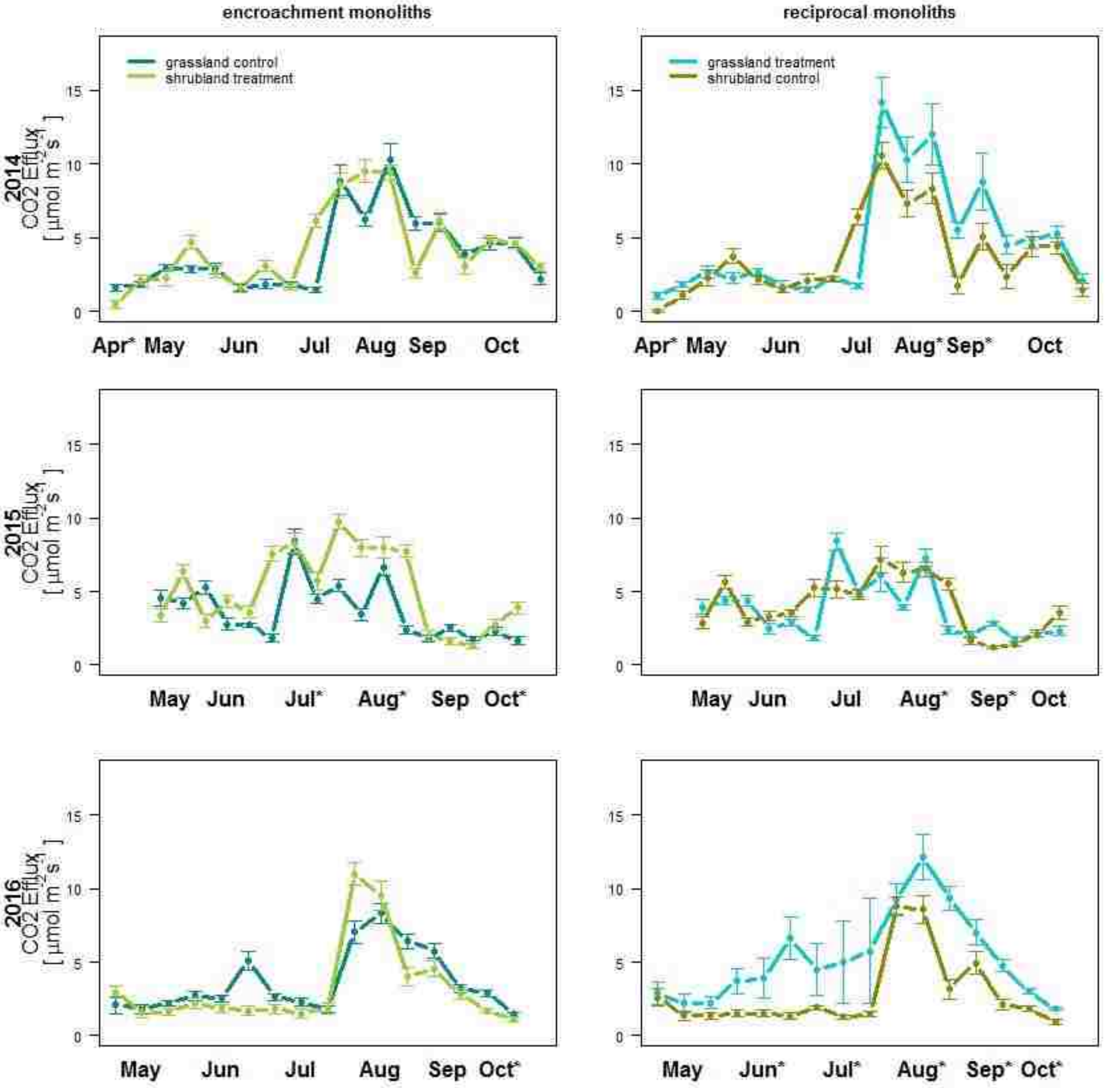
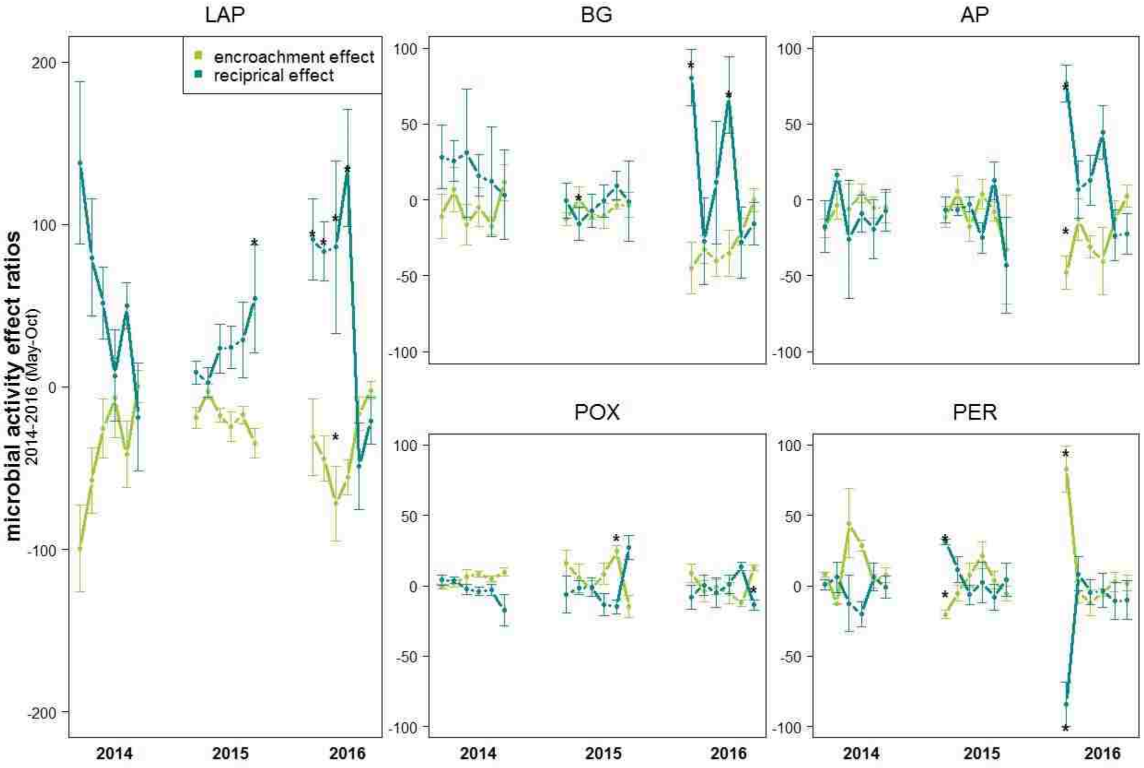


Figure 3.4. Mean monthly extracellular enzyme activities (EEA) effect ratios during the growing season for encroachment and reciprocal treatments from 2014-2016. Encroachment effect is EEA values of grassland monoliths moved into creosotebush shrubland (G->S) subtracted from the grassland control values (G->G). Reciprocal effect is EEA values of shrubland monoliths into grassland (S->G) subtracted from the shrubland control values (S->S). Extracellular enzyme activities are proximate measures of microbial decomposition of nitrogen (LAP), carbon (BG), phosphorous (AP) in soil. Phenol oxidase (POX) and peroxidase (PER) activities estimate lignin synthesis and degradation. Variance is in standard error. Asterisks indicate a significant effect for that month.



CONCLUSION

In this dissertation, cross-taxa comparisons in community change in mesic and semiarid grasslands were measured to assess the variation in long-term community responses to environmental presses. Further, to examine the community response of one community to a particular abiotic driver, the effects of long-term precipitation variability on a tallgrass prairie community was analyzed. Then, to determine how community change influences ecological process, the effects of shrub encroachment on soil respiration and microbial enzyme activity in semiarid grassland were examined.

Producer and consumer communities are changing over time in response to shrub encroachment and fire frequency. Chihuahuan Desert grassland and shrubland plant and breeding bird communities were undergoing different rates of directional change between sites, while grasshopper and small mammal communities were stable. Changes in grassland are being driven by higher interannual climate variability with increasing aridity, favoring black grama over blue grama (Collins and Xia 2015). Changes in shrubland are driven by the encroachment of creosotebush which outcompetes grass and forb species, reducing their richness and cover (Báez et al. 2007). Mesic tallgrass prairie vegetation, grasshopper and small mammal communities were undergoing variable rates of directional change under different fire frequencies. The frequency of disturbance by fire is known to regulate vegetation dynamics which forces the reordering of the dominate grass species (Collins and Calabrese 2012). Despite directional change, species richness of all communities was highly stable and varied within a narrow range of variation. This occurred because directional change was primarily driven by changes in abundances of species already in the community, rather than turnover in species composition. Alterations of species abundances and community composition are likely to continue under global environmental change and species abundance rather than richness will be a better indicator of future community change.

Increasing the size of rainfall events while reducing the number of events resulted in relatively limited changes in plant community composition and structure in annually burned, ungrazed, tallgrass prairie. Grass cover remained relatively stable over time. Though grass richness was higher on average in treatment plots and higher levels of forb cover and richness eventually occurred. This ultimately led to significantly different species assemblages under the altered precipitation regime. This lagged response is consistent with the temporal hierarchy of ecological responses to chronic changes in resource availability predicted by the Hierarchical Response Framework (Smith et al. 2009). Again, differences resulted from changes in abundance of species already present in the plots, rather than in new species establishing in the community. Thus, this mesic tallgrass prairie is an example of an ecosystem that is both resistant to long-term changes in precipitation variability via resistance of the dominant grass species, and resilient to short-term extremes through species reordering.

In this shrub encroachment experiment, we found much resilience in respiration and microbial activity from the effects of shrub encroachment. Both soil respiration and microbial activity were highly correlated with soil moisture availability. We found a greater response in soil respiration in plant-soil monoliths moved from under creosotebush canopies into desert grassland, with transplanted monoliths having higher respiration compared to control monoliths. This effect was driven by the timing of water availability directly and microbial activity indirectly by increases both autotrophic and heterotrophic access to carbon and nitrogen substrates (Belnap et al. 2005, Bardgett et al. 2005). Grassland soils were less responsive to treatment effects and when moved into shrubland, continuing to respond like control monoliths, suggesting grassland soils will be resistant to changes in carbon cycling under shrub encroachment. Microbial enzyme response by monoliths moved from grassland to shrubland was greater than monoliths moved from shrubland to grassland. Shrubland monoliths had higher LAP, BG and AP activities, and responded more like soils from which they originated. The amount and ratio of enzymes remained relatively stable in both grassland and shrubland soil. This also suggests that, at least in the short term, these soils are resistant to abiotic changes and potentially resilient to future environmental presses such as shrub encroachment.

Grassland communities are changing in response to chronic alterations in resource availability in soil moisture, fire frequency and shrub encroachment. Specifically, there is a reordering of species abundances over time, this being a mechanism for stability through population asynchrony or species compensatory dynamics in which trade-offs in species abundances stabilize the overall community (Hector et al. 2010, Hallett et al. 2014). When community composition is altered such as when grasslands transition into shrubland, soil respiration responds via microbial facilitated nutrient availability, but will lag behind changes in composition. Studying how communities respond to disturbances and long-term changes in resource variability is important because changes in composition dynamics can alter ecological processes.

APPENDIX A

CHAPTER 1 SUPPLIMENTARY MATERIAL

Table S1.1. Summary of long-term community datasets used to compare across taxonomic groups.

	Taxa	Sampling time range	Years sampled	Sampling dimensions	*n*
Sevilleta	black grama grassland	1989 - 2013	25	400-m transect	1
Sevilleta	creosote shrubland	1999 - 2013	15	1-m^2 plots	64
Sevilleta	grasshoppers	1992 - 2013	22	100-m transects	30
Sevilleta	small mammals	1989 - 2013	25	100-m transect web with 144 traps	3
Sevilleta	birds	1997- 2013	17	24.5 mile transect	1
Konza	tallgrass prairie	1984 - 2011	28	circular 10-m2	20
Konza	grasshoppers	1982 - 1991, 1996 - 2008, 2010	24	arc transect 20 sweeps	20
Konza	small mammals	1981-83, 85-86, 88-89, 91-92, 94-95, 97-98, 00-01, 03-04, 06-07, 09-10, 2012	22	2 transects with 20 traps every 15-m	40
Konza	birds	1981 - 2000, 2005 -2008	24	100-m transect	1

Figure S1.1. Time-lag analysis of vegetation, grasshopper, small mammal and breeding bird communities for black grama grassland and creosotebush shrubland sites at the Sevilleta NWR using presence-absence data. Time-lag analysis depicts the temporal rate of change in community composition by plotting similarity of community samples, using Euclidean distance, at increasing time lags. Insets include linear regression equation and significance values. Presence-absence data shows no directional community change, indicating that relative differences in abundance are important in driving community change.

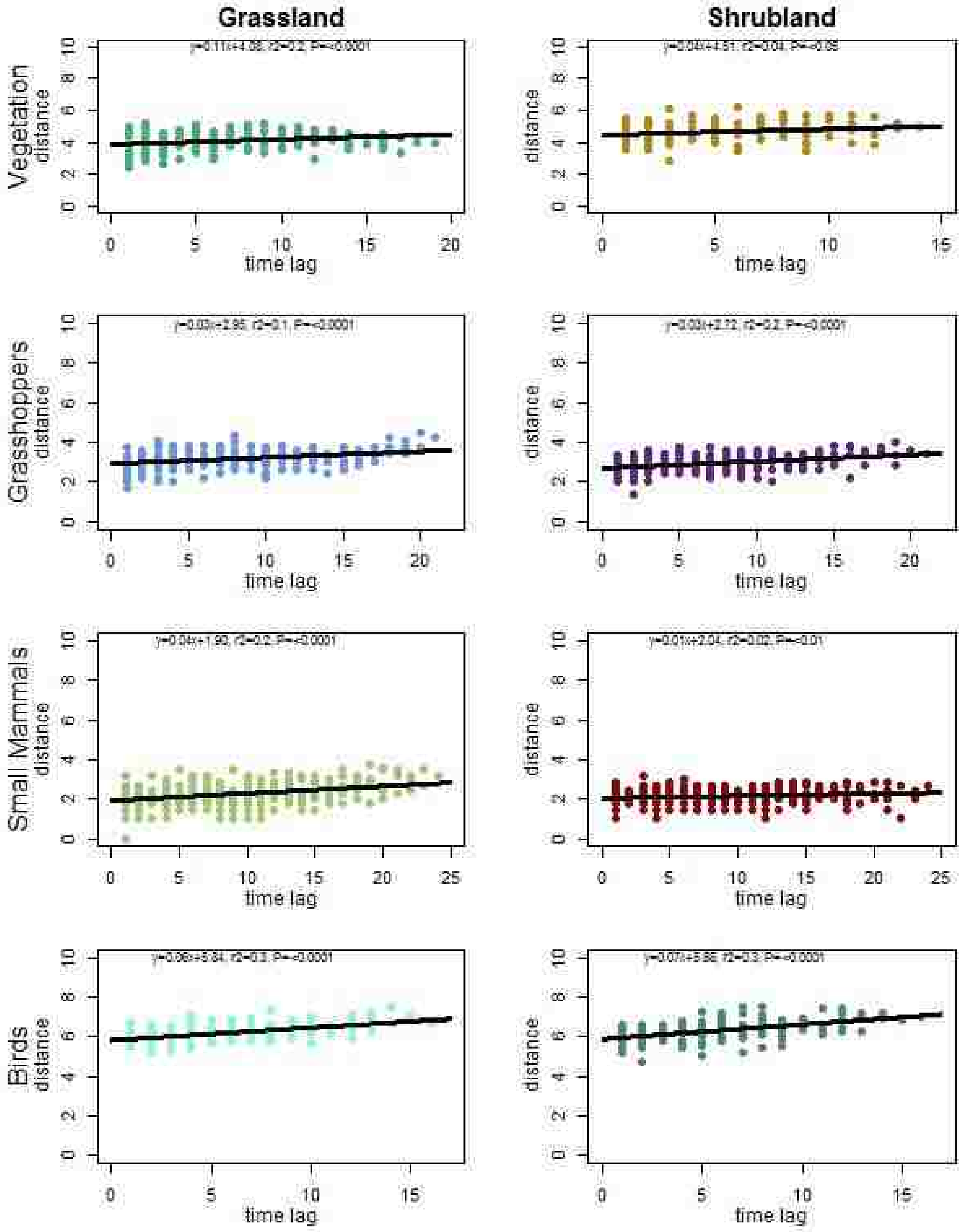
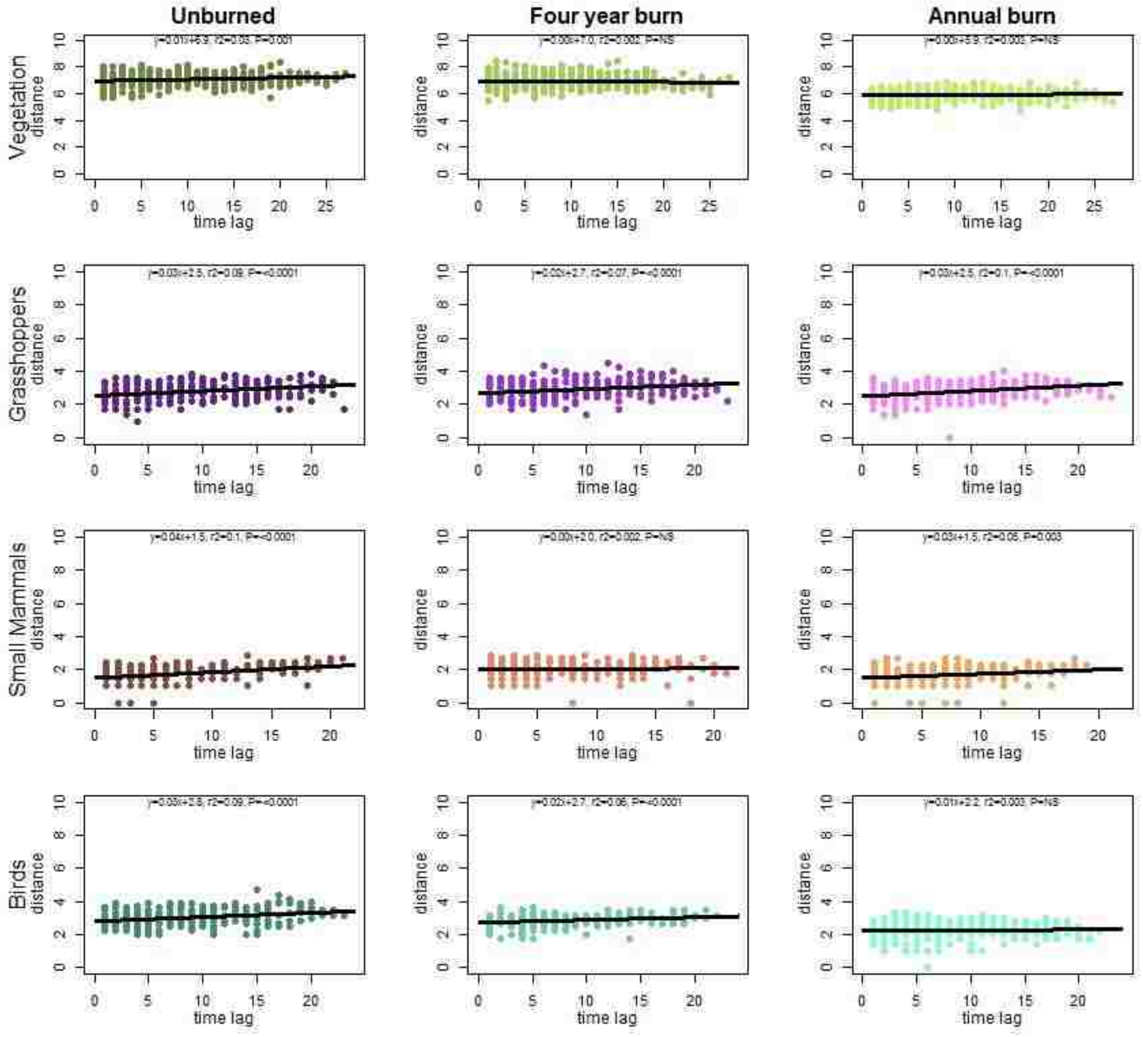


Figure S1.2. Time-lag analysis of vegetation, grasshopper, small mammal and breeding bird communities for unburned, four-yr burn and annually burned tallgrass prairie sites at Konza Prairie Biological Station using presence-absence data. Time-lag analysis depicts the temporal rate of change in community composition by plotting similarity of community samples, using Euclidean distance, at increasing time lags. Insets include linear regression equation and significance values. Presence-absence data shows no directional community change, indicating that relative differences in abundance are important in driving community change.



APPENDIX B

CHAPTER 2 SUPPLIMENTARY MATERIAL

Table S2.1. Correlation statistics of forb richness against precipitation and SWC parameters.

	total seasonal rainfall	
	r^2	P
ambient	0.05	0.4405
altered	0.02	0.6186
	avg. days between events	
	r^2	P
ambient	0.10	0.2532
altered	0.10	0.2591
	avg. seasonal SWC	
	r^2	P
ambient	0.42	0.0127
altered	0.20	0.1054
	SWC CV	
	r^2	P
ambient	0.21	0.1027
altered	0.22	0.0904

Figure S2.1. Growing season mean soil water content (**a**; % volume water content at 0-15 cm) between ambient and altered treatments (fewer, larger rain events), and ambient total growing season rainfall (**b**; mm) between 1997 to 2012. Error bars denote one standard error. Reference lines correspond to the mean annual precipitation for all 15 years. Soil water content was significantly lower in altered treatments compared to ambient during the growing season (*P* = < 0.0001).

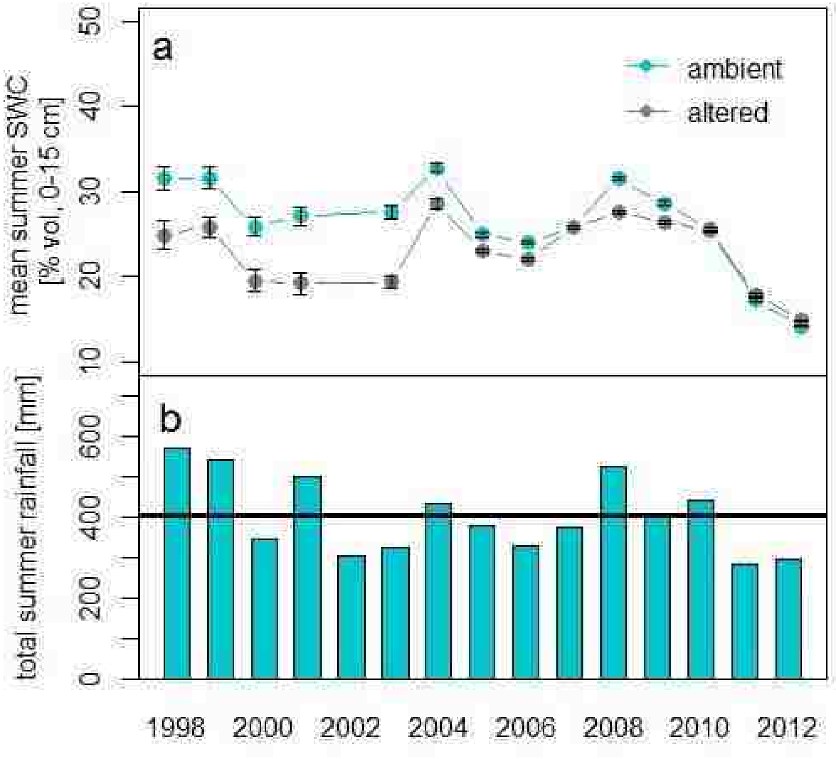
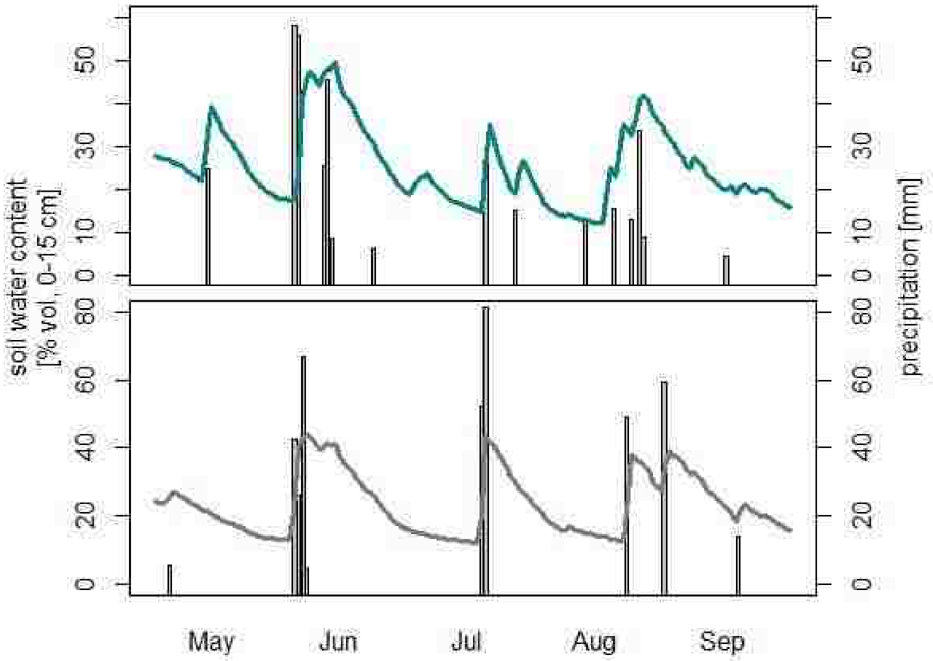


Figure S2.2. Within season soil water content (% soil water content at 0-15 cm) and precipitation by event (mm) during the 2005 growing season. Ambient treatment is shown in the top panel and altered treatment (fewer, larger rain events) in the bottom panel. Soil water content (SWC) is represented by the bold colored line, and precipitation, represented by gray bars, is shown by rain event frequency and amount. Maximum SWC was lower by 6%, and the number of days with low SWC was greater by 79% in the altered treatment compared to ambient. Over the growing season, the average deviation from ambient was 1.7%.



APPENDIX C

CHAPTER 3 SUPPLIMENTARY MATERIAL

Figure S3.1. Volumetric water content verses carbon dioxide efflux in desert grassland and creosotebush shrubland. Slopes between grassland treatment and shrubland control (i.e. reciprocal encroachment effect) and between grassland and shrubland controls were significantly different (*P*=<0.000). Slopes between shrubland treatment and grassland control (i.e. encroachment effect) was not significantly different (*P*=0.146).

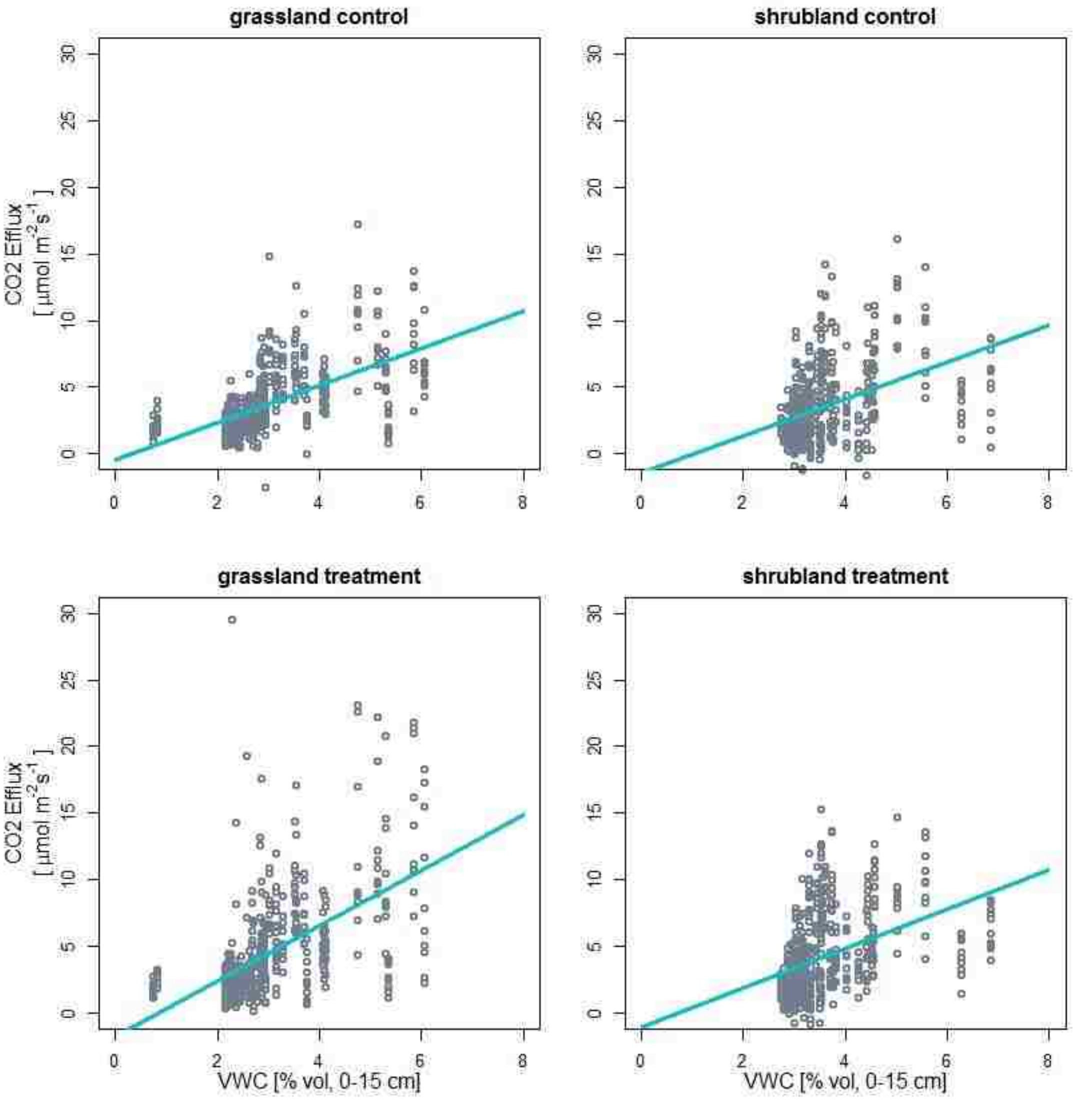


Figure S3.2. 2014 growing season extracellular enzyme activity between encroachment and reciprocal treatment and control monoliths. Hydrolase enzymes activities estimate nitrogen (LAP), carbon (BG), phosphorous (AP) availability in soil. Oxidative enzymes phenol oxidase (POX) and peroxidase (PER) estimate lignin availability. Controls are grass-soil monoliths excavated and reinstalled at respective sites. Encroachment monoliths include the shrubland treatments, grassland monoliths installed in creosote shrubland. Reciprocal monoliths include the grassland treatments, shrubland monoliths installed in blue grama grassland.

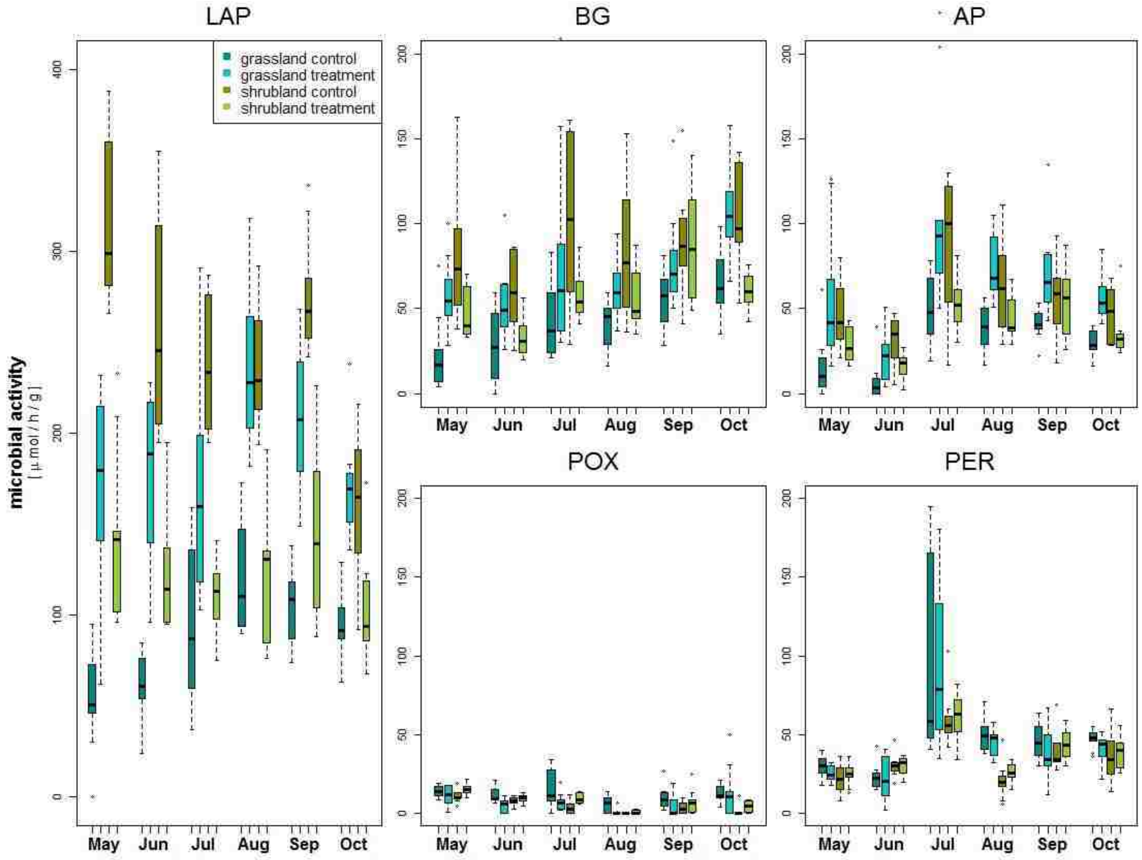


Figure S3.3. 2015 growing season extracellular enzyme activity between encroachment and reciprocal treatment and control monoliths. Hydrolase enzymes activities estimate nitrogen (LAP), carbon (BG), phosphorous (AP) availability in soil. Oxidative enzymes phenol oxidase (POX) and peroxidase (PER) estimate lignin availability. Controls are grass-soil monoliths excavated and reinstalled at respective sites. Encroachment monoliths include the shrubland treatments, grassland monoliths installed in creosote shrubland. Reciprocal monoliths include the grassland treatments, shrubland monoliths installed in blue grama grassland.

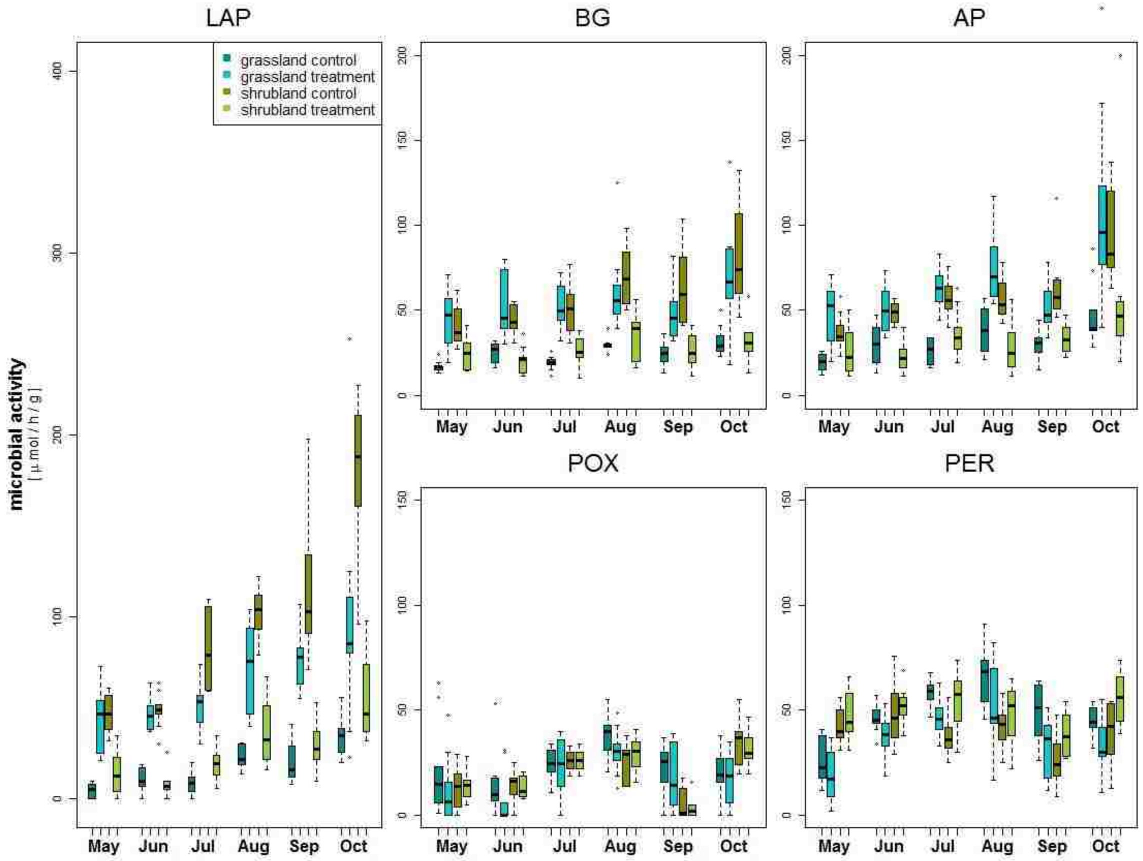
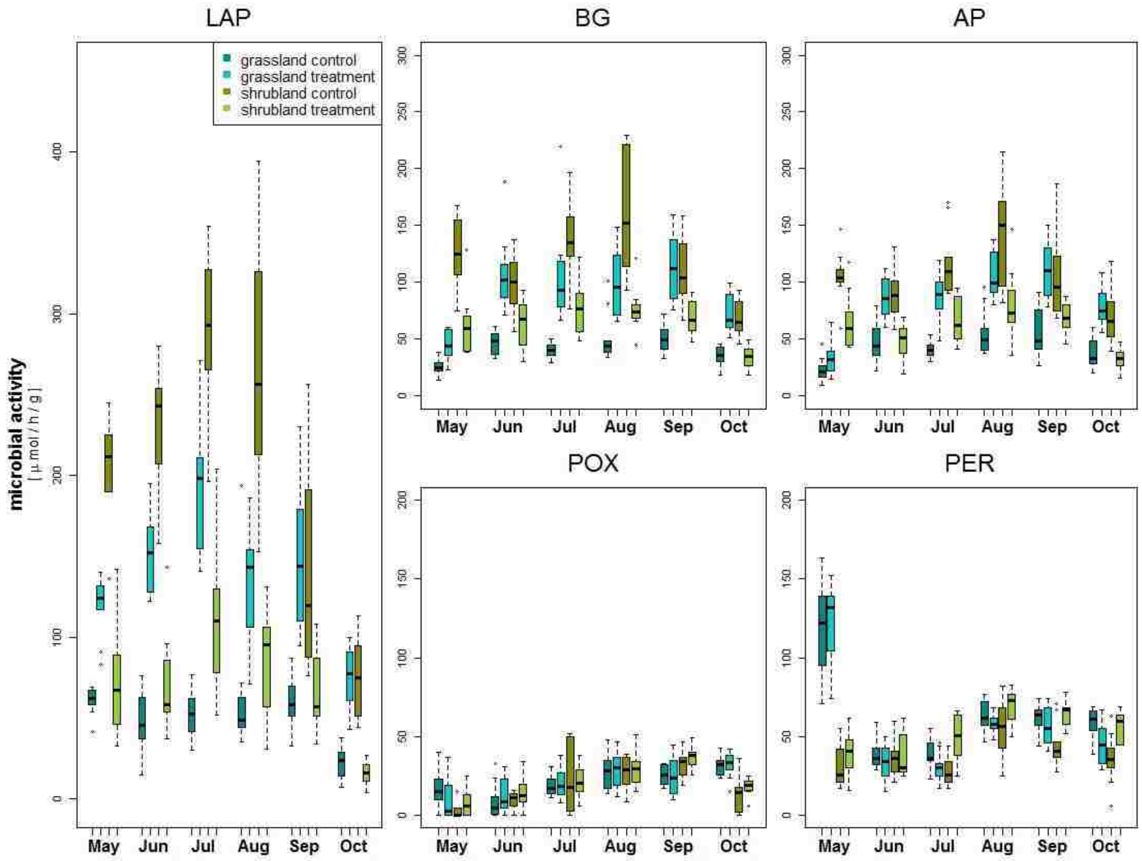


Figure S3.4. 2016 growing season extracellular enzyme activity between encroachment and reciprocal treatment and control monoliths. Hydrolase enzymes activities estimate nitrogen (LAP), carbon (BG), phosphorous (AP) availability in soil. Oxidative enzymes phenol oxidase (POX) and peroxidase (PER) estimate lignin availability. Controls are grass-soil monoliths excavated and reinstalled at respective sites. Encroachment monoliths include the shrubland treatments, grassland monoliths installed in creosote shrubland. Reciprocal monoliths include the grassland treatments, shrubland monoliths installed in blue grama grassland.



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