Role of spatial and temporal vegetation heterogeneity from fire-grazing interactions to the assembly of tallgrass prairie spider communities

by

Jesús Enrique Gómez

B.S., Universidad de Puerto Rico-Humacao, 2008

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Abstract

North American tallgrass prairie is a dynamic ecosystem that evolved with variable regimes of fire and grazing interactions (pyric herbivory), and variable mid-continental weather. Combined, these ecological factors create a shifting mosaic of plant communities that create heterogeneous and structurally complex habitats that move around across the landscape in time and space. The overarching goal of my dissertation was to study how bottom-up habitat templates created in response to fire-grazing interactions influence the community structure of spiders, key arthropod predators in grassland food-webs. Spiders are a ubiquitous and diverse group of terrestrial predators that partition their habitat at fine scales with species distributions and abundances that are sensitive to habitat structure. Primary hypotheses examined include: (H1) Spider density, species diversity, species evenness and functional richness of hunting strategies should increase as the spatial heterogeneity of habitat structure and overall habitat productivity increases, as predicted by the habitat complexity and heterogeneity hypothesis. (H2) Pyric herbivory indirectly determines spider community structure through is effect on vegetation structure and spatial heterogeneity, thereby promoting the formation of a mosaic of spider species assemblages that track changes in the distribution of key habitat resources. My research takes advantage of a long-term, watershed-level manipulations of fire frequency and bison grazing across a topographically variable landscape at Kansas State University's Konza Prairie Biological Station, a tallgrass prairie research site near Manhattan KS. Spider communities were sampled for three years at 23 sites representative of multiple habitat types ranging from low-stature grass-dominated sites to grassland-gallery forest transition zones. In addition, a field experiment was performed to test the hypothesis that vegetation structure contributes directly to web-builder abundance and web-type richness of spiders in open grasslands. Here, the availability of structure for web placement was increased by adding dead woody stems along transects in three watersheds that differed in burn histories and existing habitat structure in the absence of grazing. Results were consistent with the three key hypotheses. Species diversity and the functional diversity of spiders increased as the spatial heterogeneity and overall structure of habitat increased in response to fire-grazing interactions. Vegetation heterogeneity influenced spider community responses most strongly in the summer. Structural complexity of vegetation influenced spider diversity, species evenness and richness of hunting strategies throughout the growing season, becoming most important by the end of the growing season. The transitional ecotone between grasslands and woodlands supported a hotspot for spider density, species diversity and richness of hunting strategies along vegetation gradients (H1), and among habitat types (H2). Increasing the availability of web-anchoring structures in open grasslands led to increased web-builder density in open grassland, particularly for small and medium sized orb-web species that took advantage of increased physical structure. Disturbance from pyric herbivory indirectly promoted dynamic and malleable assemblages of spider species that coexisted in syntopy through effects on vegetation structure and its availability in time and space. Changes in habitat structure and heterogeneity as spatially and temporally shifting mosaics of habitat type increased the overall spider diversity at the landscape scale.

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Approved by:

Major Professor
Dr. Anthony Joern

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Table 5-2. Konza Prairie Biological Station spider community species list collected between summers 2011-2014. Spider species were described to the lowest taxonomic level possible (Family to species); specimens classified as unknown were either not well developed specimens tore were damaged during collection so they could not be properly identified. Each spider species received a unique numeric code (X##). Spider species were assigned to a hunting strategy based on general strategies used to capture prey known at the family level, or at the genus level if it diverged from the general strategy of the respective family. Furthermore. hunting strategy assignment was refined using literature references and field notes based on where in the vegetation a spider species was observed hunting. The Rank and Detection columns reflect the spider species collected across 23 sites using vacuum sampling from 2011-2013 at KPBS. Rank reflects how common a species was within the data sets used for Chapter 2 and Chapter 3 based or detection, not their density. The detection column shows how many times a spider species was present in a sample out of 131 samples collected across the 23 sites between 2011-2013. Since each species was counted as 0 or 1 for each sample, the maximum number of possible detections for a species was 131. 196

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Dedication

I dedicate my thesis to my parents Jesús A. Gómez and Juanita Carrasquillo and my sister Jenny M. Gómez who have shown unconditional support through my entire academic journey, beginning with the early days when I did not have a clear vision about what career path I take. Secondly, I will also dedicate this thesis to my nice Angelis Perez for being a source of inspiration to become a better person. Lastly, I will like to dedicate this thesis to the loving memory of my late-grandparents Alberto “Belto” Gómez, Daniel Carrasquillo and Damasia “Tomasita” Santana, whose early teachings and sayings helped shape my work ethic and relationship with my environment and natural communities since my childhood. Thanks to their unconditional support guidance and teachings through my I have could pursue my dreams and reach this goal and words are not sufficient to express how grateful I feel for their support but I hope I can help other has they gave help me.

Chapter 1 - Overview

It is increasingly evident that habitat heterogeneity promotes increased species diversity for many terrestrial communities (Tews et al. 2004, Allouche et al. 2012, Dennis et al. 1998, Moran 2014). At higher trophic levels, habitat is often key and the heterogeneity of habitat resources, including overall variability in plant architectural diversity, plant species composition and diversity, vegetation biomass, and the spatial distribution of vegetation resources in response to periodic disturbance are critical factors underlying the assembly of consumer communities (Diehl et al. 2013, Enders 1974, Halaj et al. 1998, 2000; Heikkinen et al. 2004, Robinson 1981). As a source of heterogeneity, disturbance often results in a shifting mosaic of habitat types arrayed across the landscape (Dennis et al. 1998, Fuhlendorf & Engle 2001, Fuhlendorf et al. 2006), which then influence the distribution and abundance of consumers. Not only is overall species diversity or the taxonomic composition of communities responding to habitat variability in time and space, but functional traits that match key habitat attributes across the landscape may also vary (Fuhlendorf & Engle 2001, Tews et al. 2004, Bonte et al. 2000, Fuhlendorf & Engle 2001, 2004; Joern 2005). In many cases, functional responses to habitat variability mediate ecosystem services provided by those communities; control and regulation of herbivore populations by natural enemies is one such example of an important ecosystem service. A primary goal of this study was to gain understanding about how spatially and temporally variable habitat complexity and heterogeneity affects the density, species diversity, species evenness, and richness of functional groups along gradients of key habitat resources for spider communities, a critically important grassland predator.

Grassland communities evolved with and respond to dynamic interactions between fire, grazing, and a variable climate, system-level drivers that underlie the origin, maintenance and function of grassland ecosystems (Anderson 2006, Archibald et. al. 2005, Bond & Keeley 2005, Gill et al. 2009, Knapp & Seastedt 1998). In particular, fire-grazing interactions (pyric herbivory) lead to spatially heterogeneous plant communities and ultimately provide multiple habitat options for consumers because of interactive effects on vegetation structure that vary in time and space (Fuhlendorf & Engle 2004, Fuhlendorf et al. 2009, Hartnett et al. 1996, Moran 2014, Tews et al. 2004, Vinton et al. 1993). Disturbance from fire-grazing interactions in grasslands moves around the landscape over time, resulting in a mosaic of vegetation states where each patch differs in the availability of key habitat resources for specific consumers. Resulting spatial mosaics of habitats alter the distribution of Southwood's habitat templates (Southwood 1988), thus affecting community assembly of consumers (Tews et al. 2004, Allouche et al. 2012). A shifting mosaic view of habitat availability (Levin and Paine 1974, Borman and Likens 1979, Fuhlendorf & Engle 2004, Pacheco & Vasconcelos 2012) is key for this study, where I sought to determine the degree to which spider assemblages track habitat patches that vary in response to periodic disturbance from fire and grazing as modified by variable weather and topography (Fig 1.1).

Spiders are ubiquitous and diverse predators in grasslands, where they can reach high abundance, local species diversity, and richness of hunting strategies (Diel et al. 2013, Schmitz & Suttle 2001, Wise 2006, Sebastian et al. 2005), each contributing to the important ecosystem service they provide. Within arthropod food webs, spiders are generalist predators that eat a wide range of invertebrate prey and are capable of subduing prey larger than their own body size/mass; prey selection is often size- rather than taxon-dependent (Nyffeler 1999, Riechert & Lockley 1984, Wise & Crawford 1994). Spider predation can regulate arthropod prey populations, and as generalist predators, spiders participate in wide ranging species interactions (especially competition and predation), or cause trait-mediated indirect interactions by prey populations that lead to trophic cascades (Denno et al. 2004, Hodge 1999, Laws and Joern 2013, Wise 2006). The complexity of habitat structure facilitates resource partitioning among species, by reducing the strength of inter/intra-specific interactions and by providing refuges to spiders for predator avoidance, and modulates microclimate. Spiders show diverse hunting strategies and feeding guilds, exhibit a wide range of body sizes and morphological variability, and spiders often partition their habitat at fine spatial scales to best exploit particular hunting locations and prey availability (Schmitz & Suttle 2001, Wise 2006). Spiders are also potential prey for vertebrate predators that can suppress spider population abundances and alter how spiders interact with their invertebrate prey (Gunnarsson 1983, 2007; Schoener & Spiller 1996, Wise & Crawford 1994). Ultimately, habitat structural heterogeneity mediated by critical habitat attributes (overall vegetation architecture and plant diversity) potentially influences the spatial distribution and abundance of arthropod species, via different foraging and competitive needs. Combined, these interactions alter the complexity of consumer assemblages at multiple spatial and temporal scales, and affect overall community diversity at the landscape level (Jones & Syms 1998, Sebastian et al. 2005, Dennis et al. 1998, Fuhlendorf & Engle 2001, Fuhlendorf et al. 2006, Jimenez-Valverde & Lobo 2007, Allouche et al. 2012). For these reasons, spiders provide an ideal ecological model for investigating how the spatial and vertical complexity of vegetation in response to fire and grazing disturbances promotes increased consumer diversity at the landscape scale.

Pyric Herbivory, Habitat Heterogeneity, and Spider Community Assembly

In my field study, variable, large-scale controlled disturbances from fire and grazing are imposed on tallgrass prairie in an experimental framework at Konza Prairie Biological Station (KPBS) to understand how pyric herbivory affects consumer communities. Here I examined how spider communities were mediated by vegetation attributes (Fig. 1.1). Recent fire affects plant growth and forage nutritional quality, in turn attracting grazing herbivores to recently burned patches throughout the landscape (Archibald et al. 2005, Bond & Keeley 2005, Fuhlendorf & Engle 2004, Fuhlendorf et al. 2009, Raynor et al. 2015, Raynor et al. 2016). Ungulate grazers, including North American plains bison (*Bison bison)*, significantly alter habitat structure and enhance spatial heterogeneity directly and indirectly through selective feeding, wallowing, and nutrient redistribution in the form of dung and urine (Vinton et al. 1993, Hartnett et al. 1996, Collins & Smith 2006, Fuhlendorf et al. 2009). Spatially explicit patterns of grazing intensity influence subsequent movement of fire through the landscape as a consequence of reduced fuel accumulation in grazed areas, and repeated grazing facilitates the development of increased forb diversity of local plant communities (Archibald et al. 2005, Moran 2014). Additionally, reduced fire frequency or intensity promotes increased woody vegetation cover shifts in plant species diversity, and alters the physical nature of vegetation structural complexity (Knight et al. 1994).

The outcome of the dynamic interactions of pyric-herbivory in combination with weather variability and topography leads to a patchwork of vegetation states interspersed in space that varies over time (Collins & Smith 2006). Shifting mosaic models of habitats are appropriate ways to view the problem when new patches are created by disturbance, mature through succession, and then progress through a sequence of different states until reset by the next disturbance event (Bormann and Liken 1979, Fuhlendorf & Engle 2004). However, one also expects that the specific location of different patch types will move around in space over time, reflecting recent disturbance history. Shifting mosaic dynamics then promote habitat heterogeneity, and one expects that the spatial distributions of consumer assemblages with strong affinities for specific habitats types should also track this habitat mosaic (Fuhlendorf & Engle 2004, Halaj et al. 1998, Heikkinen et al. 2004). Such non-trophic responses mediated by habitat-based plant structure/ architecture and spatial variability provide a predictive “bottom-up template” for understanding community assemblages at higher trophic levels (Southwood 1988, Halaj et al. 2000) from both a vegetation (structure and heterogeneity) gradient and a shifting-mosaic of habitat point of view. In each of the above cases, it is expected that biological diversity will increase at multiple trophic levels with increasing spatial and temporal heterogeneity, including responses by predator communities that only use vegetation as habitat.

Objectives and Hypotheses

The primary goal of my dissertation was to better understand how habitat structure and accompanying spatial heterogeneity, as mediated through vegetation attributes that are driven by fire and grazing interactions, influence spider community responses (a) along gradients of vegetation structure and heterogeneity (Chapter 2), (b) with respect to a shifting mosaic of vegetation communities that varies in time and space (Chapter 3), and (c) with respect to the distribution of a key woody structure (Chapter 4). To address these goals, I used spider communities as an ecological model representative of taxonomically and functionally diverse predator assemblages, and as a predator group that is critically important in grasslands. My field studies were conducted at Konza Prairie Biological Station (KPBS), where I took advantage of the long-term fire frequency (1, 2, 4 and 20 yr) and bison-grazing management treatments applied at the watershed level. I sampled spider assemblages and characterized the vegetation structure and its heterogeneity across a wide range of habitat types found at KPBS in response to the long-term fire and grazing management. In my study, I addressed three primary hypotheses: (1) the habitat complexity and heterogeneity hypothesis predicts that increases in key habitat resources (vegetation structural complexity and spatial heterogeneity) will lead to increased density, species diversity, species evenness, and richness of functional groups of spiders along key habitat gradients that are spatially and temporally reorganized across the landscape after disturbance events; and (2) the shifting mosaic hypothesis that focuses on the taxonomic composition of local spider assemblies across the landscape, which predicts that local spider assemblages track specific habitats within a spatio-temporal shifting mosaic of habitat types; i.e., the taxonomic composition of local assemblages reflects the habitat templet, reflecting the combined autecology of individuals and species interactions. The shifting mosaic view of habitat availability is key for organizing ideas in this portion of my study, where I seek to determine the degree to which identifiable spider assemblages can track habitat patches that vary with vegetation structure and heterogeneity attributes. (3) Last, I examine the broader hypothesis that influences outcomes of the first two hypotheses, where pyric herbivory is central to understanding spider communities at KPBS and probably in grasslands more broadly. The hypothesis proposes that pyric herbivory acts on spider communities indirectly through its influence on vegetation attributes (Fig 1.1).

Finally, I expect results from this thesis will be helpful in guiding habitat management decisions for grazed grassland, for grassland habitat restoration, and for cultivated crop systems such as small-scale grain operations because spiders are critically important arthropod predators in these habitats (Wise 1995, 2006; Benton et al. 2012, Weibull et al. 2000). Hopefully, lessons from this thesis, especially the need to promote habitat heterogeneity can be extended and generalized to improve habitat availability for other species as they cope with human impacted environments (Pacheco & Vasconcelos 2012, Tews et al. 2004).

Here I outline the primary approaches of my three dissertation chapters.

Chapter 2: Spider community response to increases in vegetation structure and heterogeneity driven by fire and grazing interactions

An overarching hypothesis here is that the overall abundance and species diversity of consumer communities increases with increasing spatial heterogeneity of critical habitat attributes, including the overall variability in vegetation architecture and plant species diversity (Dennis et al. 1998; Fuhlendorf & Engle 2001; Fuhlendorf et al. 2006; Jimenez-Valverde & Lobo 2007; Allouche et al. 2012). At KPBS, long-term manipulations of fire frequency and bison grazing applied at watershed scales as part of a long term experimental study-design resulted in a wide range of habitat types within the KPBS landscape. As such, the experimental landscape at KPBS sustains a broad range of ecological gradients of vegetation structure and heterogeneity required for evaluating the habitat complexity and heterogeneity hypothesis. To address this hypothesis, I first characterized the direct effects of fire and grazing on vegetation responses; then I characterized the direct responses to gradients of vegetation structure and heterogeneity. Finally I linked fire and grazing mediated responses to the structure of a grassland spider community using structural equation modeling.

Part A: Characterization of the vegetation community

In terrestrial ecosystems, the spatial and temporal distribution of plant species (including their abundance) across the landscape is influenced by the interactions among fire, grazing and climate (disturbances) that operate at different spatial and temporal scales. These interactions determine the spatial and temporal heterogeneity of vegetation structure, which in turn affects community assembly at higher trophic levels – spiders in this case. The critical vegetation template underlying spider distributions at KPBS was characterized using Akaike Information criteria (AICc) to assess how fire, grazing, precipitation, topographic position, and habitat type influenced gradients of vegetation structure and heterogeneity across KPBS. Vegetation structure was described as median vegetation height (cm), number of vegetation layers and canopy closure. Spatial heterogeneity of vegetation was described as the coefficient of variability (CV) for the median vegetation height and canopy closure.

Part B: Spider responses to vegetation structure and heterogeneity.

The habitat complexity and heterogeneity hypothesis predicts that increases in key habitat resources (vegetation structural complexity and spatial heterogeneity) will lead to increased density, species diversity, species evenness, and richness of hunting strategies of a grassland spider community. I tested the following predictions of the hypothesis:

(1) Spider density, species diversity, species evenness, and richness of hunting strategies of coexisting taxa will be positively related to increases in habitat secondary productivity (insect biomass) and the spatial heterogeneity of vegetation-structure.

(2) Increased insect biomass in response to increased vegetation structure and heterogeneity should promote increased grassland spider density, species diversity, species evenness, and richness of hunting strategies.

(3) The synergistic effects of fire and grazing disturbances across a steep sloped landscape subject to variable weather indirectly structure spider community complexity. Spider density, species diversity, species evenness, and richness of hunting strategies along gradients of habitat complexity and heterogeneity are mediated through direct effects of pyric herbivory on vegetation vertical and horizontal structural complexity and spatial heterogeneity.

Chapter 3: Spider community assembly response to a shifting mosaic of grassland habitat types driven by abiotic and biotic disturbance interactions.

Pyric herbivory drives grassland habitat variability in time and space, resulting in vegetation structure that underlies the spatial and temporal patterns of consumer diversity across the landscape at both the taxonomic and functional levels (Bonte et al. 2000, Fuhlendorf & Engle 2001, 2004; Joern 2005, Tews et al. 2004). Consumer meta-communities potentially track dynamic systems of interconnected habitat patches, where the abundance and distribution of species changes over time across the landscape (Sousa 1984; Levin and Paine 1974, Carmona et al. 2012). To address this hypothesis, I studied how the taxonomic assembly of local spider communities changed as habitats varied across the landscape in response to the effects of fire-bison grazing interactions on vegetation structure. I tested the following predicted relationships to understand how spider communities respond to a shifting habitat mosaic of vegetation structure and spatial-heterogeneity in tallgrass prairie at KPBS.

1. The taxonomic composition of local spider assemblages should track characteristic habitat structure as it varies in time and space in response to fire-grazing interactions. Unique spider assemblages (both taxonomically and functionally) will reflect specific vegetation characteristics.
2. In addition to effects on local species diversity (α-diversity), a shifting mosaic of spider assemblages should result over the growing season and across multiple years (Fig. 1.1), while leading to increased spider diversity at the landscape scale (*β*- and γ-diversity).

Chapter 4: Spider community response to availability of key-vegetation structure within grasslands.

Vegetation complexity, including the presence of woody vegetation, is recognized as an important factor influencing species presence, richness and composition of spider communities (Jimenez-Valverde & Lobo 2007). Microhabitat partitioning has been documented for web-building spiders, where webs differ in placement height, orientation, or type depending on vegetation structure (Enders 1974, Brown 1981, Schmitz & Suttle 2001, Wise 2006). Web placement most likely reflects food limitation, foraging efficiency and competitive interactions among species (Wise 1995, Wise 2006). Thus, understanding habitat characteristics that affect web placement can reveal whether and how the structural complexity of the habitat can modulate spider community assembly, species abundance and overall functional diversity (Robinson 1981, Jimenez-Valverde & Lobo 2007, Diehl et al. 2013).

My primary hypothesis in this chapter predicts that the availability of structure for web placement limits density, richness of web building species and web types, and the distribution of web-building spider guilds in open grassland. I performed a field experiment that added woody structure in grassland habitat with no woody stems to address:

> (1) how web density and web-type richness responded to the newly added structure for web anchoring (woody vegetation: manipulation) in open grasslands, and
>
> (2) how increasing the distance at which structure for web anchoring are available relative to riparian woodland edges affects web density and web-type richness.

Community responses to disturbance provide an excellent opportunity for addressing research objectives because spiders are both functionally important and also provide tractable research avenues for studying predator responses. A key challenge of addressing these types of questions with vertebrates is that native predators have been largely exterminated from large portions of their native range, resulting in novel arrangements of predator communities. Also, many vertebrate top-predators have large home ranges that may include multiple habitat types found over large distances making it difficult to address their responses to changes in habitat structure and heterogeneity, especially in an experimental setting. In this regard, arthropods are ideal study models due to their taxonomic and functional diversity, and overall abundance in natural systems that facilitate the ability to detect responses in a community to changes in the availability and distribution of key habitat resources in the landscape.

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FIGURES.

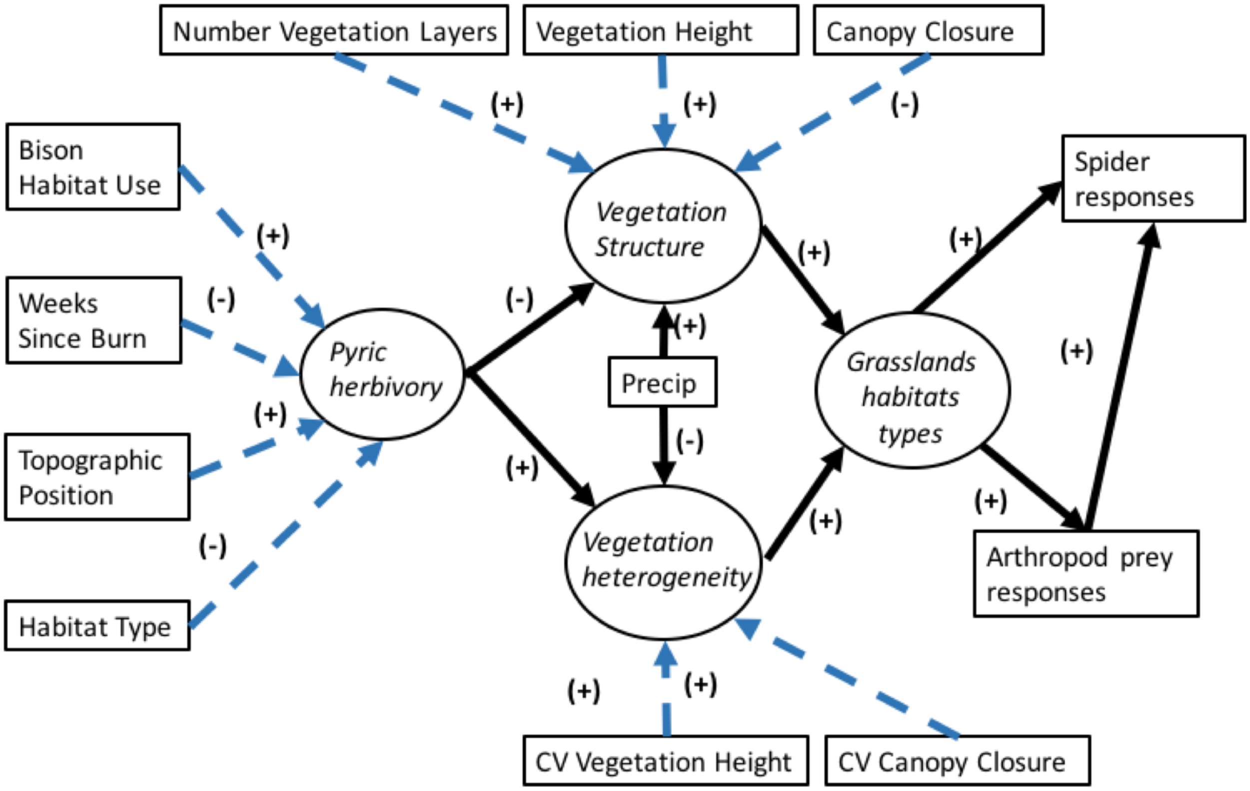

Figure 1-1 Conceptual framework for predictions of how the ecological driver *pyric herbivory* indirectly structures the richness of local spider assemblages within a spider grassland community in through its direct effects on vegetation structure and vegetation heterogeneity, which determine the diversity of grassland habitat types found by consumers. The conceptual framework was evaluated using the Structural Equation Modeling approach (SEM) and Redundancy Analysis. Boxes in the diagram represent loading factors: responses and predictor variables for which I have empirical measurements . Ellipses represent latent variables (SEM), variables inferred from other variables that represent the synergistic effects of loading factors on a ecological process/interaction. Dashed arrows show which predictor variables were used to infer each latent variable. +/- symbols indicate the expected relations among the loading factors and latent variables. Solid arrows show the interactions of interest with respect to key hypotheses. +/- symbols shows the expected interaction among predictor and responses interactions of interest in this model.

Chapter 2 - Disturbances from fire and grazing modulate tallgrass prairie spider communities through direct effects on vegetation structure and spatial heterogeneity

Abstract

North American grasslands are dynamic ecosystems that evolved under variable regimes of weather, fire and grazing disturbance, leading to spatially heterogeneous habitat structure across the landscape. In response, species abundances, diversity, and functional richness in consumer communities should increase as the spatial heterogeneity of habitat structure and overall habitat productivity increases, as predicted by the habitat complexity and heterogeneity hypothesis. My field study evaluates responses by spider assemblages to habitat in mesic tallgrass prairie managed experimentally with fire and ungulate grazing treatments applied at the landscape scale. Spiders are important terrestrial predators that partition their habitat at fine spatial and temporal scales, and where species distributions and abundances are sensitive to key habitat structure. The fire-grazing interaction indirectly affects spider community structure through direct effects on vegetation structure that promotes the formation of spatially heterogeneous, shifting gradients of vegetation structure (vegetation height, number of vegetation layers and canopy closure). Seasonally, spider diversity, species evenness, and richness of hunting strategies were higher in the late-summer than in early-summer samples. Vegetation heterogeneity influenced spider community responses most strongly in the summer. Structural complexity of vegetation influenced spider diversity, species evenness and richness of hunting strategies through the growing season, becoming most important by the end of the growing season. Spider diversity, species evenness, and richness of hunting strategies also responded positively to increases in overall prey productivity (insect biomass) in both early and late summer. In sum, spatial heterogeneity and the general structure of habitat in response to fire-grazing interactions increased species and functional diversity of spiders as predicted by the habitat complexity and heterogeneity hypothesis (HCHH).

Keywords: Konza Prairie Biological Station, spider, structural-heterogeneity/diversity hypothesis, vegetation structure, grasslands

Introduction

The habitat structural complexity and heterogeneity hypothesis (SCHH) predicts that the overall abundance, species diversity, and functional diversity of feeding/hunting strategies in consumer communities should increase with increasing total availability and spatial heterogeneity of critical habitat (Fuhlendorf et al. 2009, Fuhlendorf et al. 2010, McGranahan et al. 2012). For many arthropod consumers, heterogeneity of key habitat resources, including overall variability in plant architectural diversity, composition, density, biomass and variable spatial distribution of key vegetation resources, results in a mosaic of habitat types arrayed across the landscape (Dennis et al. 1998, Fuhlendorf & Engle 2001, Fuhlendorf et al. 2006). Such non-trophic responses by consumers mediated by habitat-based plant architecture and its spatial variability provide a predictive “bottom-up template” for understanding community assemblages at higher trophic levels (Southwood 1988, Halaj et al. 2000).

Fire prone ecosystems such as North American mesic tallgrass prairie integrate abiotic and biotic disturbances at multiple spatial and temporal scales (Knapp et al. 1998, Archibald et al. 2005, Fuhlendorf et al. 2009). In particular, fire and ungulate grazing interactions (pyric herbivory) act as critical ecological drivers (Bond & Keeley 2005, Fuhlendorf & Engle 2004, Fuhlendorf et al. 2009), resulting in spatially and temporally heterogeneous grassland dominated by non-woody vegetation. Patterns of species diversity at multiple trophic levels are mediated through vegetation architecture, its spatial heterogeneity, and structural complexity (Vinton et al.1993, Fuhlendorf & Engle 2004). Recent fire affects plant growth and forage nutritional quality, in turn attracting grazing herbivores to recently burned patches throughout the landscape (Archibald et al. 2005, Bond & Keeley 2005, Fuhlendorf & Engle 2004, Fuhlendorf et al. 2009, Raynor et al. 2015, Raynor et al. 2016). Ungulate grazers, including North American plains bison (*Bison bison)*, significantly alter habitat structure and enhance spatial heterogeneity directly and indirectly through selective feeding on warm season grasses, wallowing, and nutrient redistribution in the form of dung and urine (Vinton et al. 1993, Hartnett et al. 1996, Collins & Smith 2006, Fuhlendorf et al. 2009). Spatial patterns of grazing intensity influence subsequent movement of fire through the landscape as a consequence of reduced fuel accumulation in grazed areas, and facilitate the development of increased forb diversity of local plant communities (Archibald et al. 2005, Moran 2014). Additionally, reduced fire frequency and/or intensity promotes increased woody vegetation cover (Knight et al. 1994), shifts in plant species diversity, and alters the physical nature of vegetation structural complexity. Generally, pyric-herbivory at the landscape level promotes habitat structural diversity, leading to a spatially and temporally shifting mosaic of habitat types in response to positive feedbacks from fire-grazing interactions (Collins & Smith 2006). In turn, this variability increases opportunities for habitat partitioning and increased species diversity by consumers at fine scales (Sudhikumar et al. 2005, Malumbres et al. 2013).

Here, I examined the response of spider communities, a diverse and functionally important group of terrestrial arthropod predators, to the physical complexity and spatial variability of vegetation in response to disturbance from fire and grazing in a North American tallgrass prairie. Spiders are ubiquitous and diverse predators in grasslands, where they can reach high densities, local species diversity, with a range of hunting strategies (Diel et al. 2013, Schmitz & Suttle 2001, Wise 2006, Sebastian et al. 2005). As generalist predators, spiders participate in multiple species interactions (especially competition and predation), or cause trait-mediated indirect interactions by prey populations, often leading to trophic cascades (Denno et al. 2004, Hodge 1999, Laws and Joern 2013, Wise 2006). The complexity of habitat structure facilitates resource partitioning among species, reduces the strength of inter/intra-specific interactions, provides refuges to spiders for predator avoidance, and modulates microclimate. Spider feeding guilds include multiple active hunting, ambushing, and sedentary web-building foraging strategies, and spiders often partition their habitat at fine spatial scales to best exploit particular hunting locations and prey availability (Schmitz & Suttle 2001, Wise 2006). Ultimately, habitat structural heterogeneity mediated by critical habitat attributes of overall vegetation architecture and plant diversity potentially influences the spatial distribution and abundance of arthropod species including spiders at small scales to meet foraging and competitive needs. Heterogeneity alters consumer assemblage complexity at multiple spatial and temporal scales and overall community diversity at the landscape level (Jones & Syms 1998, Sebastian et al. 2005, Dennis et al. 1998, Fuhlendorf & Engle 2001, Fuhlendorf et al. 2006, Jimenez-Valverde & Lobo 2007, Allouche et al. 2012).

At a landscape scale, pyric herbivory creates a shifting-mosaic of key habitat resources for consumers in both time and space, providing a variable “bottom-up template” for community assembly. Grazing systems accompanied by fire are ideal for testing the habitat complexity and heterogeneity hypothesis for spiders (Southwood 1988, Halaj et al. 2000), a taxonomically and functionally diverse predator community. *The structural complexity and heterogeneity hypothesis (SCHH)) of the habitat* predicts that increases in key habitat resources (vegetation structural complexity and spatial heterogeneity) should lead to increased density, species diversity, species evenness, and richness of hunting strategies of a grassland spider community. Moreover, incremental increases in habitat structural complexity and heterogeneity may also increase secondary productivity (insect biomass), prey diversity, and abundance. *Increases in insect biomass should promote increased grassland spider density, species diversity, species evenness, and richness of hunting strategies.* I took advantage of unique, long-term experimental, landscape-level manipulations of fire frequency and bison grazing in mesic tallgrass prairie applied at the watershed level in a factorial experimental design at Konza Prairie Biological Station (KS: USA). Long-term manipulations created ecological gradients as required for evaluating the habitat SCHH. I tested the following predictions of the hypothesis: (1) spider density, species diversity, species evenness, and richness of hunting strategies of coexisting taxa should increase as habitat secondary productivity and the spatial heterogeneity of vegetation-structure increases. (2) Ecotonal grassland–woodland transitions commonly found along drainage basins or shrub islands will be hotspots of local spider species diversity and richness of hunting strategies. The transition zone contains the most heterogeneous and complex vegetation structure with increased vertical habitat layers above the grass and shrubs layers typical of open grassland habitats. I expected spider species typical of different habitat types would co-mingle in ecotonal hotspots, leading to expected increased spider species and functional diversity due to the unique vegetation profile found on these habitats. (3) The synergistic effects of fire and grazing disturbances across a steep slope landscape subject to variable weather indirectly structure spider community complexity. Spider density, species diversity, species evenness, and richness of hunting strategies along gradients of habitat complexity and heterogeneity are mediated through direct effects of pyric herbivory on vegetation vertical and horizontal structural complexity and spatial heterogeneity (Fig. 2.1). Increases in habitat structural complexity reflect changes in architectural complexity and total vegetation biomass with increasing time since last burn. Moderate increases in site use by bison promote vegetation heterogeneity and opportunities for habitat partitioning by consumers, high intensity grazing by bison reduces habitat availability for arthropods through significant reduction of biomass and vegetation structure.

Methods

Study site

This study was conducted at Konza Prairie Biological Station (KPBS), located in northeastern Kansas 10 km south of Manhattan (39°05'N, 96°35'W). KPBS is a 3,487 ha. native mesic tallgrass prairie preserve that experiences a highly variable US mid-continental climate consisting of wet-hot summers and dry-cold winters (Knapp et al 1998, Knight et al. 1994, Joern 2005). KPBS is managed with factorial treatments of long-term, landscape-level manipulations of prescribed fire at 1, 2, 4 and 20 year intervals and bison grazing (+, -). Annual precipitation and subsequent primary production is highly variable (Knapp & Seastedt 1998). Mean annual precipitation is ~835 mm (CV ~25%) with most rainfall occurring during the growing season. The topography of KPBS is characterized by steep-sloped terrain with silty-loam soils ranging from shallow soils in the upland to deep soils on the lowland areas (Knapp et al. 2006). Prescribed burning at multiple frequencies date from 1972, with more watershed-level replicates added as additional land was acquired (Collins & Steinauer 1998, Veach et al. 2014). Since re-introduction in 1992, bison were provided free access to ~1000 ha distributed among 10 watersheds with burn frequencies of 1, 2, 4 and 20 year intervals between fires (Harnett et al.

1996, Raynor et al. 2015, 2016; Veach et al. 2014). The herd size averages about ~260 adult individuals with about ~80-100 calves born each year (Raynor et al. 2015, 2016; Towne 1999); the herd is culled in autumn each year to reach the target adult number. On average, the bison herd removes about 25% of the aboveground vegetation annually on average in a patchy pattern that reflects recent prescribed burning treatments (Briggs et al. 2002, Raynor et al. 2015).

Perennial C_4 grasses dominate vegetation cover at KPBS whereas plant species richness includes a mixture of more than 600 plant species, including C_3 and C_4 grasses, forbs and woody plant species (Towne 2002, Towne et al. 2005, Collins & Calabrese 2012). Grasses comprise ~80% of the aboveground vegetation biomass and forbs contribute ~80% of the total plant species diversity (Knapp & Seastedt 1998, Joern & Laws 2013). Vegetation structure and plant species diversity diverged among watersheds over time in response to long-term fire-grazing treatments, resulting in a landscape mosaic of structurally variable habitats of potential consequence to arthropods (Joern 2004, 2005; Jonas & Joern 2007). Vegetation heterogeneity continues to shift in space in response to continued prescribed burning and bison grazing. In general, plant species diversity and richness is greatest in watersheds burned at intermediate fire (4 y) return intervals and grazed by bison (Collins & Calabrese 2012). High fire frequency (1-2 y return interval) without grazing favors C_4 grass cover and results in lower plant species diversity with a uniform plant canopy height (Collins & Calabrese 2012). Extensive woody vegetation cover is found in watersheds subjected to low fire frequency and along the riparian and drainage basin areas (Collins & Calabrese 2012). Plant diversity is highest in upland areas compared to slopes or lowlands, and in grazed watersheds associated with reduced grass cover and an increase in forb diversity (Gibson & Hulbert 1987, Hartnett et al. 1996). Overall vegetation cover and biomass is higher at lowland sites, reflecting deeper soils with a higher water-holding capacity and higher amounts of woody vegetation when compared to upland and slope areas (Collins & Calabrese 2012); soil depth and vegetation height decreases from lowlands to uplands.

For our comparisons, I selected sites with combinations of grazing activity (+, -) crossed with watershed burn frequency (1, 2, 4 and 20 y). Of the 23 sites sampled (Supplementary material, Fig. S1), 14 were distributed among seven bison-grazed watersheds and the remaining 9 sites were distributed among eight non-grazed watersheds. The non-grazed sites were selected randomly from the range of available watersheds. Use intensity of bison-grazed sites was classified with location data from up to 13 female bison fitted with GPS collars (Raynor et al. 2015). An index of bison habitat use intensity for each site and sampling period was created as an incremental scale (1-10), each unit reflecting 50 bison visits within a 100 m radius from center point of a sample location (site) within a one-month period prior to each sampling period. For example, 0 = not grazed, 1 = fewer than 50 bison visits and 2 = 51-100 visits. Bison grazed habitat types for spiders ranged from areas visited rarely by bison and characterized by abundant woody vegetation (woody-grazed grassland) to intensively used grass-dominated grazing lawns. Non-grazed habitats ranged from largely grass monoculture on watersheds burned annually to areas characterized by abundant woody vegetation (woody-grazed grassland) on infrequently burned watersheds.

Spider Community and Insect Biomass Sampling

Spider and Insect Sampling. I sampled spider and insect communities from the grass-layer and understory using a vacuum sampler constructed from a modified leaf blower (Buffington & Redak 1998, Hossain et al. 1999). Spider communities in open grassland vary seasonally (Churchill & Arthur 1999, Green 1999), and I sampled spider and insect communities once in early-summer (June) and once in late-summer (August- September) for 3 years (2011-2013) at each of the 23 sites. No samples from the woody-grasslands sites were collected in early-summer 2011. Each of three 40m^2 transects at each of the 23 sites was vacuumed once during each sampling period. To accommodate the variability in vegetation height and structural complexity among the 23 sites, transects were sampled uniformly by slowly walking along each transect and vacuuming from near the base of the vegetation up to a maximum height of 1.5 m in the woody-grassland transition sites. Arthropods were placed immediately in coolers with ice after collection in the field, and frozen that day. Spiders and insects were later sorted, and the material stored in 70% alcohol. I identified spiders to the lowest taxonomic level possible. Bulk samples of insects for each collection were dried in an oven for 48h at 70^{0}C before weighing. Insect productivity was determined by dividing the insect mass (g) by the total area vacuumed per site (g-m^{-2}). The 2^o-productivity of insects is used as a proxy for availability of potential food sources for spiders.

<u>Spider Hunting Strategies.</u> I categorized the richness of hunting strategies per site based on sixteen categories previously described for grassland spiders. Following Uetz et al. (1999), Eiseman et al. (2010) and Gomez et al. (2016), I categorized web-building spider hunting strategies into nine web-type groups based on family web morphology: *Funnel* web builders, *Doily-Sheet* web builders, *Irregular-All-directions* web builders and *Irregular-Mesh* web builders, *Purse* web and *Slingshot-Orb* webs (Table 1). Orb weaving spider exhibited much variation in web diameter, thus I followed Gomez et al. (2016) to further divide this web-type group into three size classes: *Small* (< 50 cm^2), *Medium* (> 50-740 cm^2,) and *Large* (> 740 cm^2) *Orb-Web*. Wandering spiders were classified into the following hunting groups using family- and genus-based hunting traits: *Active-Ground-hunter, Ground-Sit & Wait*, *Spider Specialist*, *Foliage-Stalker*, *Stem-Runner*, *Foliage –Sit & Wait*, *Foliage-Ground-Sit & Wait* (Uetz 1977, Uetz et al. 1999, Young & Edwards 1990, Isaia et al. 2006, Miller et al. 2014; Table 2.1); hunting strategies of some spiders were classified as unknown.

Habitat Characterization

Sites were classified into topographic regions (upland, slope and lowland) based on their relative position in watersheds (referred to as 'TopoPosition'). To assess effects of fire treatment on spider community assemblages, I compared: (a) burned vs. not-burned watersheds in year of burn from 2011-2013 ('Burned'), (b) number of weeks since a site was last burned ('Weeks-Since-Burn'-WSB), and (c) burn frequency ('BrunFreq'). Sites burned every 1 & 2 y were considered to be *frequently* burned, sites burned every 4 y are classified as *intermediate* frequency*,* and sites burned every 20 y are considered *low* frequency. Bison habitat use was described using (a) the 'Bison Habitat Use Index' (BHUI), and (b) with a categorical value to describe bison grazing treatment at each site referred as 'Bison Present'. Precipitation ('Precip') was measured with a continuously recording rain gauge located at Headquarters. Mean rain late season received from April 1 to May 31 corresponds to early-summer samples, and cumulative growing season rainfall received (April 1 to July 31) corresponds to late-summer samples. The Palmer Drought Index (PDI) ranks drought severity, and is calculated by dividing the daily average air temperature measured (^{o}C) by the daily total precipitation (mm). Reported PDI values for the early-summer and late-summer sampling periods represents mean PDI values over the growing season for the same period discussed for Precip variable.

Vegetation structural complexity and spatial heterogeneity. Sites were classified into one of three general grassland habitat types: (a) open, non-grazed, (b) open, grazed, and (c) woody-transition habitats based on the dominant vegetation cover (termed 'HAB'). An index of habitat structure and spatial heterogeneity was estimated in two ways using: (a) a modified Robel pole, and (b) the leaf area index (LAI). Mean values represent overall vegetation structural complexity, and the *coefficient of variation* (CV) from multiple samples along transects at each site characterized the spatial heterogeneity of vegetation. I measured three aspects of vegetation structure: (a) vegetation canopy closure (LAIM), (b) central tendency of vegetation height (cm) (CTVH) and (c) the number of vegetation layers (NVL), interpreted as an index for the number of strata available for spiders to partition the canopy.

Architectural/ structural complexity of vegetation at each site was measured using a modified Robel pole, consisting of a 1.5 cm diameter rod marked with 5 cm interval increments up to a height of 1.5 m. Thirty random points were recorded at each site for each sampling period. At each sampling point, the rod was placed through the vegetation perpendicular to the ground and the number of vegetation hits was counted for each 5cm interval. Vegetation height was described as the “Central Tendency of Vegetation Height” (CTVH), an estimate of canopy height (cm), was calculated as the average of the median vegetation height for each of the thirty random vegetation structure points measured at a site. I also calculated the coefficient of variation (CV) of the central tendency of vegetation height, denoted as “Central Tendency-CV” (CTCV). Last, I estimated the vertical structural complexity of the habitat [“Number of Vegetation Layers” (NVL)] at each site based on vegetation hits in each 5 cm increment interval. NVL values ranged from 0 to a maximum of 31 layers per site; at least two hits by vegetation in a layer were required for a height interval to be considered a vegetation layer. Site NVL values represent the sum of vegetation layers that meet this criterion.

Vegetation cover closure was characterized with the leaf area index (LAI). Light obstruction through the plant canopy was recorded using the LP-80 AccuPar ceptometer (bar length: 1 m, 100 sample points along the bar). At each site, 20 random sample points of light obstruction were made in every sampling period. At each sampling point, I recorded a light obstruction value at ground level and another measure at 1m in height above the vegetation. To calculate approximate LAI values using ceptometer readings, I divided the ground level measurements by the above canopy measurements; an approximate LAI was calculated as –ln(x)/ 0.86. The constant value of 0.86 was obtained from the literature (Decagon Devices 2004). Note that our samples measurements were taken over a wider range of daily time periods than is recommended for LAI measurements, so LAI results are considered approximate. The mean and standard deviation for the LAI values were then calculated for each site and sampling period to estimate the mean LAI (LAIM) and the CV of LAI (LAICV).

Statistical analyses

Characterization of Spider Habitat. Akaike's Information criterion (AICc) values were used to assess how ecological drivers (fire, grazing, precipitation, topographic position, and habitat type) influenced gradients of vegetation structure and heterogeneity. Vegetation structure was described by CTCH, NVL and LAIM, and vegetation heterogeneity by CTCV and LAICV. Grazing pressure was characterized by BHUI, fire was represented by both WSB and Burned, weather variability was evaluated as Precip and PDI, and topographic position was represented as TopoPosition. All models with a value of ΔAICc ≤ 2 were considered parsimonious and retained for evaluation (Anderson 2002). The importance of factors associated with vegetation structure and heterogeneity were determined with the function 'importance' using the package MuMin in R; this is the sum of Akaike weights (w_i) for all models with a ΔAICc ≤ 2. Linear regression was used to assess the responses of vegetation structural complexity and spatial heterogeneity with respect to time since last fire, bison habitat use, precipitation and PDI. The significance of topographic position, habitat type, and year of burning (Burned) were assessed using Kurskal-Wallis one-way analysis of variance. *Post-hoc*, pairwise comparisons were performed using the function pairwise.t.test in the package stats. Pairwise comparisons were performed using a Chi-square distribution and Holm adjusted p-values.

Spider Community Characterization. To determine if spider community composition (average density, Shannon's diversity (H') and Evenness (E) of spider species, and richness of hunting strategies) differed seasonally, I performed 2-way ANOVAs including interactions with Year (2011-2013) and Season (Summer vs. Late Season) as predictor variables. Species diversity was estimated using Shannon's Diversity Index (H′), calculated as:

$$H' = -\Sigma\, p_i \ln p_i \ ,$$

where p_i represents the relative abundance of species i in the sample of n species. Shannon's Evenness (E) was calculated as:

$$E = H' / \ln(S) \ ,$$

where S represents species richness.

Akaike's Information criterion (AICc) values were used to determine which gradients of vegetation structure, vegetation heterogeneity and arthropod productivity best predicted changes in average spider density, species diversity, species evenness, and richness of hunting strategies. Topography (TopoPosition) was included in the analysis as it has been shown to affect plant species distributions and productivity across the landscape via soil depth (Gibson & Hulbert 1987, Collins & Calabrese 2012, Hartnett et al 1996). All reduced additive models from the global model were fit using the function *dredge* in the MuMIn package (Barton 2012) in Program R version 3.1.2. Models with ΔAICc ≤ 2 were retained for evaluation (Anderson 2002) and considered equally parsimonious. The importance of environmental predictor variables at predicting spider community responses was determined using the function importance in package MuMin of R, referred to as the sum of Akaike weights (w_i) for all models with a ΔAICc ≤ 2. Linear regressions were used to assess the directionality of spider community responses in relation to gradients in vegetation structural complexity (increases: LAIM, CTVH and NVL), habitat heterogeneity (variability: LAICV and CTCV) and insect biomass.

A Kruskal-Wallis one-way nonparametric analysis of variance followed by *post-hoc* pairwise comparisons was used to assess significance of the main effects of fire (BurnFreq and Burned), grazed vs not-grazed (BisonPresent), site topographic position, year and habitat type on the spider responses measured in this study. Kruskal-Wallis tests were performed using the function kruskal.test using package stat in R 3.1.2. *Post-hoc*, pairwise comparisons were performed using the nemeyi.test with the function posthoc.kruskal.nemeyi.test in the R package PMCMR. Pairwise comparisons were performed using a Chi-square distribution to correct for tied data.

Structural Equation Models. Structural Equation Modeling (SEM) (Grace 2006, Grace et al. 2010) was performed to summarize how fire and grazing interactions influenced spider communities through direct and indirect effects on vegetation structure and heterogeneity; Figure 2.1 describes a general, *a priori* model of hypothesized relationships. In SEM models, I evaluated late-summer responses of spider density, H′, E and richness of hunting strategies in response to insect biomass and the latent variables *vegetation structure* and *vegetation heterogeneity* for both early and late season spider communities. I evaluated only spider communities in late-summer since woody-grassland transition sites were not sampled in early-summer 2011, leading to insufficient data to analyze all desired paths in my conceptual SEM model. The latent variable '*vegetation structure*' was constructed using CTVH, NVL and LAIM as loading factors, and the latent variable *Vegetation heterogeneity* included LAICV and CTCV as loading factors. Because vegetation can strongly influence insect biomass, taxonomic composition and biomass of potential prey for spiders (Dennis et al. 1998, Diehl et al. 2013, Joern 2004, Moran 2014), responses of insect biomass to *'vegetation structure'* and '*vegetation heterogeneity'* was also included in our models. To assess indirect contributions of fire and grazing interactions to spider community responses through effects on vegetation, I included the latent variable *'pyric herbivory'* with BHUI and WSB as loading factors to represent grazing and fire. I also included 'TopoPosition' and 'Habitat' to build the latent variable *'pyric herbivory'* in the model since both described how fire and grazing interactions structured gradients of '*vegetation structure'* and '*vegetation heterogeneity'* across the heterogeneous landscape of KPBS. Effects of '*pyric herbivory'* on vegetation were evaluated: (a) as a direct effect between pyric herbivory latent variables and vegetation loading factors (CTVH, NVL, LAIM, CTCV and LAICV), and (b) as a direct interaction between '*pyric herbivory* 'with the latent variables '*vegetation structure'* and '*vegetation heterogeneity'*. I included precipitation (Precip) as a path affecting both vegetation latent variables in the SEM because rainfall varied significantly over the period of my study, including a drought in 2012 that affected vegetation attributes and grazing patterns. SEMs were performed on both original data and transformed data using natural log (ln) to normalize the following variables: LAIM, LAICV, CTVH, CTCV and IB. I considered the following fit measures to select the most parsimonious SEM models: Chi square (non-significant model at alpha of 0.05), the comparative fit index (CFI) and the Tucker-Lewis

Index (TLI) (obtain a model with value is close to 1.0), and the root mean square error of approximation (RMSEA) (to obtain a model with a RMSEA value close to 0.0 and p-value < than 0.05; RMSEA is a one-sided test of H_o=0.05) (Rigdon 1996, Iacobucci 2010, Hooper et. al 2008).

SEM modeling was conducted with R 3.1.2 (R Core Team 2014) using the packages lavaan for running SEM models with latent variables, the package semPlot used for building SEM figures, the package nlme used to fit paths in the SEM model on lavaan, and the packages car and QuantPsyc for calculating summary values. Vegetation and spider community structure was analyzed using AIC, Regression, Kruskal-Wallis and *post hoc* pairwise analyses performed in R using original code and the following packages during different analysis: vegan, BiodiversityR, MuMIn, PMCMR, stats.

Results

Vegetation Structure in Response to Fire and Grazing

In general, the amount of precipitation received over the growing season (Precip), drought severity (PDI), time since last burn (WSB), bison habitat use over time (BHUI), and habitat type (HAB) designation significantly influenced vegetation attributes. Differences in vegetation structure (LAIM, CTVH & NVL) and spatial heterogeneity (LAICV & CTCV) among sites were more pronounced at the end of the growing season after vegetation growth and effects of bison grazing reached peak effects.

Precip and PDI were positively related to vegetation canopy closure (LAIM) for both early-summer (R^2 = 0.94-0.95, p <0.001; Tables 2.1 & 2.2, Fig. 2.2) and late-summer seasons (R^2 = 0.79-0.80, p < 0.001; Tables 2.1 & 2.2, Fig. 2.3). Early-summer LAIM responded positively to year of burning (Burned), changes in BHUI, site TopoPosition and Habitat designation (Tables 2.1 & 2.2, Fig. 2.2). In the late-summer season, LAIM was influenced secondarily by Habitat, TopoPosition and WSB (Tables 2.1 & 2.2, Fig. 2.3). With linear regression, PDI was negatively related to LAIM, explaining 34% of the variance in the summer (Table 2.3, Fig. 2.2), and vegetation canopy closure was significantly different among habitat types in the late-summer (Kruskal-Wallis analysis of variance) (Table 2.3, Fig. 2.3). *Post hoc* analysis of pairwise comparisons revealed no significant differences among the three habitat types when p-values were corrected for type-1 error using the Holm adjustment.

The central tendency of vegetation height (cm) (CTVH) was primarily influenced by Precip, Habitat and WSB in both early-summer and late-summer; PDI was also a primary factor in the late-summer (Tables 2.1 & 2.2, Fig. 2.2 & 2.3). In the early-summer, Burned, PDI and TopoPosition explained gradients of CTVH (Tables 2.1 & 2.2, Fig. 2.2). Cumulative effects of grazing (BHUI) over the growing season were important in explaining late-summer gradients of CTVH (Tables 2.1 & 2.2, Fig. 2.3). In general, CTVH (early-summer: $R^2 = 0.36$, $p < 0.001$; late-summer: $R^2 = 0.27$, $p < 0.001$) increased with increasing time since fire (Table 2.3, Fig. 2.2 & 2.3). Increased vegetation structural complexity at the transition between grass and woody vegetation is a legacy of intermediate and low fire frequency treatments, regardless of grazing treatment. CTVH differed among habitat types both in the early-summer ($\chi^2 = 38.52$, $p < 0.001$) and late-summer ($\chi^2 = 42.86$, $p < 0.001$) (Table 2.3). *Post hoc* analysis showed that in the early season vegetation height in woody/ grassland transition habitats was different from both grazed ($p < 0.001$) and non-grazed open grasslands ($p < 0.001$) (Fig. 2.2). In late season, CTCV in woody-grassland transitions habitats was still different from both grazed ($p < 0.001$) and non-grazed ($p < 0.001$) open grasslands, but no difference in CTVH among grazed and non-grazed habitats were observed (Fig. 2.3).

The number of vegetation layers was influenced primarily by Habitat and WSB for both early-summer and late-summer periods (AIC analysis, Tables 2.1 & 2.2). In early-summer, Burned, Precip and BHUI were significant at explaining gradients in NVL (Tables 2.1 & 2.2, Fig. 2.2). In late-summer, Drought, Precip, BHUI and TopoPosition best explained the gradient of NVL towards the end of the growing season (Tables 2.1 & 2.2, Fig. 2.3). Significant linear regressions showed that the number of vegetation layers (early-summer: $R^2 = 0.33$, $p < 0.001$; late-summer: $R^2 = 0.29$, $p < 0.001$) increased with increasing time since fire (WSB) (Table 2.3). Kruskal-Wallis analysis showed that burning reduced the NVL in the early-summer ($\chi^2 = 11.062$, $p < 0.001$) and late-summer ($\chi^2 = 7.59$, p = 5.9e-3) (Table 2.3, Fig. 2.2 & 2.3). NVL differed among habitat types in both early-summer ($\chi^2 = 31.13$, $p < 0.001$) and late-summer ($\chi^2 = 39.13$, $p < 0.001$) (Table 2.3, Fig. 2.2 & 2.3). Woody-grassland transition habitat had a higher NVL than grazed (early-summer: $p < 0.001$; late-summer: $p < 0.001$) and non-grazed (early-summer: $p < 0.001$; late-summer: $p < 0.001$) open grasslands. In the late-summer non-grazed open grassland had a higher NVL than grazed open grasslands ($p = 0.045$). NVL differed among sites in the early-summer with respect to topographic position ($\chi^2 = 7.9$, $p = 0.028$) and late-summer ($\chi^2 = 13.59$, $p = 0.001$) (Table 2.3, Fig. 2.2 & 2.3). *Post hoc* analysis showed that uplands had a significantly lower NVL than lowland habitats (early-summer: $p = 0.022$; late-summer: $p < 0.001$).

Spatial Heterogeneity of Vegetation in Response to Fire and Grazing

The LAICV was primarily influenced by Precip and PDI ($R^2 = 0.27\text{-}0.30$, $p < 0.0001$) (Tables 2.1 & 2.2, Fig. 2.2), secondarily influenced by Habitat, BHUI and Burned, and to a lesser extent by TopoPosition in the early-summer. In contrast, LAICV in the late-summer was primarily driven by the effects of BHUI ($R^2 = 0.11$, $p < 0.05$) (Tables 2.1 & 2.2, Fig. 2.3), and secondarily influenced by Precip and PDI. Habitat types differed significantly in the LAICV both in early-summer ($\chi^2 = 16.33$, $p <0.001$; Table 2.3, Fig. 2.2 & 2.3). In the early-summer, non-grazed sites had lower variation in canopy closure than bison grazed open grasslands ($p = 0.011$).

The heterogeneity in vegetation height (CTCV) was influenced by Precip, Habitat, TopoPosition in the early-summer (Tables 2.1 & 2.2, Fig. 2.2). In the late-summer, CTCV primarily reflected Habitat, WSB and BHUI and year of burning (Burned) as documented by AIC analysis (Tables 2.1 & 2.2, Fig. 2.3). CTCV increased with increased visitation by bison (BHUI) in the late-summer period (linear regression, $R^2=0.36$, $p <0.001$; Table 2.3, Fig. 2.3), resulting from grazing activity over the growing season. CTCV differed among habitat types in both the early-summer ($\chi^2 =16.33$, $p <0.001$) and late-summer ($\chi^2 = 31.99$, $p <0.001$; Table 2.3, Fig. 2.2 & 2.3). Non-grazed open grassland in both summer periods had a significantly lower variability in vegetation height than gazed open grassland (early-summer: $p <0.001$; late-summer: $p <0.001$) and woody-grassland transition habitats (early-summer: $p <0.001$; late-summer: $p <0.001$).

Spider Community Responses

I collected 132 morpho-species across 23 sites within 13 watersheds from 2011 to 2013, of which ~75% were identified to species. Spider species were distributed among 22 families and 83 different genera. The total sample included taxa from a wide range of habitat types and vegetation. Rank abundance analysis indicated that the spider community at KPBS was numerically dominated by wandering spider species (data not shown). The 15 most abundant spider species were distributed among 6 Families where only one species was a web-builder. The hunting strategies of the 15 most abundant spider species commonly found across KPBS were

Foliage-Stalker, Stem-Runner, Foliage-Sit & Wait and Medium-Orb-web spiders (Table 4), but their abundances differed among habitat types.

Median spider density in early-summer was 0.48 individuals-m^{-2} and maximum spider density was 1.22 individuals-m^{-2}. In late-summer, median spider density was higher at 0.63 indv-m^{-2} and a maximum observed density of 2.06 individuals- m^{-2} than early-summer. Median spider diversity (H′) was 1.99 per site in early-summer, and 2.4 per site in late-summer with an observed maximum H′ of 3.23 in the early-summer and 3.06 in late-summer. Spider evenness in early-summer had a median value of 0.82 and maximum observed evenness of 0.97. In late-summer, median evenness was 0.85 and maximum evenness was 0.96. In general, the median richness of hunting strategies observed at any given site was 7 for both early and late summer. Hunting strategy richness at a site ranged from 3 in heavily grazed habitats to sites with 12-13 hunting strategies in early and late-summer samples at sites with complex, heterogeneous vegetation structure, particularly along at the transition zone between grasslands and woody stands. In general, spider assemblages increased in complexity towards the late season across all habitat types sampled.

Seasonality and Differences Among Years

Spider community structure differed between seasons; late-summer spider communities showed higher species diversity, species evenness, and richness of hunting strategies than was seen in early-summer. A significant season-by-year interaction was the best predictor of spider density. Spider density was higher in late-summer than in the early-summer of 2011, but the opposite pattern was observed for 2012 and 2013 (ANOVA, $F_{2,1} = 14.58$, $p < 0.001$; Fig. 2.4a). Shannon diversity (H′) also showed a significant year*season interaction (ANOVA, $F_{2,1} = 6.82$, $p = 0.002$; Fig. 2.4b); late-summer samples in 2011 and 2013 had higher species diversity than the early-summer communities, but no difference was seen between early and late-summer communities in 2012. A significant year*season interaction was observed for species evenness (E) (ANOVA, $F_{2,1} = 5.11$, $p = 0.007$; Fig. 2.4c), where E was higher in late season 2012 and 2013, but the opposite trend was observed in 2011. Last, the richness of hunting strategies showed a pattern similar to that for species evenness (ANOVA, $F_{2,1} = 3.98$, $p = 0.02$; Fig. 2.4d). Spider diversity and richness of hunting strategies in the drought year of 2012 showed a pattern opposite to those seen 2011 and 2013, where early-summer values were higher in 2012.

Spider responses to vegetation structure and spatial heterogeneity and habitat productivity

Because spider responses showed significant seasonal responses with respect to vegetation structure, spatial heterogeneity, habitat productivity and topography, early-summer and late-summer samples were analyzed separately using AIC. Year was retained as an explanatory variable because of a drought in 2012. AICc models with a ΔAICc < 2 included variables with little capacity to explain observed measured variance in spider responses and characterized by having low importance ($\leq 20\%$). These interactions are ignored. Effects of vegetation on spiders varied seasonally.

Spider Density. Top AIC models to explain spider density in the early-summer included vegetation heterogeneity, structure and variation among years ($R^2 = 0.35$-0.36, $p < 0.001$; Tables 2.5 & 2.6, Fig. 2.5). Spider density in early-summer responded negatively to increases in mean canopy closure (linear regression, LAIM; $R^2 = 0.27$, $p < 0.001$; Table 2.7, Fig. 2.5). Spider densities varied significantly among years (Kruskal-Wallis test: $\chi^2 = 19.51$, df = 2, $p < 0.001$); a pairwise *post hoc* test showed that density in 2011 was significantly lower than both 2012 ($p < 0.001$) and 2013 ($p = 0.008$) (Fig. 2.4a).

In late-summer, spider density responded differently to vegetation structural complexity and heterogeneity; AIC models showed that spider density responded to NVL and CTCV instead of LAIM and LAICV. As in early-summer samples, variability among years was a recognized predictor of spider density; top AIC models had an $R^2 = 0.19$ ($p < 0.001$). Differences in mean spider density from lowland to upland were not significant (Tables 2.5 & 2.6, Fig. 2.6). Similar to early-summer samples, spider density in the late-summer showed significant variability among years (Kruskal-Wallis test: $\chi^2 = 13.95$, df = 2, $p < 0.001$); a pairwise *post hoc* test showed that late-summer density in 2011 was significantly higher than both 2012 ($p = 0.002$) and 2013 ($p = 0.026$) (Fig. 2.4a). In the late-summer, spider densities were lower at sites on recently burned watersheds than for sites in unburned watersheds ($\chi^2 = 3.88$, df = 1, $p = 0.049$). Fire frequency treatments at KPBS influenced spider density ($\chi^2 = 8.78$, df =2, $p = 0.012$); results showed that sites in watershed burned every 20 years had higher density than sites in frequently burn ($p = 0.028$, Fig. 8).

__Spider Diversity__. Spider diversity in early-summer responded to habitat secondary productivity, vegetation structure and its spatial heterogeneity, and topography (AIC analyses, Tables 2.5 & 2.6, Fig. 2.5). Linear regression showed that diversity responded positively to increases in insect biomass in the early-summer ($R^2 = 0.40$, $p < 0.001$). In addition to responding positively to changes in habitat secondary productivity, H’ responded negatively to increased LAIM ($R^2 = 0.23$, $p < 0.001$; Table 2.7). Spider diversity increased with increased variability in vegetation height (CTCV; $R^2 = 0.27$, $p < 0.001$; Table 2.7). Kruskal-Wallis analysis of variance showed that fire frequency treatments at KPBS influenced early-summer H′ ($\chi^2 = 10.79$, df = 2, $p < 0.001$). Accumulation of species in watersheds burned at 20 year intervals led to higher H′ in this sites than sites from watersheds burned frequently (1 & 2 y, $p = 0.006$) and at intermediate frequencies (4 y, $p = 0.017$) years in the early-summer regardless of grazing treatment (Fig. 2.7). Year influenced patterns of H′ across KPBS ($\chi^2 = 17.82$, df = 2, $p <0.001$), where diversity in 2011 was lower than 2012 ($p = 1.7e-4$) and 2013 ($p = 0.011$) (Fig. 2.4b). Finally, habitat type influenced spider diversity ($\chi^2 = 22.26$, df = 2, $p <0.001$) in the early-summer; the *post hoc* pairwise analysis revealed that H′ in bison-grazed-grasslands was more diverse than in non-grazed-grasslands ($p = 0.045$), and woody-grassland transitions were more diverse than both bison-grazed-grasslands ($p = 0.015$) and non-grazed-grasslands ($p <0.001$) (Fig. 2.7).

Late-summer spider diversity responded to habitat productivity, vegetation structure and variability in vegetation height (Tables 2.5 & 2.6, Fig. 2.6); predictor variables in linear regression analysis had low R^2 but were statistically significant at $\alpha = 0.05$ (Table 2.7). Kruskal-Wallis analysis of variance showed that habitat type influenced H′ ($\chi^2 = 15.61$, df = 2, $p <0.001$) and the *post hoc* pairwise analysis revealed that H′ in both woody-grassland transitions and grazed/ open grasslands was higher than in non-grazed sites ($p <0.001$) in the late-summer (Fig. 2.8). Similar to early-summer, fire frequency treatments at KPBS influenced patterns of spider diversity in the late-summer ($\chi^2 = 15.045$, df = 2, $p <0.001$). Sites in watersheds burned every 20 years had higher H′ than sites burned frequently ($p = 0.001$) and burned at an intermediate frequency ($p = 0.003$, Fig. 2.8).

Species Evenness. Species evenness increased with insect biomass, vegetation structure, and heterogeneity (Tables 2.5 & 2.6, Fig. 2.5) as shown by AIC analyses. Linear regression (Table 2.7) showed that individual predictors were only able to explain a small percentage of the variance in spider evenness. Habitat type influenced evenness ($\chi^2 = 6.2$, df = 2, $p = 0.045$) in the early-summer; *post hoc* pairwise analysis showed woody-grassland transitions sites had higher E than ungrazed-grasslands sites ($p = 0.05$) (Fig. 2.7).

Top AIC models showed that late-summer spider evenness was best predicted by variability in vegetation height, vegetation structure, topography and variability among years (Tables 2.5 & 2.6, Fig. 2.6). Increases in LAIM had a negative effect on E ($R^2 = 0.23$, $p <0.001$) in the late-summer (Table 2.7). Kruskal-Wallis analysis of variance showed that year influenced E in the late-summer season ($\chi^2 = 15.18$, df = 2, p =<0.001) and *post hoc* pairwise analyses showed that evenness in 2011was lower than in 2012 ($p = 0.002$) and 2013 ($p = 0.008$) (Fig. 2.4c).

<u>Richness of Hunting Strategies</u>. In general, richness of hunting strategies during early-summer increased as insect biomass and vegetation structural complexity increased from upland to lowland (TopoPosition) (Tables 2.5 & 2.6, Fig. 2.5). Richness of hunting strategies responded negatively to increased LAIM (linear regression, $R^2 = 0.35$, $p <0.001$; Table 2.7) while it increased with increasing insect biomass ($R^2 = 0.22$, $p <0.001$; Table 2.7). Early-summer richness of hunting strategies also varied among years ($\chi^2 = 27.42$, df = 2, $p <0.001$) with significantly lower richness in 2011 than in 2012 ($p <0.001$) and 2013 ($p = 0.014$) (Fig. 2.4d). Kruskal-Wallis analysis of variance showed that fire frequency treatments influenced richness of hunting strategies in the early-summer ($\chi^2 = 8.47$, df = 2, $p = 0.02$), where sites in watersheds burned at low frequency had higher richness of hunting strategies than sites burned frequently ($p=0.005$) and at intermediate frequency ($p = 0.01$) (Fig. 2.7). Finally, habitat type influenced richness of hunting strategies ($\chi^2 = 18.02$, df = 2, $p <0.001$); *post hoc* pairwise analysis showed woody-grassland transitions had higher richness than both bison grazed grasslands ($p <0.001$) and non-grazed grasslands ($p = 0.001$) (Fig. 2.7).

In the late-summer, top models explaining richness of hunting strategies included vegetation structure (NVL, LAIM, CTVH), topography and year variability as predictor variables (Tables 2.5 & 2.6, Fig. 2.6). Richness of hunting strategies in late-summer responded positively to increased vegetation structure, primarily in response to NVL (linear regression, $R^2 = 0.33$, $p < 0.001$) and to a lesser extent CTVH ($R^2 = 0.25$, $p < 0.001$). Topographic position was somewhat important in late-summer ($\chi^2 = 7.2$, df =2, $p = 0.03$), where hunting strategy richness was higher in lowland than upland sites ($p = 0.028$, Fig. 2.8). In late-summer, the burn frequency treatment influenced patterns of spider hunting richness ($\chi^2 = 18.24$, df =2, $p < 0.001$) in which hunting richness in watersheds burned every 20 y were significantly higher than frequently (1 & 2 y) ($p = 0.0013$) or intermediately (4y) burned sites ($p = 0.0002$) (Fig. 2.8). As seen in early-summer, habitat type also influenced patterns of hunting richness; in the late-summer ($\chi^2 = 30.26$, df = 2, $p < 0.001$) woody-grassland transitions had a higher richness of hunting strategies than both bison grazed grasslands ($p < 0.001$) and non-grazed grasslands ($p=0.0001$) (Fig. 2.8).

Pyric herbivory influences spider community composition.

All SEM analyses examined here were statistically significant for the χ^2 index of fit ($P<0.05$). I reported models with the closest value to 1.0 for the comparative fit index (CFI) and the Tucker-Lewis Index (TLI), and for the root mean square error of approximation (RMSEA) modelswith a RMSEA value close to 0.0 and p-value < than 0.05; RMSEA is a one-sided test of $H_o=0.05$) (Rigdon 1996, Iacobucci 2010, Hooper et. al 2008) indices to select the best available model for each analysis. I excluded interactions between insect biomass and two vegetation latent variables *habitat structure* and *habitat heterogeneity* (Fig. 2.1) because I did not have sufficient data to evaluate all pathways in our theoretical model. Because spider density was largely unresponsive to vegetation attributes, SEM models were modified by incorporating only predictor factors of importance from AICc models. Because natural log transformations of predictor variables provided only marginal gains to explanatory power of spider responses, results are reported using non-transformed data.

Spider Density. The best fit SEM model indicated that late-summer spider density was largely independent from *vegetation structure* and insect biomass ($R^2 = 0.074$). The model (Fig. 2.9a) fit for the data based was CFI = 0.624, TLI = 0.483 and RMSEA = 0.216 with $p = 0.000$. In this model, indirect effects of fire-grazing interactions on spider density were accounted for by the direct interactions between the *pyric herbivory* and *vegetation structure* latent variables and CTCV.

Species Diversity (H′). Late-summer spider diversity was primarily explained by and positively correlated with increased *vegetation structure* and *vegetation heterogeneity*. It was also positively influenced by increased insect biomass although this relationship was less important in late-summer than in the early-summer. Indirect effects of fire and grazing interactions on spider diversity were incorporated through interactions between *pyric herbivory* with the latent variables *vegetation structure* and *vegetation heterogeneity*. The fit values for this model were CFI = 0.717, TLI = 0.625, RMSEA = 16 ($p = 0.000$), and $R^2 = 0.34$ for spider diversity (Fig. 2.9b). Pyric herbivory promotes species diversity through negative effects on vegetation structure and positive effects on vegetation heterogeneity, both in the early and late summer.

Species Evenness. Spider evenness in late-summer was primarily explained and positively influenced by increased *vegetation heterogeneity*, while *vegetation structure* had low explanatory power. The moderate model fit was CFI = 0.668, TLI = 0.559 and RMSEA = 0.174 ($p = <0.001$) (Fig. 2.9c). The model only accounted for 22 percent of the variance observed in my samples ($R^2 = 0.223$). *Pyric herbivory* increased species evenness primarily through effects on *vegetation heterogeneity* in the early and late summer seasons, and to a lesser degree its effects on *vegetation structure*.

Richness of Hunting Strategies. The SEM model that best fit hunting strategy richness in late-summer (Fig. 2.19d) accounted for 40 percent of the variance observed in the data ($R^2 = 0.395$); CFI = 0.703, TLI = 0.607 and RMSEA = 0.167; p = 0.000). Spider hunting richness increased with increased *vegetation structure*. Insect biomass and *vegetation heterogeneity* were not important predictors in late-summer at explaining patterns of spider richness of hunting strategies. Effects of pyric herbivory on spider richness of hunting strategies included pathways between *pyric herbivory* and the latent variables *vegetation structure* and *vegetation heterogeneity.* As in the early-summer, *pyric herbivory* positively affected the richness of hunting strategies through its negative effects on *vegetation structure*.

Discussion

Spiders are dominant arthropod predators in grassland ecosystems with important functional roles (Schmitz 2008, 2009), and it is important to understand community level responses by this group to major and widespread disturbances from fire and grazing. Many studies have documented strong interspecific interactions among spiders at the local scale (e.g. competition, intraguild predation) (Denno et al. 2004, Hodge 1999, Polis et al. 1989, Wise 2006) that provide context for the results of my study. For example, changes in the taxonomic and functional composition of spider communities affects their role as biological control agents of arthropod populations, and their ability to create trophic cascades with implications for plant diversity and habitat productivity. Spider assemblage's effects on trophic cascades vary depending on the combination of spider species and distribution of functional traits found at a locality (Laws &

Joern 2013, Schmitz 2008, 2009). Here, I examined functional relationships affecting abundances, species diversity, hunting strategy diversity, and spatial distributions in response to habitat spatial heterogeneity and overall structure. My results will provide critical opportunities to identify conservation needs and to develop effective, alternate conservation practices.

Spatial and temporal variability in fire-grazer interactions in a grassland landscape alters habitat structure directly, and when accompanied by variable weather indirectly structures grassland spider communities at multiple spatial scales. The outcome is a shifting mosaic of habitat types and local spider assemblages that varies throughout the landscape in time and space. By taking advantage of the long-term experimental manipulations of fire-frequency and bison grazing applied at the watershed scale at KPBS, I documented how density, species diversity, species evenness and richness of hunting strategies of spiders responded to vegetation structural complexity, vegetation spatial heterogeneity, and 2^0 productivity (insect biomass). *As predicted by the overarching structural complexity and heterogeneity hypothesis (SCHH), increases in the overall vegetation height, stratification of vegetation and openness in the vegetation canopy accompanied by greater spatial heterogeneity in habitat structure led to increased species diversity, species evenness, and hunting strategy richness at the landscape scale.* SEM models (Figs. 2.9 & 2.10) and model selection with AICc analyses (Table 2.4) document these relationships. The importance of spatial heterogeneity of vegetation for explaining the spider communities declined somewhat as the growing season progressed, and the structure of the vegetation *per se* became relatively more important at explaining spider community late-summer outcomes. Similarly, species diversity, species evenness and richness of hunting strategies increased as habitat 2^0 productivity increased early-summer, but only diversity was still positively associated to 2^0-productivity in late-summer. Interestingly, overall spider density was largely unresponsive to these same habitat gradients, except for canopy closure in the early-summer where density decreased with increasing canopy closure, but the model was weak.

Spider responses to vegetation structure and spatial heterogeneity

Spider species diversity, species evenness and richness of hunting strategies responded positively to increased spatial heterogeneity of key vegetation resources as canopy closure decreased. In effect, spiders were responding to increased diversity of habitat types that likely supported increased diversity spider hunting strategies, and thus promoted increased species diversity of local assemblages at both local and landscape scales. Complex vegetation structure often plays a crucial role in maintaining a greater variety of species of taxonomically and diversity of functional groups at multiple spatial and temporal scales, in part by increasing opportunities to partition the habitat at fine scales and promote species coexistence (Sudhikumar et al. 2005, Malumbres et al. 2013, Michalko et al. 2016). Increased architectural complexity of vegetation, associated plant richness, and the heterogeneity of key vertical structure required by different spiders reduced the likelihood that communities are dominated by a small group of species (Chen & Tso 2004). Vertical complexity also promoted increased functional complexity (richness of hunting strategies) and species evenness in spider assembly by offering greater opportunities to partition their habitat both vertically and spatially to reduce the overlap of hunting zones among spider taxa while also possibly increasing hunting success (Michalko & Pekar 2015, Michalko et al. 2016, Schmitz & Suttle 2001). For example, Schmitz & Suttle (2001) documented how three wandering spiders coexisted while hunting for the same grasshopper prey species by partitioning an old field canopy. Spiders may also avoid intraspecific competition and predation by targeting prey of different sizes even when various species use the same hunting strategy. As an example, Richardson and Hanks (2009) showed how five species of orb-weavers (Araneidae) partitioned and captured prey based on the relative body-size of the spider regardless of the web size or position on the vegetation. The ability of spiders to partition resources in response to habitat physical attributes, physiological tolerance, body size and hunting strategies may reduce the intensity of competitive interactions and allow coexistence when in syntopy (Michalko et al. 2016, Richardson & Hanks 2009).

Reduced dominance and spatial connectivity of specific types of vegetation coupled to increased spatial heterogeneity promoted species and functional diversity of local spider assemblages within the landscape. Spider evenness can be important (McArt et al. 2012), where it increased in this study with increasing vertical complexity (CTVH & NVL) and heterogeneity (CTCV) of the vegetation. Also, a greater proportion of individuals comprising dominant species associated with increased canopy closure decreased evenness. Increased canopy closure led to a reduced horizontal vegetation complexity (LAIM) and heterogeneity (LAICV) and promoted the homogenization of vegetation cover. Grass dominated canopies are characterized by high canopy closure associated with not-grazed, frequently-burned areas dominated by grass. Non-grazed, frequently burned habitats generally had lower species evenness as well as lower species diversity and richness of hunting strategies. However, overall spider density was not significantly different from other habitat types, suggesting that the dominant species/hunting strategies of non-grazed frequently burned habitat occurred at high abundances compared to habitats that supported more species or hunting strategies. It could be that dominant species experienced reduced competition with other species/hunting strategies due to increased connectivity of the vegetation strata exploited by these species. For example, species from the families Anyphaenidae and Philodromidae that move about using a stem-running hunting strategy reached higher densities in non-grazed, frequently-burned habitats than in any other habitat types at KPBS.

Insect biomass was a strong predictor of spider community responses in this study, particularly early in the growing season (early-summer) when species diversity, species evenness and richness of hunting strategies were positively associated with increased 2^0 productivity. This suggests that (a) a larger prey base can support more species because of increased productivity (Gamfeldt et al. 2005) and by inference increased total primary productivity (McNaughton et al. 1989), and/or (b) increased biomass is partitioned into a greater variety of insect species of different sizes (Haddad et al. 2001, Vezina 1985) in response to increased vegetation structure and heterogeneity. These are not mutually exclusive outcomes, and these alternatives were not measured explicitly. Insect biomass was of particular importance at explaining spider community structure in the summer when insect juvenile stages are more abundant and susceptible to spider predation due to their small body size compared to their respective adults sizes (Lang et al. 1999). Increased food availability of the appropriate body size range for spider species of different body sizes, possibly reduced the likelihood of inter- and intra-specific competition and predation among spider by allowing species to coexist when in syntopy. Increases in insect biomass promoted increased richness of hunting strategies, species diversity and species evenness at multiple spatial and temporal scales. Variability in vertical and horizontal vegetation attributes (vegetation structural complexity and spatial heterogeneity) in combination with increased availability of potential prey (insect biomass) could facilitate the ability of spider to coexist by providing increased opportunities to partition their habitat along multiple key limiting resources. Coexistence in syntopy may explain why on average at KPBS, I observed twice as many species (14 species) than richness of hunting strategies (7 hunting strategies) per site, suggesting that multiple species use the same hunting strategy for at least one of the functional groups (hunting strategy type) but forage in different places.

The transition ecotone between woody stands (riparian wood-stand and shrubs islands) and grass dominated habitats were hotspots for spider diversity, species evenness and richness of hunting strategies both in early and late summer. Woody islands located within otherwise open grassland led to functionally and taxonomically more complex spider assemblages than was seen in surrounding habitats. Species richness in the woody/grassland transitions was 2x or greater than in the surrounding open-grasslands habitats, and the richness of hunting strategies was more 1.5x times higher. Ecotonal habitats are characterized by steep increases in both vertical and horizontal vegetation structural complexity and heterogeneity over relatively small spatial scales. Ecotone habitats offer a unique vegetation profile for all aspects of vegetation measured in this study. Similar patterns have been documented for butterflies on Mount Fuji, Japan, where butterfly diversity was highest at forest edge habitat than in forest interior or open-land sites (Kitahara &Watanabe 2003). Spider assemblages of these habitat hot-spots are not only the most diverse and complex spider assemblages observed across the KPBS landscape, but they are characterized by higher number of species of web-building taxa and web-types than in other grassland habitats. As demonstrated by Gomez et al. (2016) and Baldissera et al. (2004), web-building spider abundance and richness of web-types/species decreases rapidly with increasing distance from woodland-grassland edge at both KPBS and in *Araucaria forest-pasture in southern* Brazil. These transitional habitats could act as habitat refuge islands for web-builders in grasslands that otherwise would have lower abundances and low richness of web types (Gomez et al. 2016).

Spider assemblages from Konza Prairie exhibited some seasonal differences as well, where early and late summer spider community complexity differed in species diversity and richness of hunting strategies. This could reflect variation in patterns of activity and phenology of species (Sudhikumar et al. 2005). However, general responses by spiders to changes in vegetation structure and heterogeneity were the same in both seasons (Fig. 2.5 & 2.6). The availability and diversity of vegetation resources facilitate the stratification of vertical (CTVH, NVL and CTCV) and horizontal (LAIM and LAICV) components of the habitat, reducing the overlap of hunting zones among spider species (Michalko & Pekar 2015). Stratification promotes increased species diversity and richness of hunting strategies through niche partitioning and habitat filtering (Michalko & Pekar 2015), and also explains the observed increases in species diversity, species evenness and richness of hunting strategies (Figs. 2.5 & 2.6).

Fire and grazing modulate consumer assemblages indirectly through habitat modification

A central premise of the pyric herbivory paradigm in grasslands is that fire-grazing interactions promote spatially and temporally shifting mosaics of habitat structure at multiple spatial scales, leading to increases in consumer assemblage diversity (Fuhlendorf et al. 2009, 2010; McGranahan et al. 2012). My SEM models for spiders document this pattern (Figs. 2.9) and extend the concept to include the diversity of hunting modes in spiders. The long-term, manipulative fire-grazing experiment at the landscape-level at KPBS allowed me to causally link pyric herbivory to consumer community responses as modulated through variable habitat (vegetation) characteristics. It is key to recognize that pyric herbivory sets the stage through effects on vegetation that in turn influences spider community's complexity across the landscape. Alternatively, but not exclusive of direct effect of vegetation on spider community complexity, increases in complexity and heterogeneity in the vegetation template promotes increases in insect biomass, which in turn positively influences spider community complexity. Unfortunatley, this was not tested in my SEM due to lack of sufficient data. Still, my study shows that secondary consumer community complexity is structured by ecosystem driver disturbance interactions mediated through their direct effects on the physical structure and heterogeneity of the habitat (bottom-up processes). Fire mediates plant community composition (Knapp et al. 1998, 1999; Collins and Calabrese 2012, Trager et al. 2004), where fire return intervals at intermediate levels (3-4 years) promoted increased plant diversity compared with frequent fire that result in communities dominated by warm season grasses. Long-term suppression of fire promotes increased cover of woody plants (Collins et al. 1998, Trager et al. 2004). Recent burning positively affects abundance and nutrient quality of palatable grasses that attracts and influences grazer distribution across the landscape (Archibald et al. 2005, Fuhlendorf et al. 2009, Raynor et al. 2015, 2016; Trager et al. 2004). In turn, intensive grazing decreases the likelihood that the recently grazed patches will burn again until the fuel load builds up (Archibald et al. 2005, Fuhlendorf et al. 2009, Trager et al. 2004). Fire-grazing interactions drive habitat heterogeneity and species diversity (Towne et al. 2005, Fuhlendorf & Engle 2001) at multiple spatial and temporal scales. For example, Yarnell et al. (2007) found that the interaction of rainfall variability, fire and moderate grazing helped to maintain small mammal biodiversity in South African grasslands through positive effects on habitat heterogeneity and availability of habitat types for mammals. At KPBS, bison prefer recently burned patches, and abandoned recently used but not burned patches early in the summer (Raynor et al. 2015, 2016). Grazing intensity levels out among watersheds toward the end of the growing season in response to increased homogenization of forage quality as the vegetation matures (Raynor et al. 2015, 2016). Grazing in combination with other physical disturbances like trampling and wallowing promotes increased forb abundance and promotes spatially heterogeneous vegetation canopy structure by reducing grass cover dominance when compared to non-grazed sites (Collins et al. 1998, Collins & Calabrese 2012, Hartnett et al. 1996, Towne et al. 2005). Thus, increasing habitat availability and diversity for consumers at multiple trophic levels, including spiders, creates gradients of vegetation structure and heterogeneity and associated distribution of key habitat resources that vary from year to year across the landscape (Figs. 2.9).

Changes in the physical characteristics of the habitat mediated through key vegetation resources can affect consumer species distribution, such as in the abundance and species richness distribution of flower-visiting insects (Sjödin et al. 2008), or the distribution of spider families whose presence was closely correlated to key vegetation resources such as habitat refuges and hunting grounds (Malumbres et al. 2013). At KPBS, species diversity and density of thomisids increased with increasing abundance of flowering plants and was highest on grazed open grasslands burned at 4-year intervals. Similarly, the distribution of other spider families was also closely related to the distribution of key vegetation resources or physical characteristics. In contrast, habitat generalists like spiders from the family Oxyopidae occurred at similar abundances across all habitat types. It is clear that habitat shifts will preferentially favor some groups of taxa over others based on basic biological needs and thus influence shifts in community diversity and taxonomic composition.

Along with fire and grazing, the topography at KPBS also influences vegetation patterns, which potentially affects the distribution of grazing within the landscape along an elevation gradient and the distribution of habitat types for other consumers in the community. For example, Uetz (1976) documented how flooding occurrence influenced taxonomic dominance of ground dwelling spider communities in response to altered vegetation structure along an elevation gradient. The families Clubionidae, Gnaphosidae, Hahniidae and Thomisidae were more dominant in uplands where litter accumulated, and the Lycosidae were dominant where the terrain was more open at lower elevations. Similar patterns were observed at KPBS where species richness and abundance of the family Thomisidae was higher towards the upper plateau areas of grazed watersheds were abundance of flowering plants is higher. In contrast, agelenids (funnel web spiders) dominate in lowland areas along riparian stands where appropriate structure for web-attachments is abundant (unpublished data). I also found that richness of hunting strategies was higher in slope and lowland habitats in both early-summer and late-summer in association with woody vegetation islands encroaching on open grassland along an elevation gradient on watersheds subject to intermediate and low burning frequency (Briggs et al. 2002, Ratajczak et al. 2012, Veach et al. 2014).

β-diversity may increase in spatially heterogeneous landscape. Cano and Leynaud (2010) found that amphibian β-diversity in the Argentinian Humid Chaco benefited from the vegetation mosaic generated fire and grazing where local amphibian assemblages were surrounded by a mosaic of patches at different successional stages. At KPBS, the β species richness of spiders at the landscape scale is 9.4x higher than the average richness found at local sites, and species richness is 7.8 times higher than the maximum number of hunting strategies observed. Including woody-grassland transition habitats, where species diversity was 1.5x to almost double the number of maximum number of hunting strategies describe for KPBS. Spider species richness at the landscape level was ~ 4.4 higher than that of woody-grasslands transition habitats the local hotspot of spider diversity at KPBS. Results from all habitat types described here showed that spider species richness within sites were on average twice as great as the richness of hunting strategies. Thus, a mosaic of habitat types in response to topography, fire and grazing structures the spatial coexistence of spider species within patches of similar physical and microclimate even if these species do not co-occur in the same patches within the landscape. *Pyric herbivory not only promoted increases in species diversity, species evenness and richness of hunting strategies across the landscape through indirect effects on habitat structure, it promoted the coexistence of species in syntopy at multiple spatial and temporal scales mediated through direct effect on vegetation structure and heterogeneity and indirectly on arthropod* 2^0 *productivity.*

Conclusions

Synergistic effects of fire and grazing disturbances in combination with variable weather and topography increased the total diversity of habitat types and the configurational landscape heterogeneity with number, size and arrangement of habitat patches (Perović, et al. 2015). Spider assemblages responded to these disturbances at multiple spatial and temporal scales across the landscape through direct responses to vegetation attributes as predicted by the habitat complexity and heterogeneity hypothesis. Richness of taxonomic and functionally (richness of hunting strategies) distinct spider assemblages across the landscape reflects the diversity of microhabitat availability determined by local vegetation attributes (Sudhikumar at al. 2005). Increased species diversity, species evenness and richness of hunting strategies can be attributed to two equally important factors for explaining community assembly. (1) *Increased vertical and horizontal vegetation structural complexity and heterogeneity* leads to increased availability of microhabitat types and provides opportunities to reduce intra-guild predation and competition through niche partitioning at multiple spatial and temporal scales. Moreover, (2) *increased secondary productivity* (insect biomass) which also responds to increased vegetation structural complexity and heterogeneity provides a possible complementary trophic mechanism for spider community assembly, leading to taxonomically and functionally more diverse spider assemblages through higher abundance of food resources and more opportunities to partition this limiting resource. Moreover, increased β-diversity results from the shifting mosaic of patches with different vegetation structure in time and space. My study contributes to our understanding of the dynamic nature of spider community assembly in response to changes in the physical structure of it habitat. Results provide important insights for managing biodiversity, heterogeneity and ecosystem services in the form of insect population management from natural enemies in natural and anthropogenic landscapes, including agricultural fields or city gardens.

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Figures and Tables

Table 2-1. *Early-summer* and *late-summer* samples 2011-2013 summarizing vegetation responses to abiotic and biotic grassland ecosystem drivers. AIC results for models with ΔAICc < 2 are summarized here and considered parsimonious; where AICc = AIC corrected for small ample size, LL = log likelihood, df = degrees of freedom, R2 = adjusted regression coefficient, P = model P-value, ΔAICc = difference between the top model and given model AICc, wi = model weight.

Early-summer

Model Variables	AICc	LL	df	adj.R^2	P	ΔAICc	w_i
A. LAIMean							
Drought, Precip, Burned, Habitat	778.52	-381.22	7	0.95	2.2e-16	0	0.40
Drought, Precip, BisonHabitatUseIndex, TopoPosition	779.57	-383.02	6	0.95	2.2e-16	1.05	0.24
Drought, Precip, Burned, TopoPosition, Habitat	779.91	-380.54	8	0.95	2.2e-16	1.27	0.21
Drought, Precip, BisonHabitatUseIndex	780.40	-384.67	5	0.94	2.2e-16	1.88	0.16
B. LAICV							
Precip, Drought, BisonHabitatUseIndex	21.36	-5.14	5	0.28	6.34e-5	0	0.20
Precip, Habitat	21.68	-5.31	5	0.28	7.33e-5	0.32	0.17
Precip, Drought, Habitat	21.86	-4.16	6	0.29	9.20e-5	0.50	0.15
Precip, Drought, Habitat, Burned	22.43	-3.18	7	0.30	1.22e-4	1.07	0.12
Precip, Drought, Habitat, BisonHabitatUseIndex	22.46	-3.19	7	0.30	1.23e-4	1.10	0.11
Precip, Habitat, Burned	22.79	-4.63	6	0.28	1.38e-4	1.44	0.10
Precip, Drought, BisonHabitatUseIndex, TopoPosition	23.01	-4.74	6	0.28	1.51e-4	1.65	0.09
Precip, Habitat, BisonHabitatUseIndex	23.28	-4.88	6	0.27	1.70e-4	1.92	0.08
C. Central Tendency of Vegetation Height							
Precip, Habitat, WeeksSinceBurn, Burned	398.84	-191.38	7	0.72	3.6e-15	0	0.42
Precip, Habitat, WeeksSinceBurn, Burned, Drought	400.31	-190.80	8	0.72	1.2e-14	1.46	0.20
Precip, Habitat, WeeksSinceBurn, Burned, TopoPosition	400.34	-190.81	8	0.72	1.2e-14	1.50	0.20
Precip, Habitat, WeeksSinceBurn	400.64	-193.55	6	0.70	3.5e-15	1.79	0.17
D. Central Tendency CV							
Precip, Habitat	-81.76	46.42	5	0.51	8.9e-10	0	0.53
Precip, Habitat, TopoPosition	-80.16	46.85	6	0.51	3.19e-9	1.60	0.24
Precip, Habitat, Burned	-80.08	46.80	6	0.51	3.32e-9	1.69	0.23
E. Number of Vegetation Layers							
Habitat, WeeksSinceBurn, Burned, Precip	329.98	-156.95	7	0.75	2.2e-16	0	0.56
Habitat, WeeksSinceBurn, Burned	331.67	-159.07	6	0.74	2.2e-16	1.69	0.24
Habitat, WeeksSinceBurn, Burned, Precip, BisonHabitatUseIndex	331.96	-156.62	8	0.75	6.1e-16	1.98	0.21

Late-summer

Model Variables	AICc	LL	df	adj.R^2	P	ΔAICc	W_i
A. LAIMean							
Drought, Precip, Habitat	884.79	-435.72	6	0.79	2.2e-16	0	0.33
Drought, Precip, Habitat, TopoPosition	885.26	-434.71	7	0.79	2.2e-16	0.47	0.26
Drought, Precip, Habitat, WeeksSinceBurn	885.42	-434.79	7	0.79	2.2e-16	0.64	0.24
Drought, Precip, Habitat, TopoPosition, WeeksSinceBurn	885.98	-433.79	8	0.80	2.2e-16	1.19	0.18

B. LAICV							
BisonHabitatUseIndex	289.81	-141.72	3	0.11	3.54e-3	0	0.47
BisonHabitatUseIndex, Precip	290.85	-141.11	4	0.11	8.21e-3	1.04	0.28
BisonHabitatUseIndex, Drought	300.00	-141.19	4	0.11	8.83e-3	1.19	0.26
C. Central Tendency of Vegetation Height							
Drought,Precip, Habitat, WeeksSinceBurn	538.72	-261.44	7	0.61	9.1e-13	0	0.59
Drought, Precip, Habitat, WeeksSinceBurn, BisonHabitatUseIndex	539.51	-260.51	8	0.61	2e-14	0.71	0.41
D. Central Tendency CV							
Habitat, WeeksSinceBurn, BisonHabitatUseIndex, Burned	-64.67	40.25	7	0.52	6e-10	0	0.70
Habitat, WeeksSinceBurn, BisonHabitatUseIndex	-62.97	38.16	6	0.50	8.2e-10	1.70	0.30
E. Number of Vegetation Layers							
Drought, Precip, Habitat, WeeksSinceBurn, BisonHabitatUseIndex, TopoPosition	389.20	-184.07	9	0.77	2.2e-16	0	0.33
Drought, Precip, Habitat, WeeksSinceBurn, TopoPosition	389.49	-185.54	8	0.77	2.2e-16	0.29	0.29
Drought, Precip, Habitat, WeeksSinceBurn	389.65	-186.91	7	0.76	2.2e-16	0.45	0.26
Drought, Precip, Habitat, WeeksSinceBurn, BisonHabitatUseIndex	391.18	-186.39	8	0.76	2.2e-16	1.99	0.12

Table 2-2. Abiotic and biotic predictor variable importance at describing different attributes of vegetation structure and spatial heterogeneity on *early-summer* and *late-summer* samples 2011-2013. Results best describe the habitat template encounter by spiders. Variable importance was estimated as the proportion of models with ΔAICc < 2 that included the respective variable.

Predictor variables	**Early-summer**					**Late-summer**				
	LAIM	**LAICV**	**CTVH**	**CTCV**	**NVL**	**LAIM**	**LAICV**	**CTVH**	**CTCV**	**NVL**
BisonHabitatUseIndex	0.39	0.47			0.21		1.0	0.41	1.0	0.45
Burned	0.61	0.21	0.83	0.23	1.0				0.7	
WeeksSinceBurn			1.0		1.0	0.42		1.0	1.0	1.0
Drought	1.0	0.66	0.20			1.0	0.26	1.0		1.0
Precip	1.0	1.0	1.0	1.0	0.76	1.0	0.28	1.0		1.0
Habitat	0.61	0.72	1.0	1.0	1.0	1.0		1.0	1.0	1.0
TopoPosition	0.45	0.09	0.20	0.24		0.44				0.61

Table 2-3. Patterns of grassland vegetation structure and heterogeneity driven by fire, grazing, weather and topographic position.

Early-summer	**WSB**	**Burned**	**BHUI**	**Drought**	**Precip**	**Habitat**	**Topo Position**
Response variables	F(df)	X^2 (df)	F(df)	F(df)	F(df)	X^2 (df)	X^2,(df)
	adj.R^2, p	p	adj.R^2, p	adj.R^2, p	adj.R^2, p	p	P
A. LAIMean	0.22 (60)	2.3 (1)	0.03 (60)	**31.89 (60)**	**556.3 (60)**	5.45 (2)	0.3,(2)
	-0.013, 0.64	0.13	-0.016, 0.87	**0.34, 4.73e-7**	**0.9<2.2e-16**	0.07	0.86
B. LAICV	0.072 (60)	1.27 (1)	**7.7 (60)**	**7.026 (60)**	**12.98 (60)**	**16.33 (2)**	1.86 (2)
	-0.016, 0.79	0.26	**0.10, 7.4e-3**	**0.09, 1.03e-2**	**0.16, 6.4e-4**	**0.00028**	0.39
C. Central Tendency of Vegetation Height	**35.79 (60)**	**9.13 (1)**	**10.59 (60)**	1.55 (60)	1.74 (60)	**38.59 (2)**	**6.89 (2)**
	0.36, 1.31e-7	**0.0025**	**0.14, 1.87e-3**	0.01, 0.22	0.012, 0.19	**4.18e-9**	**0.032**
D. Central Tendency CV	1.39 (60)	1.14 (1)	**7.24 (60)**	**5.12 (60)**	**15.49 (60)**	**25.81 (2)**	0.22 (2)
	0.006, 0.25	0.29	**0.09, 9.2e-3**	**0.06, 0.027**	**0.19 2.19e-4**	**2.49e-6**	0.90
E. Number of Vegetation Layers	**30.33 (60)**	**11.06 (1)**	**5.28 (60)**	2.46 (60)	0.04 (60)	**31.13 (2)**	**7.19 (2)**
	0.33 8.03e-7	**8.81e-4**	**0.07, 0.025**	0.023, 0.12	-0.016, 0.84	**1.74e-7**	**0.028**

Late-summer	**WSB**	**Burned**	**BHUI**	**Drought**	**Precip**	**Habitat**	**Topo Position**
Response variables	F(df)	X^2 (df)	F(df)	F(df)	F(df)	X^2 (df)	X^2 (df)
	adj.R^2, p	p	adj.R^2, p	adj.R^2, p	adj.R^2, p	p	P
A. LAIMean	0.026 (67)	0.29 (1)	3.38 (67)	2.77 (67)	1.42 (60)	**11.09 (2)**	0.085 (2)
	-0.015, 0.87	0.59	0.034, 0.071	0.025, 0.10	0.0061, 0.24	**0.0039**	0.96
B. LAICV	0.06 (67)	0.014 (1)	**9.14 (67)**	1.32 (67)	1.92 (67)	**31.99 (2)**	0.23 (2)
	-0.014, 0.81	0.91	**0.11, 0.0035**	0.0047, 0.25	0.013, 0.17	**1.13e-7**	0.89
C. Central Tendency of Vegetation Height	**25.9 (67)**	**6.041 (1)**	**6.83 (67)**	1.99 (67)	0.31 (67)	**42.86 (2)**	**10.88 (2)**
	0.27, 3.12e-6	**0.014**	**0.08, 0.011**	0.014, 0.16	-0.01, 0.58	**4.93e-10**	**0.0044**
D. Central Tendency CV	1.64 (67)	0.56 (1)	**39.93 (67)**	0.23 (67)	0.45 (67)	**28.05 (2)**	0.12 (2)
	0.0094, 0.20	0.45	**0.36, 2.45e-8**	-0.011, 0.63	-0.008, 0.51	**8.1e-7**	0.94
E. Number of Vegetation Layers	29.19 (67)	**7.59 (1)**	**8.66 (67)**	**4.03, (67)**	1.63 (67)	**39.13 (2)**	**13.59 (2)**
	0.29, 9.35e-5	**0.0059**	**0.10, 0.0045**	**0.043, 0.049**	0.0092, 0.21	**3.18e-9**	**0.0011**

Table 2-4. Richness of spider hunting strategies found at KPBS and spider families associated with each hunting group. Sample specimens were collected from early-summer 2011 to late-summer 2013 and identified to lowest taxonomic level possible.

		Web size (cm^2)	
Hunting Strategies	**Family**	**Minimum**	**Maximum**
Web-morphology			
Small-Orb	Araneidae	4	< 50
	Uloboridae		
Medium-Orb	Tetragnathidae, Araneidae	> 50	740
Large-Orb	Araneidae	> 740	3239
Funnel-Web	Agelenidae	9.43	2842
	Amphinectidae		
	Cybaidae		
Doily- Web	Linyphiidae	5	506
	Hahniidae		
All-Direction-Web	Theridiidae	55	566
	Mysmenidae		
	Nesticidae		
Mesh-Web	Dictynidae	4	12
Purse-Web	Atypidae		
Slingshot-Orb-Web	Theridiosomatidae		
Wandering			
Active-Ground-hunter	Gnaphosidae		
	Salticidae		
Ground-Sit & Wait	Lycosidae		
Spider Specialist	Mimetidae		
Foliage-Stalker	Oxyopidae		
	Salticidae		
Stem-Runner	Anyphaenidae		
	Philodromidae		
Foliage –Sit & Wait	Pisuaridae		

	Thomisidae
Foliage-Ground-Sit & Wait	Thomisidae
Ant-mimic	Salticidae
Unknown	

Table 2-5. *Early-summer* and *Late-summer* (2011-2013) spider community responses to vegetation structure, vegetation spatial heterogeneity, habitat secondary productivity, rainfall variability, and topography. AIC results for models with ΔAICc < 2 are summarized here and considered parsimonious; AICc = AIC corrected for small ample size, LL = log likelihood, df = degrees of freedom, R^2 = adjusted regression coefficient, P = model P-value, ΔAICc = difference between the top model and given model AICc, wi = model weight.

Early-summer

Model Variables	AICc	LL	df	adj.R^2	P	ΔAICc	w_i
A. Spider Density							
LAICV, LAIMean, Year	-2.98	7.03	5	0.36	2.65e-6	0	0.70
LAICV, LAIMean, Year, NumberVegetationLayers	-1.31	7.42	6	0.35	7.38e-6	1.67	0.30
B. Spider Diversity							
InsectBiomass, LAIMean, NumberVegetationLayers,TopoPosition	57.74	-22.10	6	0.51	2.93e-9	0	0.17
InsectBiomass, LAIMean, NumberVegetationLayers,TopoPosition, CentralTendencyCV	57.92	-20.92	7	0.52	4.72e-9	0.19	0.16
InsectBiomass, LAIMean, NumberVegetationLayers,TopoPosition, LAICV	58.50	-21.21	7	0.52	6.06e-9	0.76	0.12
InsectBiomass, LAIMean, NumberVegetationLayers, CentralTendencyCV	58.83	-22.65	6	0.51	4.76e-9	1.09	0.10
InsectBiomass, LAIMean, TopoPosition, CentralTendencyCV, CentralTendencyVegHeight	58.95	-21.44	7	0.52	7.37e-9	1.22	0.09
InsectBiomass, LAIMean, CentralTendencyCV, CentralTendencyVegHeight	59.10	-22.79	6	0.50	5.38e-9	1.37	0.09
InsectBiomass, LAIMean, NumberVegetationLayers	59.28	-24.10	5	0.50	3.47e-9	1.54	0.08
InsectBiomass, LAIMean, NumberVegetationLayers,TopoPosition, Year	59.53	-21.73	7	0.51	9.46e-9	1.79	0.07
InsectBiomass, LAIMean, NumberVegetationLayers, LAICV	59.66	-23.07	6	0.50	6.91e-9	1.92	0.07
InsectBiomass, LAIMean, NumberVegetationLayers,TopoPosition, CentralTendencyVegHeight	59.71	-21.82	7	0.51	1.02e-8	1.97	0.06
C. Evenness of species richness							
InsectBiomass, LAIMean, NumberVegetationLayers,	-103.17	57.12	5	0.19	1.83e-3	0	0.18
InsectBiomass, LAIMean, NumberVegetationLayers , LAICV	-103.12	58.32	6	0.20	1.85e-3	0.05	0.17
InsectBiomass, LAIMean	-102.31	55.51	4	0.16	2.41e-3	0.85	0.12
InsectBiomass, LAIMean, CentralTendencyCV	-102.16	56.61	5	0.17	2.86e-3	1.01	0.11
InsectBiomass, LAIMean, NumberVegetationLayers, CentralTendencyCV	-102.14	57.83	6	0.19	2.77e-3	1.03	0.11
InsectBiomass, LAIMean, NumberVegetationLayers, CentralTendencyVegHeight	-102.04	57.78	6	0.19	2.89e-3	1.13	0.10
InsectBiomass, LAIMean, CentralTendencyCV, Year	-101.43	57.48	6	0.18	3.72e-3	1.74	0.08
InsectBiomass, LAIMean, LAICV	-101.40	56.24	5	0.16	3.99e-3	1.77	0.07
InsectBiomass, LAIMean, NumberVegetationLayers, LAICV, CentralTendencyVegHeight	-101.25	58.66	7	0.20	3.52e-3	1.91	0.07
D. Richness of hunting strategies							
CentralTendencyVegHeight, LAIMean, InsectBiomass	219.66	-103.07	6	0.57	7.6e-10	0	0.66
CentralTendencyVegHeight, LAIMean, InsectBiomass, TopoPosition	221	-102.46	7	0.58	2.11e-9	1.34	0.34

Late-summer

Model Variables	AICc	LL	df	adj.R^2	P	ΔAICc	W_i
A. Spider Density							
Year, NumberVegetationLayers	68.99	-30.18	4	0.19	3.22e-4	0	0.54
Year, NumberVegetationLayers, CentralTendencyCV	70.61	-29.83	5	0.19	8.41e-4	1.61	0.24

Year, NumberVegetationLayers, TopoPosition	70.73	-29.89	5	0.19	8.90e-4	1.74	0.23
B. Spider Diversity							
InsectBiomass, CentralTendencyCV, CentralTendencyVegHeight	31.33	-10.19	5	0.29	1.10e-5	0	0.53
InsectBiomass, CentralTendencyCV, CentralTendencyVegHeight, NumberVegetationLayers	32.94	-9.79	6	0.29	2.82e-5	1.62	0.24
InsectBiomass, CentralTendencyCV, NumberVegetationLayers	33.02	-11.04	5	0.28	2.38e-5	1.70	0.26
C. Evenness of species richness							
CentralTendencyCV, LAIMean, TopoPosition	-170.50	90.73	5	0.30	7.50e-6	0	0.27
CentralTendencyCV, LAIMean	-169.92	89.27	4	0.28	6.38e-6	0.58	0.20
CentralTendencyCV, LAIMean, TopoPosition, CentralTendencyVegHeight	-169.34	91.35	6	0.30	1.61e-5	1.65	0.15
CentralTendencyCV, LAIMean, TopoPosition, Year	-169.21	91.28	6	0.30	1.70e-5	1.29	0.14
CentralTendencyCV, LAIMean, Year	-169.03	89.99	5	0.29	1.47e-5	1.47	0.13
CentralTendencyCV, Year	-168.96	88.79	4	0.27	1.01e-5	1.55	0.12
D. *Richness hunting strategies*							
NumberVegetationLayers, LAIMean,	244.77	-118.07	4	0.37	1.12e-7	0	0.43
NumberVegetationLayers, Year	246.25	-118.81	4	0.37	2.27e-7	1.48	0.21
NumberVegetationLayers, LAIMean, CentralTendencyVegHeight	246.46	-117.75	5	0.39	4.38e-7	1.68	0.19
NumberVegetationLayers, LAIMean, TopoPosistion	246.50	-117.78	5	0.39	4.47e-7	1.73	0.18

Table 2-6. Predictor variable importance for *early-summer* and *late-summer* (2011-2013) spider community responses. Variable importance was estimated as the proportion of models with ΔAICc < 2 that included the respective variable.

Predictor variables	**Early-summer**				**Late-summer**			
	Density ($\#/m^2$)	**Species Diversity (H')**	**Species Evenness (E)**	**Richness of Hunting Strategies**	**Density ($\#/m^2$)**	**Species Diversity (H')**	**Species Evenness (E)**	**Richness of Hunting Strategies**
Year	1.0	0.07	0.07	1.0	1.0		0.39	0.2
TopoPosition		0.67		0.34	0.22		0.55	0.18
CentralTendencyVegHeigth		0.24	0.17	1.0		0.77	0.15	0.19
NumberVegetationLayers	0.3	0.82	0.63		1.0	0.47		1.0
LAIMean	1.0	1.0	1.0	1.0			0.88	0.8
CentralTendencyCV		0.43	0.29		0.24	1.0	1.0	
LAICV	1.0	0.18	0.32					
InsectBiomass		1.0	1.0	1.0		1.0		

Table 2-7. Changes in vegetation structure and spatial heterogeneity affect spider community complexity. Spider community responses include: Density, Richness, Diversity, Evenness of species richness and Evenness of hunting strategies, are influenced differently by different aspects of vegetation structure and heterogeneity and insect biomass. Spider community responsiveness to changes in vegetation structure and spatial heterogeneity varied with sampling period. Vegetation canopy closure and its spatial heterogeneity are represented by LAIM and LAICV, respectively. Vegetation height (cm) and its spatial heterogeneity are represented by CTVH and CTCV, respectively. Number of vegetation layers is identified by NVL and insect biomass by IB.

Early-summer	**LAIM**	**LAICV**	**CTVH**	**CTCV**	**NVL**	**IB**
Model Variables	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p
A. Spider Density	**23.49 (60)** **0.27, 9.24e-6**	0.49 (60) -0.0084, 0.49	0.27 (60) 0.012, 0.61	3.06 (60) 0.033, 0.085	0.18 (60) -0.014, 0.67	6.11 (60) 0.077, 0.016
B. Spider Diversity	**19.08 (60)** **0.23, 5.05e-5**	**7.44 (60)** **0.10, 0.0083**	2.03 (60) 0.017, 0.16	**23.2 (60)** **0.27, 1.03e-5**	**9.7 (60)** **0.13, 0.0028**	**41.95 (60)** **0.40, 1.94e-8**
C. Evenness of species richness	2.95 (60) 0.031, 0.091	0.28 (60) -0.012, 0.60	0.65 (60) -0.006, 0.43	2.46 (60) 0.023, 0.12	**3.99 (60)** **0.047, 0.05**	3.75 (60) 0.043 0.058
D. Richness of hunting strategies	**33.25 (60)** **0.35, 3.01e-7**	**5.97 (60)** **0.08, 0.018**	**4.75 (60)** **0.06, 0.033**	**11.94 (60)** **0.15, 0.001**	**8.29 (60)** **0.11, 0.0055**	**18.62 (60)** **0.22, 6.05e-5**

Late-summer	**LAIM**	**LAICV**	**CTVH**	**CTCV**	**NVL**	**IB**
Model Variables	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p	F(df) adj.R^2, p
A. Spider Density	**5.16 (67)** **0.06, 0.026**	0.31 (67) -0.01, 0.58	0.99 (67) -0.0002, 0.32	0.60 (67) -0.006, 0.44	2.12 (67) 0.016, 0.15	1.86 (67) 0.013, 0.18
B. Spider Diversity	**6.21 (67)** **0.071, 0.015**	0.49 (67) -0.0075, 0.49	**8.97 (67)** **0.11, 3.85e-3**	**9.06 (67)** **0.11, 3.67e-3**	**11.75 (67)** **0.14, 1.05e-3**	**7.13 (67)** **0.08, 9.5e-3**
C. Evenness of species richness	**21.14 (67)** **0.23, 1.95e-5**	1.02 (67) 0.00022, 0.32	0.93 (67) -0.0011, 0.34	**11.19 (67)** **0.13, 1.35e-3**	0.32 (67) -0.01, 0.57	**4.77 (67)** **0.053, 0.033**
D. *Richness hunting strategies*	0.10 (67) -0.013, 0.75	0.67 (67) -0.005, 0.42	**23.32 (67)** **0.25, 8.31e-6**	0.10 (67) -0.013, 0.75	**34.58 (67)** **0.33, 1.43e-7**	0.011 (67) -0.015, 0.92

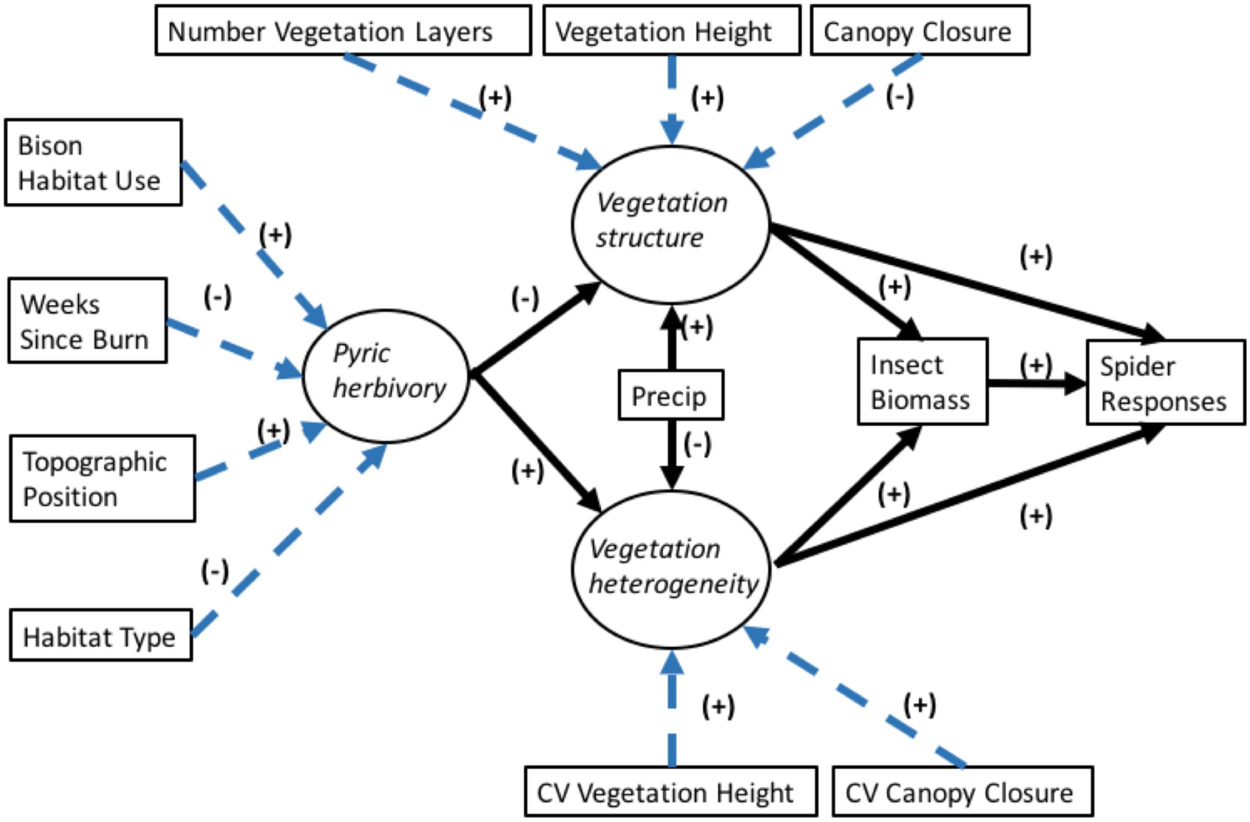

Figure 2-1. Conceptual framework showing predictions of how the ecological driver *pyric herbivory* indirectly structures the richness of local spider assemblages within a spider grassland community through its direct effects on vegetation structure and vegetation spatial heterogeneity. Vegetation attributes determine the diversity of grassland habitat types used by consumers. The conceptual framework was evaluated using the Structural Equation Modeling approach (SEM) and Redundancy Analysis. Boxes represent loading factors: responses and predictor variables for which I have empirical measurements. Ellipses represent latent variables (SEM), variables inferred from other measured variables that describe the synergistic effects of loading factors on a ecological process/interaction. Dashed arrows show which predictor variables were used inferred each latent variable. +/- symbols indicates the expected relation among the loading factor and latent variable. Solid arrows show the interactions of interest. +/- symbols shows the expected interaction among predictor and responses interactions of interest in this model.

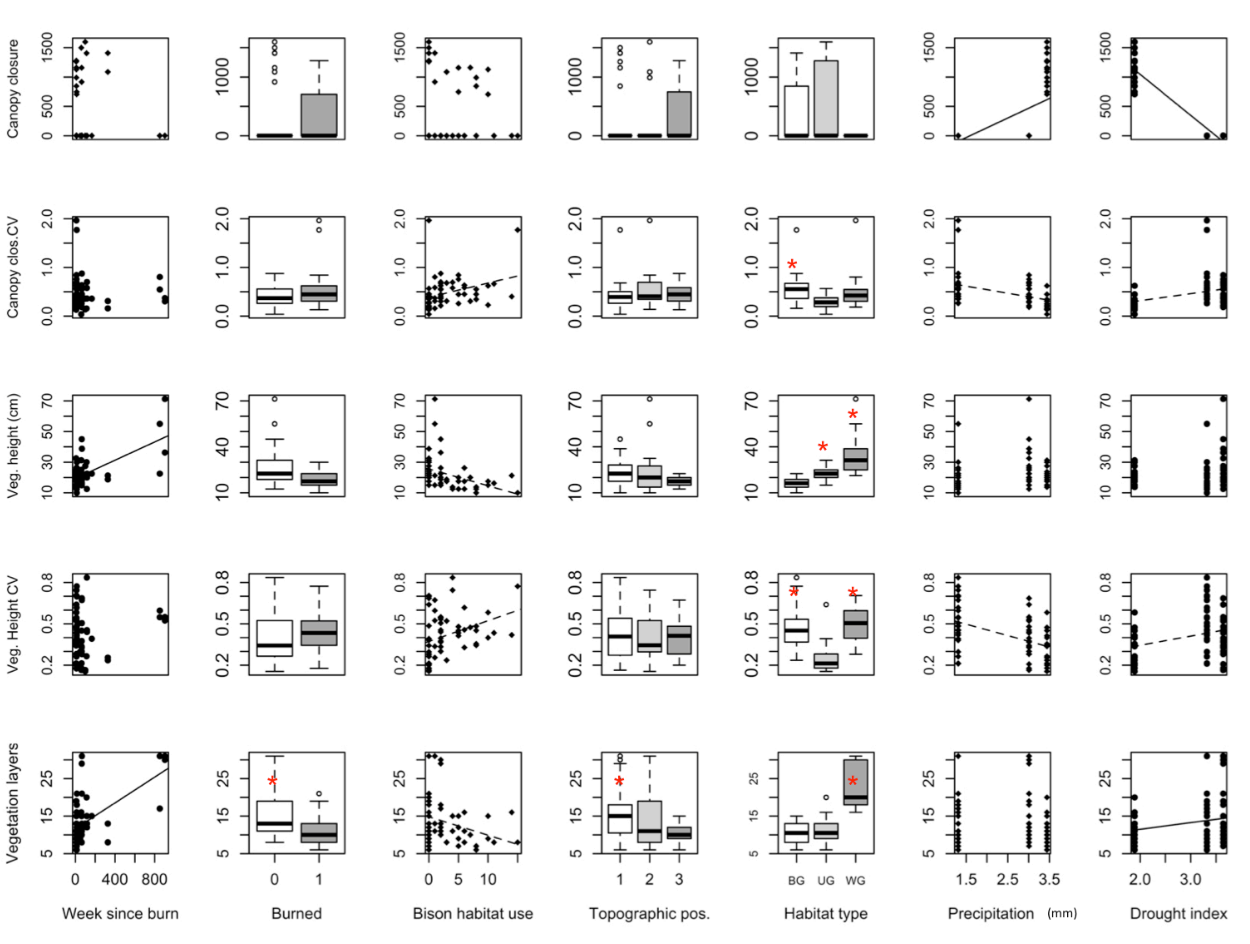

Figure 2-2. ***Early-summer*** **vegetation responses to environmental drivers: fire, grazing, topography and weather. Top to bottom, vegetation responses are as follow: Top row-mean canopy closure (LAIM), second row from top shows variation in canopy closure (LAICV), middle row shows mean vegetation height (CTVH), the second row from the bottom up represents the variability in vegetation height (CTCV) and the bottom row shows the NVL responses. The predictor variables are arrayed from left to right. To assess the effects of fire on vegetation characteristics I looked at (a) time since last burn, measured in weeks (WSB). (b) Burned, where I classified the sites as burned in the spring (1) or not burned in the spring (0) prior to the sampling period in the same year. Grazing effects were characterized using the BHUI, where increases in bison visitation rate to a site were scaled from 1 to 10+, and non-grazed site are classified as 0. The middle column is topographic position, where sites were classified into lowland sites (1), slope-sites (2) and upland sites (3). The next column to the right of the predictor response is the Habitat type where sites were classified into bison-grazed, open-grassland (BG), non-grazed, open-grassland (UG) and woody/grassland transitions (WG) habitat based on dominant vegetation characteristics. The next predictor variables and last two columns show effects of weather variability on vegetation structure and the amount of precipitation received over the growing season until the sampling period (Precipitation), and the Palmer Drought Index values (Drought index). Solid lines in regression plots represent predictor and response interactions with an R^2 equal or greater than 0.20; dashed lines represent**

interactions with an R^2 of less than 0.20. The asterisks on box-plots highlight models with significant response differences from analysis of variance. The box plot elements represent the following: box vertical dimension= interquartile range; horizontal line= median; whiskers= minimum and maximum values; open points= maximum observation 1.5 (IQR) above the 75th percentile.

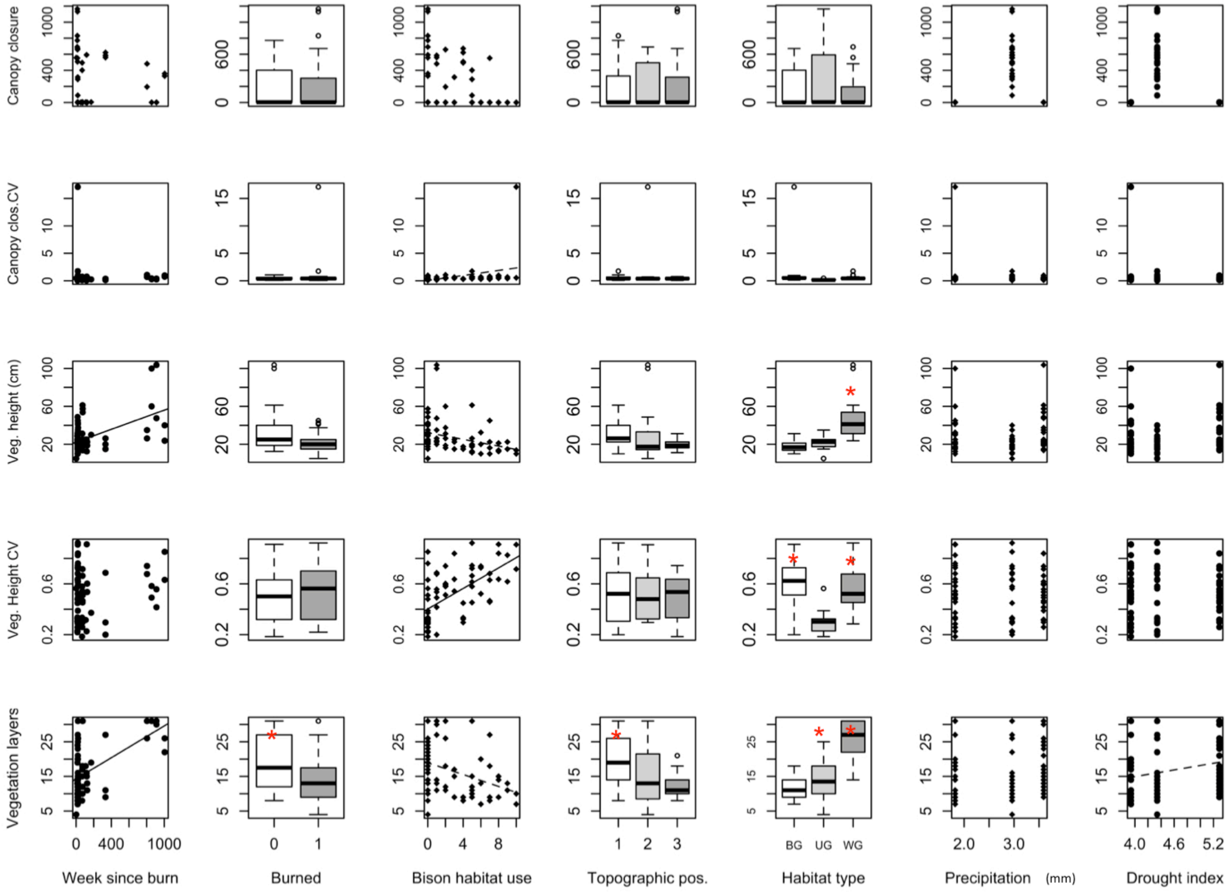

Figure 2-3. ***Late*-summer vegetation responses to environmental drivers: fire, grazing, topography and weather. Top to bottom, vegetation responses are as follow: Top row- mean canopy closure (LAIM), second row from top shows variation in canopy closure (LAICV), middle row shows mean vegetation height (CTVH), the second row from the bottom up represents the variability in vegetation height (CTCV) and the bottom row shows the NVL responses. The predictor variables are arrayed from left to right. To assess the effects of fire on vegetation characteristics I looked at (a) time since last burn, measured in weeks (WSB). (b) Burned, where I classified the sites as burned in the spring (1) or not burned in the spring (0) prior to the sampling period in the same year. Grazing effects were characterized using the BHUI, where increases in bison visitation rate to a site were scaled from 1 to 10+, and non-grazed site are classified as 0. The middle column is topographic position, where sites were classified into lowland sites (1), slope-sites (2) and upland sites (3). The next column to the right of the predictor response is the Habitat type where sites were classified into bison-grazed, open-grassland (BG), non-grazed, open-grassland (UG) and woody/grassland transitions (WG) habitat based on dominant vegetation characteristics. The next predictor variables and last two columns show effects of weather variability on vegetation structure and the amount of precipitation received over the growing season until the sampling period (Precipitation), and the Palmer Drought Index values (Drought index). Solid lines in regression plots represent predictor and response interactions with an R^2 equal or greater than 0.20; dashed lines represents**

interactions with an R^2 of less than 0.20. The asterisks on box-plots highlight models with significant response differences from analysis of variance. The box plot elements represent the following: box vertical dimension= interquartile range; horizontal line= median; whiskers= minimum and maximum values; open points= maximum observation 1.5 (IQR) above the 75th percentile.

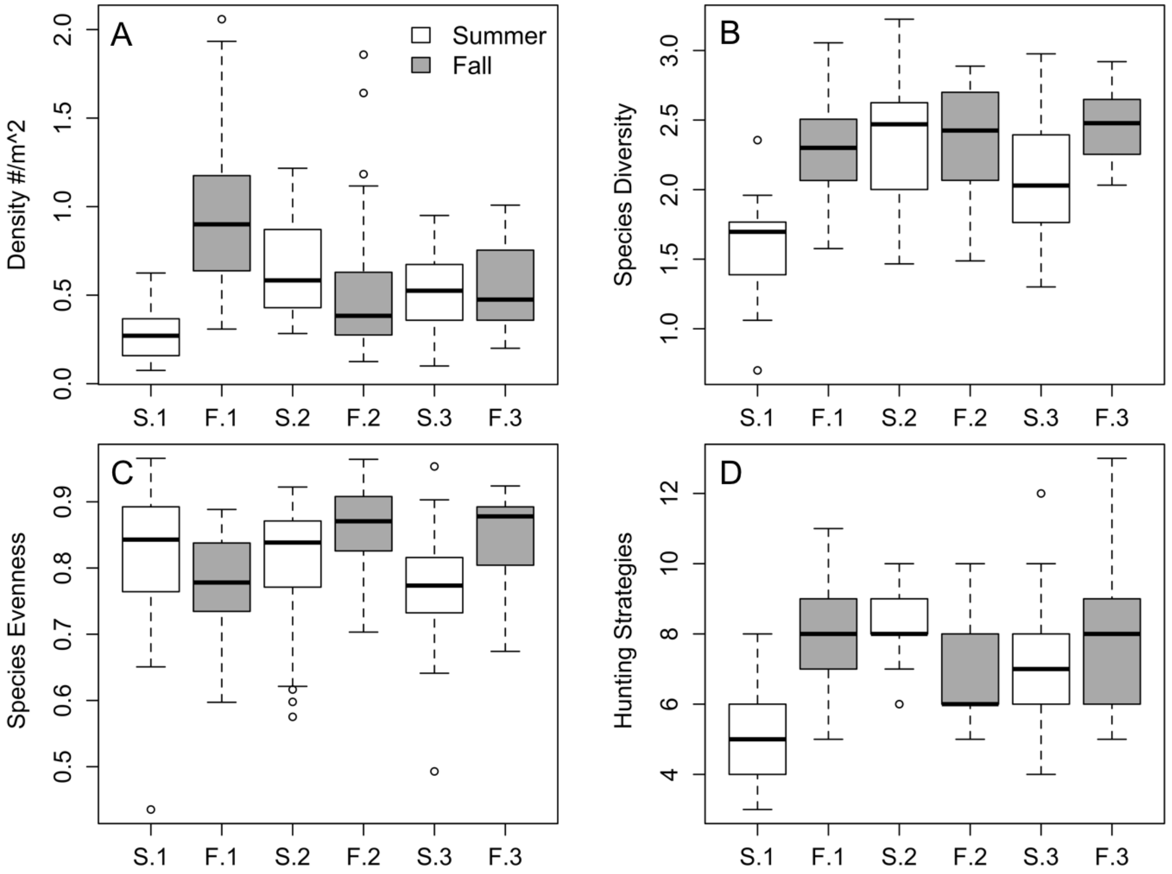

Figure 2-4. Annual variation in seasonal spider community responses represented as box plots. The X-axis represents season (S= early-summer, F= late-summer) and year (2011-2013, respectively). Spider community responses include: (a) mean spider density (# individuals /m^2), (b) Shannon's species diversity (H'), (c) species evenness (E), and (d) number of hunting strategies identified per season and sampling year. The box plot elements represent the following: box vertical dimension= interquartile range; horizontal line= median; whiskers= minimum and maximum values; open points= maximum observation 1.5 (IQR) above the 75th percentile.

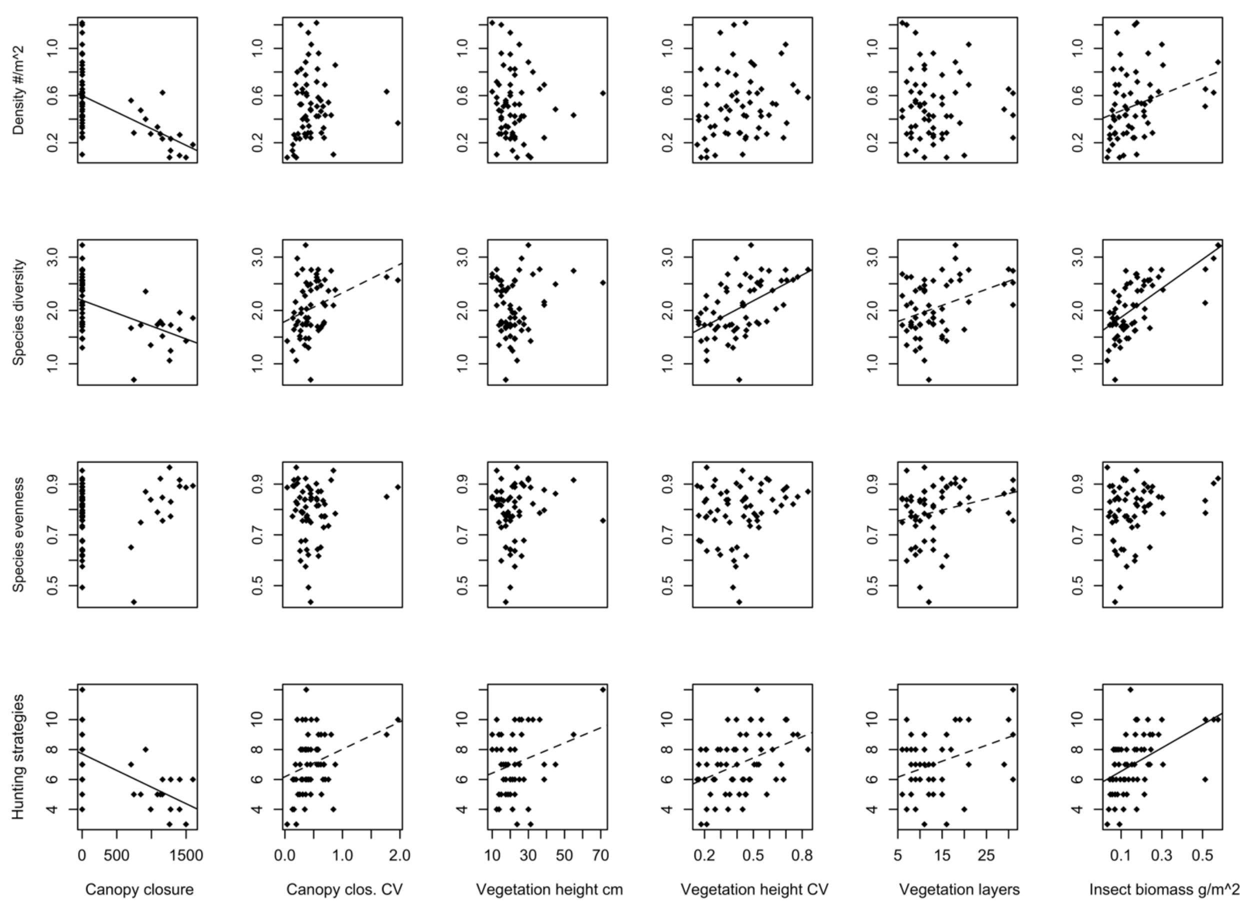

Figure 2-5. *Early-summer* spider community responses to various aspects of vegetation structure, vegetation spatial heterogeneity, and habitat 2^0 productivity in the form of insect biomass. Spider responses from top to bottom are: spider density (top row), species diversity (second row from top), species evenness and richness of hunting strategies (bottom row). The predictor variables from left to right are: canopy closure (LAIM), variability in canopy closure (LAICV), vegetation height (CTVH), variability in vegetation height (CTCV), number of vegetation layers (NVL) and insect biomass. Vegetation structure is represented by LAIM, CTVH and NVL; while vegetation heterogeneity is represented by LAICV and CTCV. Solid lines in regression plots represent predictor and response interactions with an R^2 equal or greater than 0.20; dashed lines represents interactions with an R^2 of less than 0.20.

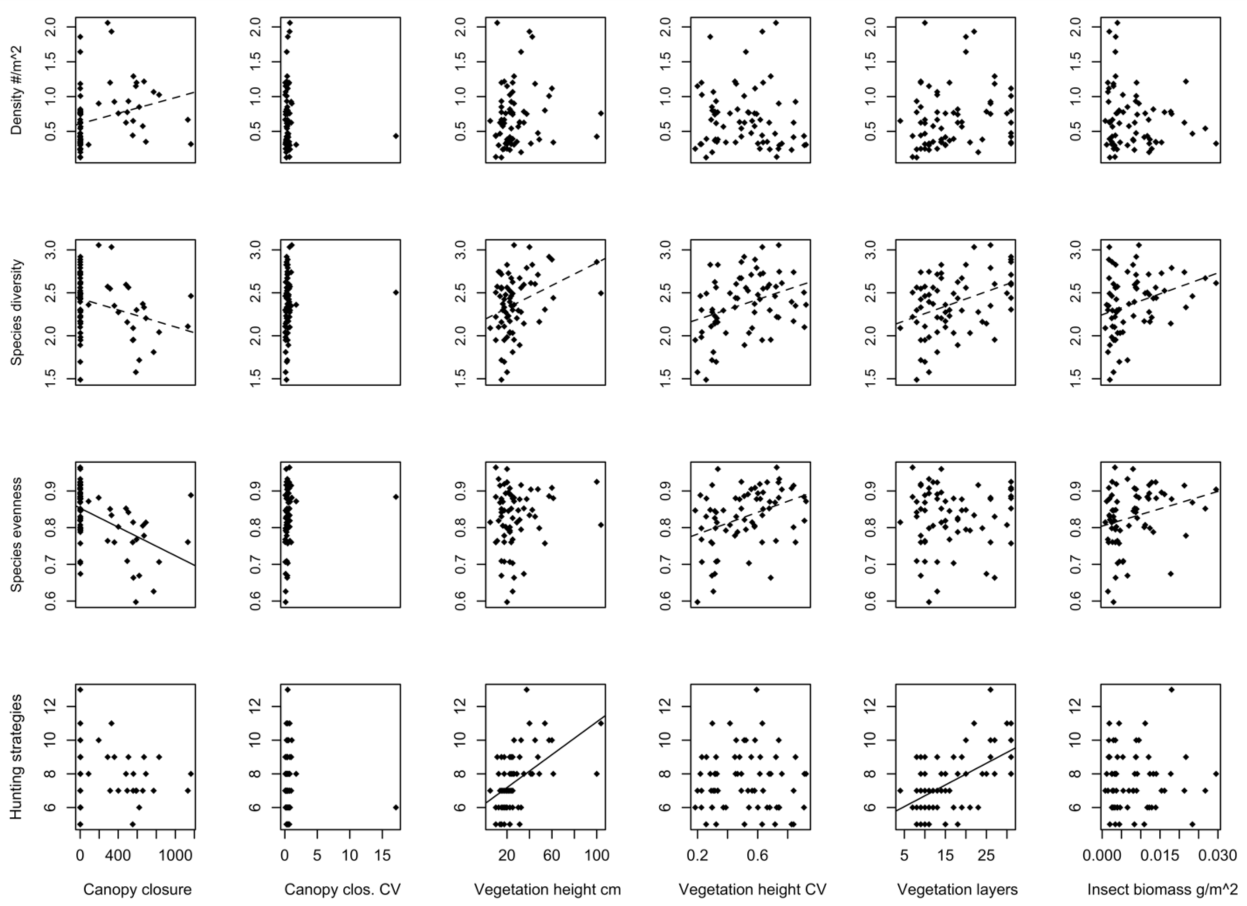

Figure 2-6. ***Late-summer*** **spider community responses to various aspects of vegetation structure, vegetation spatial heterogeneity and habitat 2^0 productivity in the form of insect biomass. Spider responses from top to bottom are: spider density (top row), species diversity (second row from top), species evenness and richness of hunting strategies (bottom row). The predictor variables from left to right are: canopy closure (LAIM), variability in canopy closure (LAICV), vegetation height (CTVH), variability in vegetation height (CTCV), number of vegetation layers (NVL) and insect biomass. Vegetation structure is represented by LAIM, CTVH and NVL; while vegetation heterogeneity is represented by LAICV and CTCV. Solid lines in regression plots represent predictor and response interactions with an R^2 equal or greater than 0.20; dashed lines represents interactions with an R^2 of less than 0.20.**

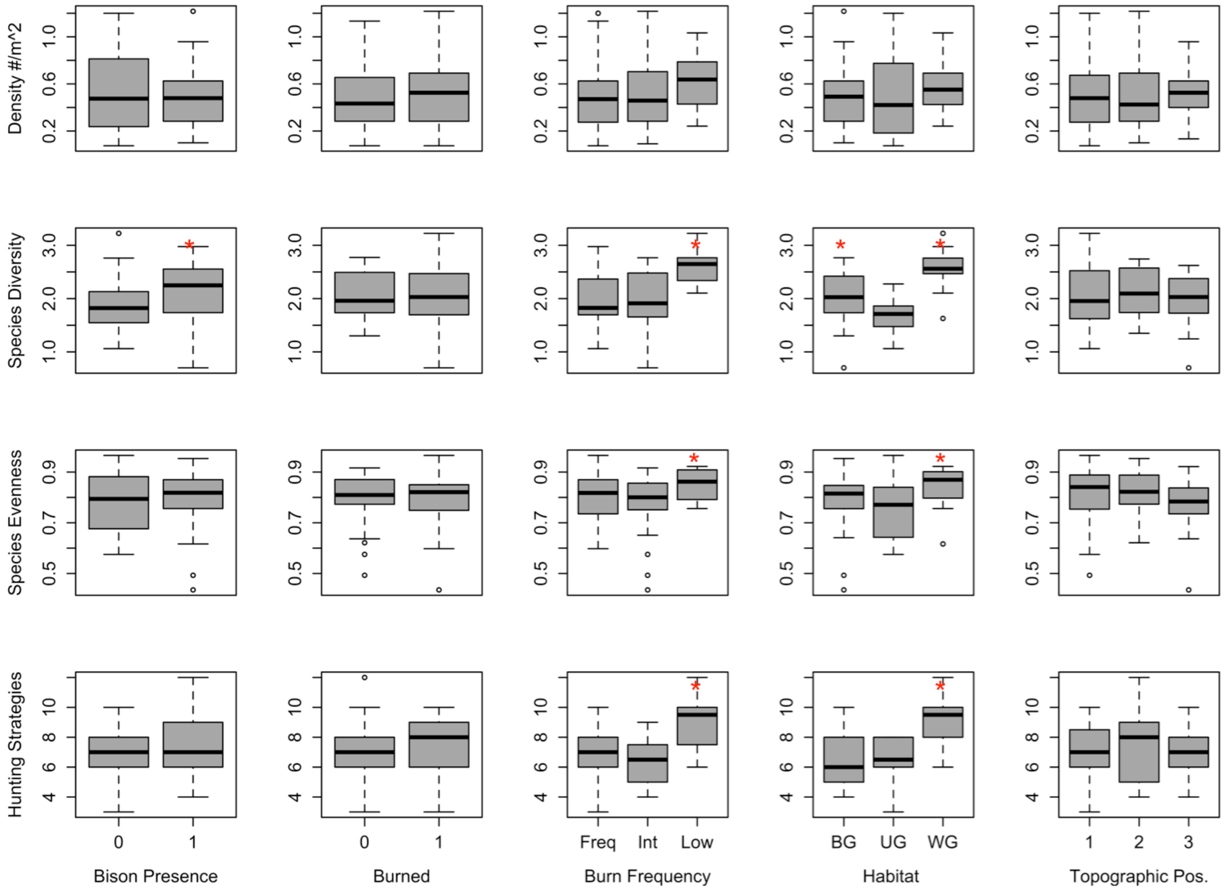

Figure 2-7. *Early-summer* spider community responses to grasslands ecosystem drivers. Spider responses from top to bottom are: spider density (top row), species diversity (second row from top), species evenness and richness of hunting strategies (bottom row). Grazing is represented by Bison presence were non-grazed sites are scores as 0 and grazed sites as 1. Fire was represented by two variables: a) Burned were 0 represent sites that sere not burned in the spring before sampling, and 1 represents sites burned the spring prior to sampling. (b) Burn Frequency, where sites were classified into one of three categories: frequently burnws (Freq. burned every 1 & 2 year), intermediately burned (Int. burned every 4 years), and low burn frequency (Low burn every 20 years). Habitat predictor variables represent the dominant trends in vegetation cover at a site classified as follows: bison grazed open grassland (BG), non-grazed open grasslands (UG) and woody/grassland transitions (WG) habitat based on dominant vegetation cover characteristics. The far right column shows the effects of topographic position on spider community responses were sites were classified into low-land sites (1), slope-sites (2) and upland sites (3). The asterisks on box-plots highlight models with significant response differences for analysis of variance. The box plot elements represent the following: box vertical dimension= interquartile range; horizontal line= median; whiskers= minimum and maximum values; open points= maximum observation 1.5 (IQR) above the 75th percentile.

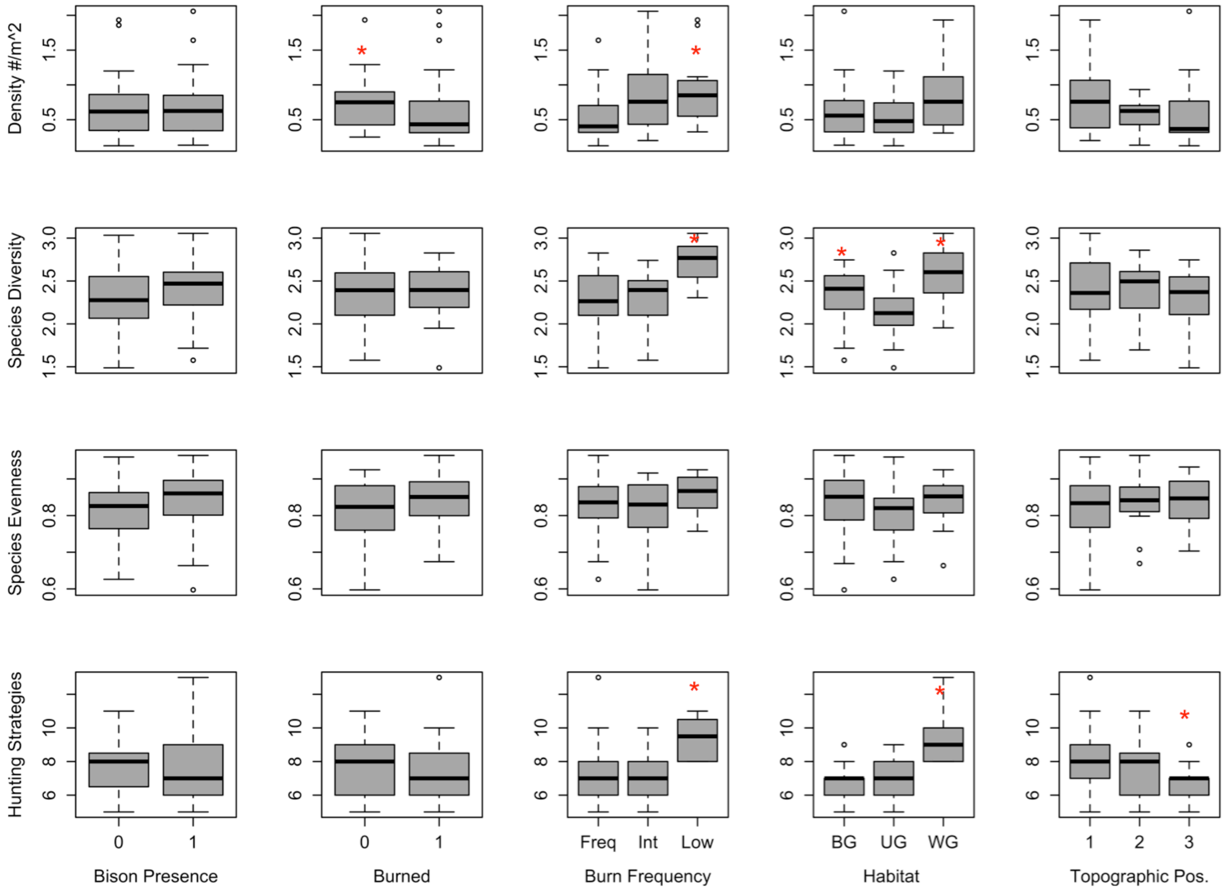

Figure 2-8. *Late-summer* spider community responses to grasslands ecosystem drivers. Spider responses from top to bottom are: spider density (top row), species diversity (second row from top), species evenness and richness of hunting strategies (bottom row). Grazing is represented by Bison presence were non-grazed sites are scores as 0 and grazed sites as 1. Fire was represented by two variables: a) Burned were 0 represent sites that sere not burned in the spring before sampling, and 1 represents sites burned the spring prior to sampling. (b) Burn Frequency, where sites were classified into one of three categories: frequently burnws (Freq. burned every 1 & 2 year), intermediately burned (Int. burned every 4 years), and low burn frequency (Low burn every 20 years). Habitat predictor variables represent the dominant trends in vegetation cover at a site classified as follows: bison grazed open grassland (BG), non-grazed open grasslands (UG) and woody/grassland transitions (WG) habitat based on dominant vegetation cover characteristics. The far right column shows the effects of topographic position on spider community responses were sites were classified into low-land sites (1), slope-sites (2) and upland sites (3). The asterisks on box-plots highlight models with significant response differences for analysis of variance. The box plot elements represent the following: box vertical dimension= interquartile range; horizontal line= median; whiskers= minimum and maximum values; open points= maximum observation 1.5 (IQR) above the 75th percentile.

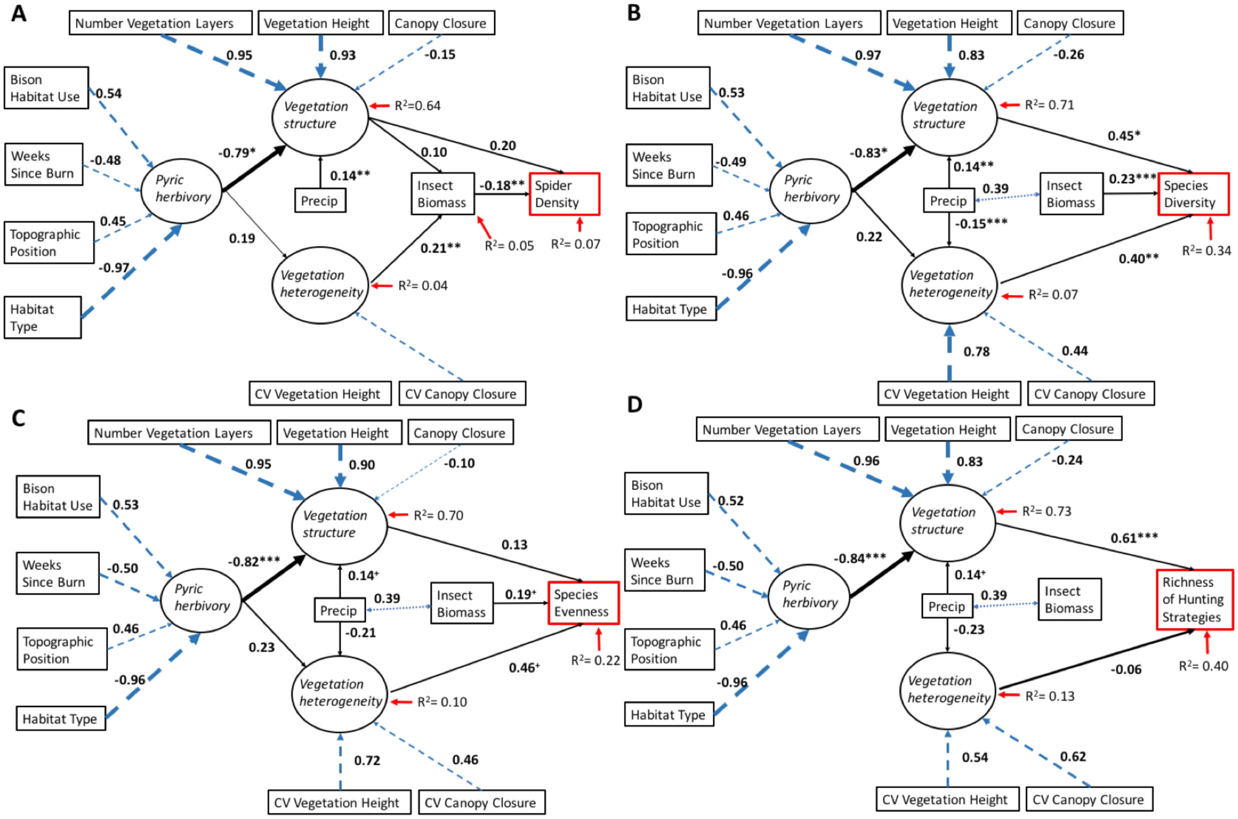

Figure 2-9. Structural equation models that shows how fire and grazing interactions (pyric herbivory) in *late-summer* indirectly structures spider community complexity through direct effects on on latent variables describing vegetation structure and vegetation spatial heterogeneity. Spider responses measured include (a) density, (b) species diversity, (c) species evenness, and (d) richness of hunting strategies. The latent variable 'pyric herbivory' representd the synergistic effect of fire (Weeks Since Burn) and grazing (Bison Habitat Use) interactions across a topographically variable landscape (Topographic Position) that sustain various vegetation communities (Habitat Type) differing in availability and palatability of forage for grazers. The loading factors vegetation height, number of vegetation layers, and canopy closure defined the latent variable habitat structure. The loading factors CV vegetation height and CV canopy closure defined the latent variable 'habitat heterogeneity'.

Chapter 3 - Spider communities respond to shifting mosaic in mesic grassland resulting from fire-grazing interactions across an experimental landscape

Abstract

In grassland ecosystems, fire, grazing, topography and climate interact to create a shifting mosaic of spatially heterogeneous and structurally complex habitats that move around in time and space. A shifting mosaic of habitats becomes the spatially variable template that underlies the assembly of local consumer communities and affects species diversity at multiple trophic levels at the landscape scale. Spiders are a functionally important, diverse and ubiquitous group of arthropod predators in terrestrial ecosystems, including grasslands. Spatial and temporal distribution of spider species and functional groups (hunting strategies) as well as the taxonomic and functional composition of local assemblages reflect variability in vegetation structure. Using decadal, watershed-level manipulations of fire frequency and bison grazing across a topographically variable landscape, my study assessed bottom-up contributions from fire-grazing interactions as mediated through vegetation structure to understand spider community assembly at the landscape level. Spider communities were sampled over three years at 23 sites representative of multiple habitat types resulting from large-scale experimental treatments, ranging from low-statured, grass-dominated sites to grassland-gallery forest transition zones. The taxonomic composition of spider assemblages differed among habitat types in response to recent fire-grazing interactions and in accordance with the shifting mosaic hypothesis. A shifting mosaic of habitat availability to local spider assemblages supported increased overall spider diversity at the landscape scale. The transitional ecotone between grassland and woodlands supported a hotspot for overall spider

density, species diversity and richness of hunting strategies. The shifting mosaic of vegetation habitat observed at Konza tallgrass prairie site resulted in dynamic, malleable spider assemblages reflecting changes in habitat templet structure.

Introduction

Mesic grassland biomes in North America evolved with and continue to respond to disturbance from fire-grazing interactions, coupled to a variable mid-continental climate (Knapp et al. 1998, 1999, Anderson 2006, Gill et al. 2009) variable topography which influences plants species distribution in response to soil depth and other soil attributes (Abrams & Hulbert 1987). Combined, influences from these four factors lead to temporally dynamic and spatially heterogeneous plant communities with variable vegetation structure (Fuhlendorf & Engle 2001, Fuhlendorf & Engle 2004, Fuhlendorf et al. 2009, Tews et al. 2004, Bond & Keeley 2005). In turn, habitat variability in time and space can dictate the spatial and temporal patterns of consumer diversity at both taxonomic and functional levels across the landscape (Bonte et al. 2000; Fuhlendorf & Engle 2001, 2004; Tews et al. 2004, Joern 2005). Consumer meta-communities potentially track dynamic systems of interconnected habitat patches, where the abundance and distributions of species change over time across the landscape (Levin and Paine 1974, Sousa 1984, Carmona et al. 2012). In this field study, I examined the taxonomic assembly of local spider communities as habitats vary in response to the effects of fire-grazing interactions on vegetation structure.

A shifting mosaic view of habitat availability is central to this study. Populations and communities often track specific habitats – Southwood's (1988) habitat templet – reflecting the combined autecology of individuals and local species interactions. Natural ecosystems typically experience variable environmental conditions that shape vegetation composition and structure, including weather and/or critical disturbances including fire, grazing, hurricanes, and floods. The outcome of these dynamic interactions leads to a patchwork of vegetation states interspersed in space that varies over time. Shifting mosaic models of habitats exist when new patches are created in response to disturbance (Bormann and Liken 1979), mature during succession, and become different states until they are reset by the next disturbance event. If a steady state is eventually achieved, the relative proportion of patches throughout the landscape becomes relatively constant when averaged over a sufficiently long time or large area. However, one also expects that the specific location of different patch types will move around in space over time reflecting recent disturbance history. Shifting mosaic dynamics promote habitat heterogeneity, and one expects spatial distributions of consumer assemblages with strong affinities for specific habitat types should track the mosaic of habitats (Halaj et al. 1998, Heikkinen et al. 2004). The shifting mosaic view of habitat availability underlies the current study, where I seek to determine the degree to which identifiable spider assemblages track habitat patches that vary in response to periodic disturbance from fire and grazing in association with variable weather and topography.

Spiders are ubiquitous, morphologically diverse, and functionally important arthropod predators in grasslands, often reaching high levels of local species richness and abundance (Riechert & Lockley 1984, Schmitz & Suttle 2001, Sebastian et al. 2005, Wise 2006, Diel et al. 2013). Within arthropod food webs, spiders are generalist predators that eat a wide range of invertebrate prey and are capable of subduing prey somewhat larger than their own body size/mass; prey selection is often size- rather than taxon-dependent (Riechert & Lockley 1984, Wise & Crawford 1994, Nyffeler 1999). Spider play important functional roles in terrestrial ecosystems, where predation can regulate arthropod prey populations and can cause ecosystem-level trophic cascades (Hodge 1999, Finke & Denno 2002, Denno et al. 2004, Laws & Joern 2013). Spiders show diverse hunting strategies and feeding guilds, and exhibit a wide range of body sizes and morphological variability. As generalist predators, many species overlap in size and general habitat distribution, leading to an increased likelihood that spiders participate in competitive, predator-prey and cannibalistic interactions with other spiders (Polis et al 1989, Finke & Denno 2002, Denno et al. 2004, Wise 2006). Variability in spider morphology and associated hunting modes facilitates habitat and prey partitioning at fine spatial scales (Schmitz & Suttle 2001, Schmitz 2008, 2009; Wise 2006), which improves the ability of spider species to exploit hunting locations and prey availability (Schmitz & Suttle 2001, Wise 2006, Malumbres-Olarte et al. 2013). Spiders are also potential prey for vertebrate predators that can suppress spider population abundances and alter how spiders interact with their invertebrate prey (Gunnarsson 1983, 2007; Wise & Crawford 1994, Schoener & Spiller 1996). For example, removal of arboreal lizards on small islands leads to rapid increases in web densities in the understory vegetation of both habitats (Schoener & Spiller 1996), and bird predation in spruce forest decreased winter survival of spiders (Gunnarsson 1983). Constant pressure on spiders from predation risk coupled with the need to find invertebrate prey in the presence of multiple spider competitors/ predators can be mediated by the structural complexity and spatial heterogeneity of the habitat, ultimately allowing coexistence among spider species (Schmitz & Suttle 2001, Finke & Denno 2002, Denno et al. 2004, Gamfeldt et al. 2005, Wise 2006). Overall, spiders provide an ideal ecological model for investigating how the spatial and vertical complexity of vegetation in response to fire and grazing disturbances as a shifting habitat mosaic promotes increased consumer diversity at the landscape scale.

Previously, Chapter 2 documented how fire, grazing and topography promoted multiple gradients of vegetation structure and spatial heterogeneity of canopy closure, vegetation height, and number of vegetation layers that helped explains spider assemblage diversity. Such structural diversity leads to increased opportunities for habitat partitioning by spiders, which in turn affect community diversity and abundance along these habitat complexity gradients across the landscape. According to the ***habitat shifting mosaic hypothesis*** *(HSMH):* (a) the taxonomic composition of local spider assemblages should track characteristic habitat structure as it varies in time and space in response to fire-grazing interactions; and (b) a shifting mosaic of local spider assemblages should result over the growing season and across multiple years (Fig. 3.1), leading to increased β–diversity of spiders at the landscape scale. I tested the following expected relationships to understand how spider communities respond to a shifting habitat mosaic of vegetation structure in tallgrass prairie at KPBS. (1) The taxonomic composition of local spider assemblages should track characteristic habitat structure as it varies in time and space in response to fire-grazing interactions. Unique spider assemblages (both taxonomically and functionally) will correspond to specific vegetation characteristics. (2) Recent fire resets vegetation growth and spatial heterogeneity at multiple spatial scales such that increasing the time since the last fire determines the patchiness of vegetation successional states. Synergistic effects of fire and grazing interactions (pyric herbivory) will result in differentiated, unique habitat states that support different spider assemblages along the fire-frequency gradient. For example, in the year of a prescribed burn, spider community responses to watersheds burned at intermediate frequencies (<2 - 4y) will be most similar to watersheds burned every year in ordination space, followed by an increased distance from yearly burned watersheds in ordination space as time since fire increases. The understory vegetation (vegetation in the grass layer) in woody-grassland transition habitats in the year of fire is expected to become similar to sites burned every 4 years as vegetation cover in both habitats will have a greater mixture of forbs, woody vegetation and grasses compared to frequently burned habitats. (3) Effects of bison grazing/ no-grazing treatments on habitat structure lead to characteristic taxonomic shifts in spider assemblages and the distribution of associated hunting strategies. Bison grazing opens up the vegetation canopy in a heterogeneous fashion, and bison grazed sites have more plant species and are more variable in structure (Fuhlendorf & Engle 2001, Towne et al. 2005, Marion et al. 2010, Collins & Calabrese 2012). Thus, spider assemblages in non-grazed/ open-grassland habitat should be dominated by active hunters such as wandering spiders with relatively slender bodies and a small number of web-builder species that use grasses as web-anchoring structures. Bison-grazed sites should support more diverse spider assemblages including greater morphological diversity and increased richness of hunting strategies of both wandering and web-building taxa when compared to not-grazed sites as a result of greater vegetation heterogeneity both vertically and spatially than non-grazed sites. (4) The ecotonal transition zone between grassland and woody stands of riparian woodland or clonal shrub islands will be hotspots for spider diversity and richness of hunting strategies (functional groups) (Traut 2005, Muff et al. 2009) as seen for other taxa (Peet 1978, Antvogel & Bonn 2001, Traut 2005). Transition zones offer unique vegetation profiles compared to other sites at KPBS, and are composed of high plant diversity that are more spatially heterogeneous, diverse and structurally complex (Peterson & Reich 2008, Peet 1978). Transitional habitat type provides opportunities for increased vertical and horizontal habitat partitioning by consumers. Combined, my hypotheses predict the presence of taxonomically unique spider assemblages that move around in time and space in response to effects of fire-grazing interactions.

Methods

Study site

Tallgrass prairie in the Flint Hills ecoregion of Kansas and Oklahoma is one of the largest remaining regions of tallgrass prairie in North America with a landscape dominated by warm-season grasses that is traditionally managed with annual spring burning and grazing by cattle during the growing season (Collins et al. 1998, Knapp et al. 1998). Coupled to changes associated with variable mid-continental weather, management practices determine habitat availability to consumers, where fire-grazing interactions promote landscape diversity. My field study was conducted in an experimental landscape at Konza Prairie Biological Station (KPBS), a tallgrass prairie research preserve of 3,487 ha. located in the Flint Hills ecoregion of northeastern Kansas near Manhattan (39°05'N, 96°35'W). The site experiences a highly variable US mid-continental climate characterized by dry-cold winters and wet summers with a mean annual precipitation of 835 mm (C.V. = ~25%) with most falling during the growing season (Knight et al. 1994, Knapp & Seastedt 1998, Knapp et al. 1998, 1999, Joern 2005). Primary productivity is also highly variable. KPBS is managed with long-term prescribed burning and grazing (bison and cattle) treatments applied at the watershed scale (Collins et al. 1998, Knapp et al. 1998). Prescribed burning at 1, 2, 4, and 20 y intervals (mostly in the spring) began in 1972 followed by the addition of watersheds as KPBS expanded (Collins & Steinauer 1998, Veach et al. 2014). Grazed and not-grazed watersheds comprise the grazing treatments. Bison grazing treatments used here occur in 10 watershed units (~1000 ha overall) with different burn frequencies in a factorial design, where individuals graze freely among all watersheds year round (Harnett et al. 1996, Veach et al. 2014, Raynor et al. 2015, Raynor et al. 2016). Bison herd size is maintained at ~280 adult individuals year-round (plus new calves) (Raynor et al. 2015, Raynor et al. 2016, Towne 1999); bison remove about 25% of the aboveground primary production on average (Briggs et al. 2002, Raynor et al. 2015).

In response to long-term fire and grazing interactions, vegetation at the watershed level varies from open grassland habitat with little woody cover to extensive woody vegetation in watersheds subjected to low fire frequency and along the riparian corridors (Collins & Calabrese 2012). The KPBS flora includes more than 600 plant species, including a mixture of warm-season and cool-season grasses, legumes, other forbs and woody plants. Application of fire and grazing treatments over the long term leads to higher forb diversity in grazed watersheds, especially in the uplands (Gibson & Hulbert 1987, Collins & Calabrese 2012). The lowest plant diversity is found in watersheds managed with a high fire frequency (1-2 y return interval) in the absence of grazing that promote dominance by C_4 grasses (Collins & Calabrese 2012). Overall vegetation biomass is greater in lowlands because of deeper soils when compared to upland and slopes areas of KPBS (Collins & Calabrese 2012).

Spider Community and Insect Biomass Sampling

Grassland spider communities were characterized at 23 sites across a wide variety of habitat types distributed among 15 watersheds (Table 5.1 & Fig. 5.1, Supplementary material). From the 23 sites sampled in this study, 14 were located in bison grazed habitats and 9 in not-grazed habitat. Bison-grazed sites included a gradient of habitat use (low to high) ranging from frequently visited grazing lawns characterized by short-statured vegetation cover, to rarely visited areas characterized by woody/grassland transition areas. Not-grazed sites were distributed in watersheds that ranged from homogeneous grass-dominated habitats to watersheds with abundant woody vegetation. At each of the 23 sites, three 40 x 1 m transects placed 10 m apart were sampled. Spiders and insects along each transect were vacuum sampled (Buffington &

Redak 1998, Hossain et al. 1999) once in early summer (June) and once in late summer (August-September) for 3 years (2011-2013); no samples of woody-grassland sites were taken in early summer in 2011. Arthropods were sampled (Buffington & Redak 1998, Hossain et al. 1999) using a modified Ryobi leaf blower (model RY09050). Samples were collected by slowly walking along transects once per sampling period, while vacuuming uniformly from near the base of the vegetation up to a maximum height of 1.5 m. Arthropod samples were placed in coolers with ice in the field immediately after collection, and frozen later that day. Arthropods were later sorted and stored in 70% alcohol. Spiders were identified to the lowest taxonomic level possible. Insect samples were bulked and air dried for 48 h at 70^0C in a drying oven, and weighed. Insect biomass is reported in this study as the total mass divided by the total area vacuumed per site and is an index of total food available to spiders.

Characterizing ecosystem drivers

Prescribed fire and bison grazing interact as experimentally manipulated ecosystem drivers in this study system. I characterized the effects of fire treatments on spider assemblages in two ways: (a) time since last burn, calculated as the number of weeks from the last burn to the beginning of a sampling period (Week Since Burn-WSB), and (b) recent burn history – whether a site was burned or not in spring of a season under consideration from 2011-2013, regardless of burn frequency treatment (referred to as Burned-BUR). Because plant species diversity, vegetation structure and cover varied with topographic position, I also classified sites by topographic region (upland, lowland and slope) based on their relative position in the watersheds (‘TopoPosition’-TOP).

Relative bison activity was classified in grazed areas (“Bison Habitat Use Index”-BHUI) using GPS data for up to 13 female bison in a year. Site use intensity was determined by tallying the number of visits by collared female bison within 100 m from each site for a one-month period prior the first week of each sampling period from 2011-2013. Site BHUI was also estimated by dividing the collared female bison visitation rate in increments of 50 (25 visits were scored as 1, 75 visits as 2, etc.). BHUI values ranged from 1 to 10+, and not-grazed sites were scored as 0. For example, sites with BHUI values of 1 were located in woody stand-grassland transitions habitats, and sites with BHUI values of ≥ 10 were associated with heavily used sites such as grazing lawns.

Vegetation: structural complexity and spatial heterogeneity

Vegetation height and the number of vegetation layers were measured using a modified Robel pole, and canopy closure was measured using an estimate of the leaf area index (LAI). Spatial heterogeneity was reported as the coefficient of variation (CV) for vegetation height and canopy closure. At each site, vegetation architectural complexity was measured at 30 random points using a modified Robel pole, constructed from a 1.5 m copper rod (1.5 cm diameter) marked with a 5 cm interval scale. At each point, the rod was placed through the vegetation perpendicular to the ground and the number of hits by vegetation (leaf or branches) that touched the rod in each 5 cm height interval was counted. The mean vegetation height is calculated as the mean of the median vegetation height measurements (cm) for each of the 30 randomly measured vegetation structure points at a site, and is referred to as “Vegetation Height” (Central Tendency of Vegetation Height-CTVH). To describe the heterogeneity in vegetation height at each site, I calculated the coefficient of variation (CV) of the central tendency of vegetation height, denoted as “Central Tendency-CV” (CTCV). The fine-scale vertical complexity of the vegetation was described as the “Number of Vegetation Layers” (NVL) based on the number of the habitat (vegetation) hits at each 5 cm increment interval across all 30 measured vegetation points. A minimum of two hits within a sampling period was required for a height interval to be considered a vegetation layer, values ranged from 0 (bare ground) to 31 (vegetation is higher than 150cm). The NVL value for a site was the count of all vegetation-height interval that met the criteria.

Vegetation closure was characterized as the leaf area index (LAI). An LP-80 AccuPar ceptometer was used to measure the light obstruction through a plant canopy at 20 random points per site per sampling period. Light interception was estimated by comparing ceptometer values at ground level and at 1m in height within/or above the canopy. LAI values were approximated using light obstruction measurements, first determining the value of x which was calculated by dividing the ground level measurement by the measurement taken at 1m in height,and then using the relationship $-\ln(x)/0.86$ to estimate LAI for each sampling point. The constant value of 0.86 was obtained from the literature (Decagon Devices 2004). The average site LAI (LAIM) and the CV of LAI (LAICV) values were estimated by calculating the mean and standard deviation from the 20 LAI values measured at each site per sampling period.

Statistical analyses

Community Assemblages respond to a mosaic of grassland types

Rank abundance analysis was performed using both density and presence-absence data to determine the most abundant spider species/ families and taxonomically defined hunting strategies for: (a) the overall spider community, (b) web-building spiders only, and (c) wandering spiders only. This allowed me to assess whether or not common species were distributed homogeneously across the landscape in time and space.

All statistical analyses were performed with R 3.1.2 (R Core Team 2014). Multivariate Redundancy Analysis (RDA) links species ordinations with environmental gradients (Borcard et al. 2011), and was used here to investigate how fire-grazing interactions structure grassland spider communities through effects on vegetation structure. Samples collected at the same locality at different time periods are treated as independent from one another due to variability in times since last fire, variable weather, and ever changing bison use of sites, all of which influenced vegetation attributes (structure and heterogeneity). It has been shown that other consumer community assembly/ species distributions within the landscape reflect effects of fire and grazing disturbance regimes mediated through the vegetation template encountered by consumers (Matlack et al. 2001, Yarnell et al. 2007, Coppedge et al. 2008, Little et. al. 2013). I included such variables in my analyses to determine if a taxonomically diverse group such as spiders shows predictable species associations with fire or grazing disturbances directly, or if responses are more subtle and only mediated through indirect effects of vegetation (structure and heterogeneity) and prey (insect biomass) availability or interactions. Combined, these factors described a shifting mosaic of local habitat types in time and space across 23 sites. RDA was performed for each individual year (2011-2013) to assess the effects of vegetation growth on structure and heterogeneity in response to fire and grazing on local spider assemblages at two end points of the growing season. Data were analyzed separately for the late-summer over the three years to determine if patterns of local spider assemblages at end points of the growing season remained stable over time regardless of effects of fire and grazing on vegetation. Redundancy analysis was performed on hellinger pre-transformed vacuum density matrices. The hellinger transformation accounted for species with low abundance, but that were otherwise biologically important for the questions addressed (Peres-Neto et al. 2006). To reduce collinearity among explanatory variables in RDA models, I performed variance inflation analysis using the function vif.cca in the vegan package (Oksanen et al. 2011); only variables with variance inflation values of less than 10 were retained for model evaluation. Forward selection analysis was used to determine the predictor variables that make a significant contribution to the RDA analysis. The analysis was performed using a double-stopping criterion with 100,000 permutations per steps using the function ordistep in the vegan package (Oksanen et al. 2011). A parsimonious RDA model was extracted based on results from the variance inflation and forward selection analyses. Data were then reanalyzed to obtain adjusted R^2. Parametric bootstrapping, with 100,000 iterations for each test, were performed to determine the overall significance of the parsimonious RDA model, and the significance of each of the RDA canonical axes and environmental variables included in the final RDA model.

In addition to RDA analyses, I performed hierarchical cluster analyses on the hellinger pre-transformed data. I first computed the dissimilarity indices using the function vegdist and the Bray-Curtis (bray) index in the package vegan. A hierarchical analysis was then performed using the hclust function using Ward's minimum variance as the clustering method to determine sites grouping patterns based spider species composition per site. To determine the number of distinct spider assemblages from the grass-layer across KPBS, I used the K-means clustering approach with the function cascadeKM in vegan, and I used both calinski and ssi ("Simple Structure Criterion") criteria to evaluate the number of significant clusters in the datasets. For each of the K-means analysis, a total of 100,000 permutations were calculated to determine the number of clusters to account for the large variability in species detectability in my data. Results from the parsimonious RDA and hierarchical cluster analysis were combined, allowing us to plot the RDA results identified as clusters (color coded in the RDA) that corresponded directly to the dendrogram generated with the hierarchical cluster analysis. I plotted the suggested number of clusters by both k-means approaches and calculated the centroids of each cluster using the function ordiellipse in vegan package. In my results, I report the maximum number of clusters, that little of no overlap in among their centroids, and had ecological meaning.

Results from RDA analyses for both individual years and late-summer season combined across three years showed that at least three distinct spider communities were detected, reflecting broad scale differences in vegetation communities; (a) woody-grassland transitions either shrub island and riparian woody-stands, open grass dominated habitat, (b) not–grazed, and (c) grazed-habitats. To determine how different components of the spider community were associated with environmental variables and/ or habitat types, I analyzed presence-absence, pre-transformed matrices for web-building and wandering spiders with RDA and cluster analysis as described above. To evaluate how habitat type influenced density richness and richness of hunting strategies of wandering and web-building spiders, a non-parametric Kruskal-Wallis one-way analysis of variance followed by *post-hoc* pairwise comparisons were used to evaluate how web-builder and wandering spider richness differed among the three habitat types.

My goal was to determine if spiders in the three grassland habitats at KPBS differed in the total number of hunting strategies present, or whether some habitats include more species or increased density for some functional groups. I performed a 2-way ANOVA using late-summer samples over 2011-2013 where the predictor variables included habitat type and hunting strategy. The dependent variable was species richness per hunting strategy and density per hunting strategy. Species richness per hunting strategy was calculated for each sample. Functional groups as hunting strategies were determined first by dividing the spider community among wandering and web-building species, and then each wandering spider species was assigned to a functional group based on their general hunting mechanism of capturing prey and relative position in the vegetation. Web-builder classification was based on the web-type and

Gomez et al. (2016) classifications. The density for each functional group was determined by adding the density of all spider species present for each functional group per site. To evaluate how habitat type influenced density and species richness across functional groups among the three habitat types, *post-hoc* pairwise comparisons were performed using the function posthoc.kruskal.nemeyi.test in the package PMCMR (Pohlert 2014). Pairwise comparisons were performed using a Chi-square distribution to correct for tied data.

Structural Equation Modeling (SEM) (Grace 2006, Grace et al. 2010) was used to summarize how fire and grazing interactions coupled with topography affected spider assemblages across the landscape in response to a shifting mosaic of grassland types and biomass of potential prey for spiders (Dennis et al. 1998, Joern 2004, Diehl et al. 2013, Moran 2014). Local, late-summer spider assemblages, represented as RDA-1 and RDA-2 scores, responses to *vegetation structure, vegetation heterogeneity*, and insect biomass were used to develop general, *a priori* models of hypothesized relationships for spider assemblages sampled between 2011 and 2013. I also included the response of insect biomass to *vegetation structure* and *vegetation heterogeneity* in my model. CTVH, NVL and LAIM were used as loading factors to construct *vegetation structure* latent and the latent variable *vegetation heterogeneity* included LAICV and CTCV as loading factors. In addition to direct effects, the indirect contributions of fire and grazing to the composition of local spider assemblages (RDA-1 and RDA-2) were assessed through effects on vegetation by constructing the latent variable *pyric herbivory* using BHUI and WSB as loading factors to represent grazing and fire. I included TopoPosition and HAB to build the latent variable *pyric herbivory* in the model since both described how fire and grazing interactions structured gradients of *vegetation structure* and *vegetation heterogeneity* across the KPBS heterogeneous landscape. Effects of *pyric herbivory* on vegetation were evaluated as a direct interaction with the latent variables *vegetation structure* and *vegetation heterogeneity*. The influence of precipitation (Precip) on vegetation was assessed as a direct path between Precip and vegetation latent variables because it varied significantly over the period of my study. Precip included a significant drought period in 2012 that greatly affected vegetation attributes and grazing patterns. SEMs were performed on original non-transformed data and I used the following goodness-of-fit measures to select the most parsimonious SEM models: Chi square (non-significant model at alpha of 0.05), the comparative fit index (CFI) (obtain a model with a value close to 1.0), the Tucker-Lewis Index (TLI) (obtain a model with a value close to 1.0), and the root mean square error of approximation (RMSEA) (obtain a model with a RMSEA value close to 0.0 and p-value < than 0.05; RMSEA is a one-sided test of H_o=0.05) (Rigdon 1996, Hooper et. al 2008, Iacobucci 2010). SEM was performed with R 3.1.2 (R Core Team 2014) using the packages lavaan (Rosseel 2012) for running SEM models with latent variables, the package semPlot (Epskamp 2015) used for building SEM figures, the package nlme (Pinheiro et al. 2009) used to fit paths in the SEM model on lavaan, and the packages car (Fox et al. 2007) and QuantPsyc (Fletcher & Fletcher 2010) for calculating summary values.

Results

Spider community structure

Based on quantitative vacuum samples, a total of 22 families, 83 genera and 132 morpho-species from the grass-layer were captured from 2011-2013 (Table 5.2 Supplementary Material). About 75% of these taxa were identified to species; the remaining taxa are given species-specific codes. Numerical estimates of density and diversity of ground dwelling species (families Lycosidae, Gnaphosidae, and Linyphiidae) may be underrepresented, especially in habitats with dense litter. Rank-abundance curves indicated that the 15 most abundant (based on density) and widespread (based on presence-absence) spider species at KPBS belong to the families: Thomisidae, Oxyopidae, Philodromidae, Salticidae, Anyphaenidae and Araneidae, and each family was represented by 4, 1, 2, 5, 2 and 1 species respectively (Table 3.1). The hunting guilds most commonly found at KPBS, based on the 15 most abundant spider species, include: Foliage-Stalker (Oxyopidae and Salticidae), Stem-Runner (Philodromidae and Anyphaenidae), Foliage-Sit & Wait (Thomisidae) and Medium-Orb-web spiders (Araneidae) (Table 3.1). Within KPBS spider community wandering spider species represented ~65 % (86 species) and web-builders represented ~35 % (46 species) of the species collected in my samples (Table 5.2 Supplementary Material).

Among the 10 most commonly found web-building spiders species, only 3 were associated with open grassland habitats, and the remaining 7 species were commonly found in woody-grassland transition regions (Table 3.2). Orb weaver species, primarily the family Araneidae, dominated the richness of web-builders, including 6 of the 10 most common web-building spiders, followed by spiders that use "all-directions" webs (unorganized silk threads attached in many directions) with 25 and 8 species respectively. Web-builder diversity represented a small proportion of the spider fauna sampled at each site, particularly in open grassland. About 75% of the samples contained only 4 or fewer web-builder species per sample per site. For the 10 most common wandering spiders, 1 species was associated with woody habitats, 4 with open-grassland, and 5 were habitat generalists. The most commonly found hunting strategies were foliage-stalker followed by foliage sit-and-wait, and stem-running (Table 3.2, Table 5.2 Supplementary Material). Species richness of wandering spiders was dominated by jumping spiders (Salticidae, 40 species), followed by crab spiders (Thomisidae, 14 species) (Table 5.2 Supplementary Material).

Spider community responses to a mosaic of grassland types among growing seasons

Spider community responses were highly dynamic with respect to changes in vegetation state as mediated by fire and grazing along multiple spatial and temporal scales, including over a growing season. Spider assemblages also differed significantly among years, again in response to changes in vegetation cover driven in part by variable climatic conditions and drought. For this reason, I present results from individual years to highlight spider community responses to this shifting mosaic of habitats. Overall, responses by the grassland spider community at KPBS can be partitioned into open grassland vs. woody grassland transitions, early vs. late summer periods, and pre-drought vs. drought/ post-drought spider assemblages. In general, local spider assemblages at KPBS were primarily influenced by temporal changes along RDA-1 either within a growing season or among different growing seasons (2011-2013). RDA-2 primarily represented changes in vegetation structure and heterogeneity setting up the vegetation template encounter spider species influencing patterns of spider's assemblages across the landscape.

In 2011, I detected three distinct spider assemblages over the growing season using RDA and cluster analysis ($R^2 = 0.35$, $F = 5.05$, $p = 0.001$; Fig. 3.2a). RDA-1 was explained primarily by season, while CTCV, LAICV, NVL and Burned explained RDA-2. KPBS spider assemblages grouped as an early-summer spider assemblage and two distinct spider assemblages for the late-summer spider community. Early-summer assemblages were negatively associated with RDA-1, and included all open-grassland sites that were both grazed and not-grazed (black circles; Fig. 3.2a). Woody sites were not sampled for early-summer 2011. Taxa that were negatively associated with RDA-1 represented spiders from open-grassland habitat (Fig. 3.3a), most of which use flowering structures and proximal plant parts as hunting grounds (Thomisidae, Salticidae, Philodromidae, Anyphaenidae and Oxyopidae). Late-summer samples were positively associated with RDA-1 and separated into: (a) the open-grassland containing both grazed and not-grazed sites and (b) woody-grasslands transition habitats. The open-grassland containing both grazed and not-grazed sites, including two shrub-island grassland transition sites were positively associated with RDA-2 (red squares; Fig. 3.2a). Spider taxa with positive scores along both RDA axes represent spider commonly found in open grassland on plant stems and grass leaves (Salticidae, Oxyopidae and Philodromidae; Fig 3.3a). The woody-grassland transition habitat community showed a negative association with RDA-2 (green diamonds; Fig. 3.2a). Spider taxa found in the quadrat with positive RDA-1 scores and negative RDA-2 scores include species commonly found in woody-habitat or habitat with greater heterogeneity in vegetation structure along either vertical (vegetation height) or spatial dimensions (Araneidae, Anyphaenidae, Salticidae, Theridiidae and Thomisidae; Fig. 3.3a).

In 2012, spider assemblages were best predicted by Season, Habitat, CTVH and BHUI, where Season and BHUI contributed the most to explaining RDA-1 and Habitat, and CTVH best explained RDA-2. Four distinct spider assemblages were detected through the growing season ($R^2 = 0.34$, $F = 3.1$, $p = 0.001$; Fig. 3.2b). Spider assemblages from the woody-grassland transition sites formed a cluster that included sites from both early and late summer samples and were positively associated with RDA-2 and the environmental factor CTVH. Along the RDA-1 axis, woody grassland sites sampled in the early-summer were mostly negatively associated with RDA-1 while late-summer samples were positive. Woody grassland transition sites were orthogonal to the open grassland sites along RDA-2 (green diamonds, Fig. 3.2b). Woody-grassland transition habitat was closely associated with CTVH, reflecting the importance of increased habitat structure that escaped the effects of fire and grazing. Both wandering and web-building spider species (Fig. 3.3b) were positively associated with RDA-2 and the environmental vector CTVH. In general, spider species richness is higher in the transition habitat of riparian woody habitat or woody islands within open habitat than in neighboring open-grassland habitats. Common spider species in woody-grassland transition habitats tended to be small bodied when compared to their open-habitat counterparts (Oxyopidae, Philodromidae, Linyphiidae, Salticidae, Araneidae) (Fig. 3.3b). Distinct early vs. late summer assemblages were not as evident in ordination space in 2012 as in 2011 and 2013, probably reflecting the effects of drought on reduced vegetation growth that coincided with the burning of more than usual 4-year watersheds in the bison unit. As indicated by BHUI values for grazed sites during 2012, bison visitation rates and associated grazing activity in open-grassland sites were higher than in 2011, including responses to grazing lawns sites that experienced intense use. Three clusters of spider taxa were still evident in open-grassland habitat (one late-summer cluster and two early-summer clusters). The late-summer, open-grassland cluster was positively associated with RDA-1 and negatively associated with RDA-2 (blue triangles; Fig. 3.2b). Spider species occupying positive RDA-1 and negative RDA-2 ordination space include wandering species (Thomisidae and Philodromidae) and a web-builder (Araneidae) that uses grass inflorescence stalks as web anchoring structures. Similarly, Thomisidae are found on grass flowers and any other late blooming flowering plant. While the open grassland clusters in early-summer were both negative along RDA-2, bison-grazed /open grassland taxa are negatively aligned along RDA-1 (black circles, Fig. 3.2b), and not-grazed/open-grassland taxa were located near the center of RDA-1 (red squares, Fig. 3.2b). Finally, spider taxa found in the negative RDA-1 and negative RDA-2 ordination quadrat (lower left) consisted of a group of wandering spiders commonly found in open grassland, both in grazed and not-grazed habitat. This group is represented by 4 families of active hunters

(Salticidae, Philodromidae, Oxyopidae and Anyphaenidae) and a ambush hunter (Thomisidae) (Fig. 3.3b).

Post-drought structure in spider communities returned in 2013, where spider assemblages were best predicted by Season and CTCV along RDA-1, and by Habitat, WSB, LAIM and CTVH along RDA-2. All early-summer sites were negatively associated with RDA-1 and all late-summer sites were positively associated with RDA-1. Five spider assemblages were identified in 2013 ($R^2 = 0.43$, $F = 3.64$, $p = 0.001$; Fig. 3.2c), three of which were characteristic of open-grassland communities and two were associated with woody sites. Taxa from early-summer open grassland habitat formed one cluster that includes both grazed and non-grazed sites; these sites were generally negatively associated with RDA-1 and both positively and negatively associated to RDA-2. This cluster also included four woody-grassland transition sites that were also negatively associated with RDA-2 (black circles, Fig. 3.2c). Open grassland in late-summer formed two distinct clusters reflecting grazing treatment (grazed and not-grazed assemblages), but both clusters are positively associated with RDA-1 and negatively associated with RDA-2. Sites from the grazed / open-grassland showed the most negative values along RDA-2 (green diamonds, Fig. 3.2c) compared to sites from non-grazed/ open grassland in late-summer (blue triangles, Fig. 3.2c). The two clusters represent woody-grassland transition habitats and are positively associated with RDA-1 and with the environmental factors CTVH, WSB. (1) Early-summer woody (tree)/ grassland transitions were mostly negative along RDA-1 and included two late-summer sites with a species composition quite similar to early-summer assemblages (red squares, Fig. 3.2c) and lower species richness than other late-summer woody (tree)/grassland transition habitats (light blue downward triangle, Fig. 3.2c). (2) Woody-grassland transition habitats were closely associated with WSB and CTVH, reflecting the importance of habitat structure at supporting spider assemblages that differed from open grassland assemblages. In contrast, CTCV was generally correlated with late-summer/ open-grassland communities, highlighting the importance of vegetation heterogeneity in supporting diverse spider assemblages. Spiders (Fig 3.3c) commonly found on open grasslands were negatively aligned along RDA-2, including wandering, (Thomisidae, Oxyopidae, Philodromidae, Salticidae, Anyphaenidae) and web-building taxa (Araneidae and Tetragnathidae; Fig 3.3c). Open grassland was dominated by wandering spiders at both the family and species taxonomic level. Spider assemblages from the woody habitat included wandering (Thomisidae, Anyphaenidae) and web-building spiders (Araneidae, Theridiidae, Linyphiidae, Agelenidae. Web-building spider at the family and species level drives spider species diversity along woody habitat. Most of the species found in woody habitat were small-bodied spiders with a total body length of less than 2 cm.

Spider assembly response to a mosaic of grassland types across three years

To address how spider assembly responded across three years, we selected late-summer samples because spider species richness reaches it peak towards the late-summer at our site. Second, vegetation growth in response in combination pyric-herbivory influence on vegetation structure and heterogeneity results in differentiated habitat template for spiders. Last, woody-grassland transition sites were not sampled in early-summer 2011. Hierarchical cluster analysis combined with RDA indicated that spiders in late-summer were divided into five distinct spider groupings ($R^2 = 0.31$, $F = 3.72$, $p = 0.001$; Fig. 3.2d) in association with the environmental variables LAIM, Year and Habitat type influences for both RDA-1 and RDA-2, in addition to CTCV for RDA-2. The first cluster was closely associated with LAIM and included 17 of 23 the sites sampled in 2011; this cluster associated positively with both RDA axes (red squares, Fig. 3.2d). The next cluster, which was also positively associated with both axes, included all sites from woody-grassland transition habitats sampled in 2011 (blue triangles, Fig. 3.2d). A group of spiders (Fig 3.3d) that occupied the positive ordination space for both RDA axes consists of wandering spider from the families Philodromidae, Oxyopidae, Salticidae, Thomisidae, Anyphaenidae. A third cluster consisted of sites found on woody-grassland transition habitats, particularly in the riparian areas sampled 2012 and 2013, and was positively correlated to RDA-1 and negatively to RDA-2 (light blue, downward triangle, Fig. 3.2d). This group of spiders is closely associated with woody habitats. Scores were positive along RDA-1 and negative along RDA-2, and included wandering spiders from the families Thomisidae and Anyphaenidae and web-building spiders from the families Araneidae, Theridiosomatidae, and Linyphiidae (Fig. 3.3d). Two additional clusters were negatively associated with RDA-1 and represented open grassland (both grazed and non-grazed). Ordination space of grazed habitat sites (black circles, Fig. 3.2d) spreads along RDA-2 and is relatively smaller than that seen for not-grazed ones (green diamonds, Fig. 2d). These two clusters are composed of sites sampled in 2012 and 2013. The last group of spiders recognized was negatively associated with RDA-1 and included medium sized wandering spiders from the families Philodromidae, Thomisidae, Salticidae and Lycosidae; a few web-builder species commonly found associated with grasses from the families Araneidae and Dyctinidae were also found (Fig. 3.3d).

Pyric herbivory influences spider community composition

I examined taxonomic composition of assemblages with SEM (RDA-1 and RDA-2 scores were treated as separate models) of late-summer spider assemblages for all years combined (2011-2013) using a modified version of Figure 3.1. Because I did not have sufficient replication to evaluate all pathways in my primary model, I excluded the latent variable richness of habitat types and the interactions between insect biomass and two-vegetation latent variables *habitat structure* and *habitat heterogeneity*. I used the indices CFI, TLI and RMSEA to assess which model best fit the data. The SEM for both RDA-1 and RDA-2 late-summer 2011-2013 samples were statistically significant for the χ^2 index of fit ($P<0.05$) instead of the preferred non-significant relationships.

Pyric herbivory influenced the diversity of spider assemblages (RDA-1 & RDA-2) across the landscape through synergistic interactions with vegetation, primarily by resetting plant community succession at multiple spatial (local-landscape) and temporal (within-growing season to among years) scales. In turn, fire history influences grazing patterns throughout the landscape as it affects fuel load accumulation and the likelihood that a specific area will burn in the near future. The synergistic effects of fire and grazing interactions leads to the creation and maintenance of a shifting gradient of vegetation structure and heterogeneity over the landscape, and a shifting mosaic of habitat structure and heterogeneity for use by spiders.

For RDA-1, late-summer spider assemblages responded positively to the latent variable '*vegetation structure*', and negatively to insect biomass (CFI = 0.631, TLI = 0.511, RMSEA = 0.189 with $p < 0.001$ & $R^2 = 0.29$; Fig. 3.4a). The latent variable '*vegetation heterogeneity'* was not informative in the SEM model of spider assemblage composition for RDA-1 responses. Spider assemblages along RDA-1 were positively influenced by vertical complexity of the habitat at both at a fine-plant scale (NVL) and as overall vegetation height (CTVH). *Pyric herbivory* was negatively associated with habitat structure for RDA-1.

For RDA-2, late-summer spider assemblage responses responded negatively to the latent variable '*habitat structure*', to *habitat heterogeneity*, and to a lesser extent with insect biomass (CFI = 0.65, TLI = 0.536, RMSEA = 0.19 with $p < 0.001$ & $R^2 = 0.51$; Fig. 3.4b). Spider assemblages along RDA-2 were negatively influenced by increased vertical complexity of the habitat at both the individual plant scale (NVL) and overall vegetation height (CTVH). *Pyric herbivory* had a negative effect on habitat structure along RDA-2.

Distribution trends of two hunting groups: web-builder vs. wandering spiders

Hunting groups assembly in response to a shifting mosaic of habitat types

RDA and cluster analyses of web-building spider assemblages using presence/absence data revealed 5 distinct web-building spider assemblages ($R^2 = 0.12$, $F = 2.41$, $p = 0.001$; Fig. 3.5a). Web-building spiders were associated with LAIM, Year and Season along RDA-1 and NVL and HAB along RDA-2. Sites grazed by bison in the late-summer 2011 and 2013 comprise a spider assemblage with both positive and negative scores along both RDA axes (green diamonds, Fig 3.6a). The spider assemblages from the woody/grassland transition sites were mostly negatively associated with RDA-2 and included sites sampled both in early and late summer (blue triangles, Fig. 3.5a). Additionally, this cluster includes sites from both grazed and not-grazed/ open habitats, characterized by large differences in vegetation height between grass layers and presence of forb (e.g., goldenrod) or woody islands (dogwood and smooth sumac) that encroached into open habitats (blue triangles, Fig. 3.5a). This spider assemblage was mostly positively associated with RDA-1. Open grassland from both grazed and not-grazed habitats in early-summer 2011 and characterized with significant grass and forb cover are negative along RDA-1 and positive along RDA-2 (red squares, Fig 3.5a). Another spider assemblage was associated with open grassland in the early- and late- summer mostly from 2012 and 2013, and exhibited greater variation in vegetation height among grazed and not-grazed patches (black circles, Fig. 3.5a). A final cluster includes open-grassland habitat (both grazed and not-grazed) in late-summer 2011-2013 where the sites were characterized by moderate vegetation height and high vegetation heterogeneity driven by: (a) differences among grazed patches vs. not-grazed patches in the bison grazed watersheds, and (b) differences in height among different grass species, and grasses vs. forbs and shrubs (light blue downward triangles, Fig. 3.5a). Additionally, this cluster included sites grazed by bison in early-summer 2013. Web-builder species richness was significantly different among habitats types ($\chi^2 = 53.6$, $p < 0.001$), and woody grassland transitions had higher richness than grazed open-grassland ($p = <0.0012$) and not-grazed open-grassland ($p < 0.001$). Web-builders that were positively associated with both RDA axes are species that exhibited great variation in density among years. Regardless of their variation among years, web-builders are commonly found in both open grasslands or woody-grasslands transition habitats (Fig. 3.5b), but species richness and web-type richness was higher in woody-grasslands transition habitats. Species negatively associated along RDA-2 are species for which their distribution and abundances are closely related to the woody-grassland transition habitats (Fig. 3.5b). Spiders negatively associated with RDA-1 and positively associated with RDA-2 are those species positively associated with open grasslands habitats (Fig. 3.5b).

Results from the combination of RDA with cluster analysis identified four distinct wandering spider assemblages ($R^2= 0.18$, $F= 3.14$, $p=0.001$; Fig. 3.5c). Clusters along RDA-1 are driven by environmental variables that reflect temporal heterogeneity: Year, Season, LAIM and BHUI. RDA-2 is driven by the variables Habitat and NVL, variables associated with vegetation structural complexity. The first cluster that was positively associated with both RDA 1 and 2 included sites sampled in early-summer 2011 (black circles, Fig. 3.5c). The second cluster, which is negative along RDA-2, consisted of woody grassland transitions habitats and open-habitats, grazed and not-grazed, with islands of tall forbs and shrubs sampled 2011-2013 (blue triangles, Fig. 3.5c). Another cluster included sites from open grassland habitat (grazed and not-grazed) from early-summer 2012 and 2013. This cluster is positive and negative along both RDA axes (red squares, Fig. 3.5c). A final cluster contains sites from open grassland (grazed and not-grazed) habitats sampled in the late-summer 2012 and 2013, and is positive along RDA-2 and negative along RDA-1 (green diamond, Fig. 3.5c). Habitat type influenced wandering spider species richness, differed among habitats types ($\chi^2 = 21.96$, p <0.001). Not-grazed /open grassland had lower values than grazed /open grassland (p = 0.0011) and woody/ grassland transitions (p = <0.001). Spiders with positive scores along RDA-1 were positively associated with open grassland habitats both grazed and not grazed (Fig. 3.5d). Spiders with negative RDA-2 scores were positively associated with habitat with greater diversity and availability of vegetation structure and heterogeneity along woody/ grassland transitions and open habitats (Fig. 3.5d). Spiders found along the negative RDA-1 scores were associated with woody-grassland transition habitats while whereas the species associated with the positive values of RDA-1 were associated with open grasslands, particularly grazed habitats (Fig. 3.5d). Spiders found within negative RDA-1 and positive RDA-2 region (lower right) exhibited greater year to year variability while spiders found near the center of the RDA plot included both rare species and habitat generalists (Fig. 3.5d).

Habitat type influences hunting strategies composition of spider assemblages.

Spider community was divided into two broad scale functional group wandering and web-builder spiders to evaluated if spider density and/or species richness within each these group exhibited affinity towards on of the three commonly identified habitat type at KPBS: grazed/ open grassland, not-grazed/ open grassland and woody-grassland transitions, respectively. Results show that there was no difference in wandering spider density among habitat types ($\chi^2 = 2.81$, p = 0.25, Fig. 3.6a). Web-builder density was higher in woody-grassland transitions than in other two habitats (χ^2= 40.32, $p < 0.001$, Fig. 3.6b). Wandering spider species richness was higher in both grazed/ open grasslands and woody-grassland transition habitats than in not grazed/ open grasslands (χ^2= 21.96, $p < 0.001$, Fig. 3.6c). Web-builder species richness was higher on woody-grasslands transition habitat than on open grasslands both gazed and not grazed (χ^2= 53.6, $p < 0.001$, Fig. 3.6d).

A more detailed study of the functional composition (hunting strategies) of spider assemblages per habitat type revealed that the functional composition of grassland spiders showed a significant interaction between habitat type and proportional contribution per hunting strategy group to the structure of a spider assemblages at both species richness ($F_{30,1056}$ = 4.358, $p <0.001$) and density ($F_{30,1056}$ = 2.857, $p <0.001$; Fig. 3.7) levels. In general, 13, 12, 15 hunting strategies were identified on grazed/ open grassland, not-grazed/ open grassland and woody-grassland transitions, respectively. Spider species richness per functional group differed among the three habitats type, as did the density per functional groups (Fig. 3.7). Not-grazed/ open grassland habitat supported the lowest spider densities of 8 individuals/m^2 compared to 13 and 15 individuals/m^2 in grazed/ open-grassland and woody-grassland transitions, respectively. Total species richness per habitat type also varied, where woody-grassland transition (95 spp.; Fig. 3.7e) and grazed/ open grassland (82 spp.; Fig. 3.7a) supported 1.4-1.6 times mores species than was observed in not-grazed/ open grassland (59 spp.; Fig. 3.7c). Pairwise comparisons among functional groups showed that 4 functional groups were significantly different from all others in terms of their species richness and density (p-values < 0.001) when compared to other groups. Those functional groups are Foliage Stalker (FS: Salticidae, Oxyopidae), Stem Runner (SR: Anyphaenidae and Philidromidae), Foliage Sit & Wait (FSW: Thomisidae) Medium Orb-Weaver (MOW: Araneidae and Tetragnathidae), which include some of the most diverse and easily detected spider families in my survey. Some of the species within each family are widespread habitat generalists and/or achieve high abundance in some habitats. The proportional contribution of functional groups (including richness and density) to spider community assembly may be different among habitats. For example, woody-grassland transition habitats supported more species per functional group than was seen in the other habitats, and grazed/ open grassland and woody/ grassland transitions supported more species of wandering spiders per functional group than did not-grazed/ open grassland. The proportional composition of species richness and density across three habitat types for a grassland community shows that FS was the most abundant and diverse group for all habitat types, where it accounted from 25 to 40 % of the species and ~30% of the total spider density. The proportional species richness of stem runners was similar across all habitats, but their density was greater in open grazed grassland and woody-grassland transitions where the group represented ~ 25% of the density compared to 15% for not-grazed open grassland. The proportional richness of foliage-sit and wait (FSW) was similar across all habitats at ~9%, but FSW density was greater in open grazed grassland and woody-grassland transitions, representing 28% and 22%, respectively; the availability of flowering plants on these habitats likely explains this response. The proportional richness of medium orb-web (MOW) was slightly greater in not-grazed/ open grassland and woody-grassland transitions (Fig. 3.7). The proportional density of this group was higher (15%) in not-grazed/ open grassland than in other habitats (less than 10%), largely driven by the spike in abundance of *A. stellata* in 2012. For small orb web (SOW), the proportional species richness and density was higher in woody/ grassland transition sites than for other habitats, reflecting abundance of web-anchoring structure (woody vegetation).

Discussion

My field study documented how variable fire, grazing, and climate interactions underlie the observed mosaic of unique spider assemblages in tallgrass prairie at KPBS, where they act through their direct effects on vegetation structure and heterogeneity across the landscape throughout the growing season, resulting in a different number of distinct spider assemblages in different years. As documented in Chapter 2, spider communities did not respond directly to fire and grazing, but rather spider community diversity, evenness and richness of hunting strategies tracked changes in habitat structure and heterogeneity as mediated through vegetation. This study further investigates the taxonomic composition and structure of spider community assembly in response to shifting habitat mosaics in time and space. The synergistic effects of fire and grazing in combination with variable weather and topography increased the total diversity of habitat types and the configurationally landscape heterogeneity (number, size and arrangement of habitat patches) (Perović et al. 2015). A key goal here is to link the taxonomic assembly of identifiable spider clusters to habitats formed by specific environmental factors.

Mesic grassland such as tallgrass prairie at KPBS is maintained at a landscape scale by interactions among key drivers, including fire, grazing, and climate (Anderson 2006, Gill et al. 2009, Knapp et al. 1998). Combined, these ecological factors determine species diversity, the taxonomic composition of plant communities, net primary production, the physical structure of vegetation, and how each varies in time and space (Bormann and Liken 1979, Fuhlendorf & Engle 2001, 2004; Fuhlendorf et al. 2009, Tews et al. 2004, Bond & Keeley 2005). For consumers, these same site attributes define the availability of suitable habitats, which in turn determines the spatiotemporal patterns of the abundances, diversity of taxa and taxonomic composition of communities at higher trophic levels (Halaj et al. 1998, Bonte et al. 2000, Fuhlendorf & Engle 2001, 2004; Tews et al. 2004, Heikkinen et al. 2004, Joern 2005). Most importantly, outcomes of such interactions are often considered non-equilibrial (Knapp et al. 1998), reflecting the variable application and intensity of variable drivers, the inherent interactions between fire and grazing, and the variable nature of ecosystem responses in time and space that contribute to ecosystem heterogeneity (Fuhlendorf & Engle 2004, Tews et al. 2004, Archibald et al. 2005). For example, recent fire at sites preferentially attracts grazers that in turn remove forage within a patch in a heterogeneous fashion, leading to a reduced fuel load and an extension of the inter-fire interval until sufficient fuel to support a burn has accumulated. Variable fire frequencies at a landscape level promote heterogeneity of habitat attributes across multiple spatial and temporal scales from the site to landscape scale (Knapp et. al 1998, Fuhlendorf & Engle 2001, 2004; Fuhlendorf et al. 2009).

At KPBS, long-term experimental management at the watershed level included varying fire frequency over (40 + years) and bison grazing (20+ years) across a steep topographic gradient and accompanied by variable weather resulted in a shifting-mosaic of vegetation communities at multiple spatial and temporal scales across the landscape. Heterogeneity of key habitat attributes can be important for supporting increased species diversity of consumers including spiders, especially at larger spatial scales (Chapter 2, Fuhlendorf et al. 2006, 2010; Isaia et al. 2006). Moreover, consumer species each have unique habitat preferences, where individual species track habitat attributes that best suit their needs. As such, the spatial and temporal heterogeneity inherent in this variable system should also include consumer species assemblages that are characteristic of specific habitat types, and these assemblages should move about in time and space as basal vegetation (structural) habitat varies in response to actions of ecosystem drivers (Halaj et al. 1998, 2000; Fuhlendorf et al. 2006, 2010). Ultimately, community assembly processes based on species-specific responses underlie the general changes in community species diversity described above.

Spider assembly in response to a shifting mosaic of vegetation communities

This study documented the flexible nature of spider assemblages at the local scale from a grassland spider meta-community as they tracked changes inherent in local vegetation communities (Fig 3.2). The resulting species clusters differed both taxonomically and functionally in response to major trends in habitat structure and heterogeneity (Figs. 3.6 & 3.7). At a minimum, the KPBS landscape includes three spider assemblages that respond to specific habitat structure. (a) The woody-grassland transition promotes richness of foliage-stalker (FS), foliage-sit & wait (FSW), stem-runner (SR) spiders that benefit from complex vertical vegetation structure which promoted increases in density of small orb-web (SOW) groups reflecting the availability of structure for web-anchoring (Fig 3.7e & f). (b) The grazed/ open-grassland habitat is similar to woody-grassland transitions, where the mosaic of vegetation patches results from grazing activity and promotes increased richness and density of FS, FSW, SR (Fig 3.7a & b). (c) Not-grazed/ open grassland was the least diverse habitat and had the lowest overall spider density, but the distribution of functional hunting strategy groups (species richness and density per functional group) was more evenly distributed than is seen in the other two habitats (Fig 3.7c & d). A closer look reveals that the number of distinct spider clusters varied both within a growing season and changed from year to year (Fig 3.2). An advantage of addressing this type of questions about community structure with arthropods is that I can gain insights about the importance of a shifting mosaic of habitats to community assembly at a relatively small spatiotemporal scale, as revealed by the distance of sites described by cluster analysis dendrogram (Supplementary material, Fig. 5.2) and in ordination space. For example, few grazed sites from 2011 and 2013 located in different watersheds burned at 1, 2 and 4-year intervals formed distinct sub-groups within grazed open-grassland sites; the taxonomic and/or proportional density of spiders in these sites had a high abundance and richness of flowering plants. Another example from open grassland includes sites located in a 4 yr burned watershed that was a grazing lawn in 2011, but was encroached by sumac in subsequent years when bison reduced grazing activity. At this point, the spider species composition started to look more similar to the spider composition of shrub island (dogwood)/ grassland transitions compared to the composition from other grazing lawns. Last, orb-weaving spider density of *A. stellata* increased during the 2012 drought, and became one of the most common spiders in not-grazed/open grassland in late-summer while grasses were flowering. *A. stellata* density dropped in 2011 and 2013 at these sites. Changes in abundance of a species and/or functional groups can trigger shifts in the dynamics of the spider assemblage as predators in the community by altering how spiders interact among themselves (competition and predation) and how they regulate their prey. Different species and functional group may differ in their success rates at capturing different arthropod groups, which can influence plant and plant predator interactions.

Temporal and spatial variation in species diversity can influence community composition, resulting in distinct season-specific assemblages (Uetz 1975, Sudhikumar et al. 2005). The number of distinct clusters observed in early- vs. late-summer also differed for at least one distinct spider assemblage. The within-season pattern could be driven by increased species richness observed over the growing season as more species emerged and developed (Uetz 1975, Hatley & Macmahon 1980, Sudhikumar et al. 2005). The interaction of multiple factors may influence seasonal differences. Species often have different emergence times and growth rates, and spiders prefer different habitats and prey-size as they grow and mature, affecting their detectability in the habitat (Lubin 1978, Hatley & MacMahon 1980, Reed & Nicholas 2008). For example, web-builder species richness and the associated richness of different web-types at KPBS showed spikes in species richness and abundance towards the late-summer period, a pattern that was also documented for a sage spider community in Utah (Hatley & MacMahon 1980) and by a web-building spider on Barro Colorado Island, Panama (Lubin 1978). Vegetation biomass and structure reached its maximum in late season (Hatley & Macmahon 1980, Lubin 1978), and it became more differentiated with respect to plant species, vegetation types, topographic position and grazing intensity in response to recent spring-fire disturbances at KPBS. Late season habitat provided increased availability and opportunities for habitat partitioning by spider across the landscape.

Weather variability, including rainfall patterns and especially extreme events like drought, may also play crucial roles in structuring natural consumer communities through its effect on plant community species composition and vegetation growth. The severe drought of 2012 offered the opportunity to document how severe-drought early in the summer affected spider community assembly, particularly driven by changes in vegetation structure and heterogeneity. In part, responses to drought reflected an interaction with bison grazing pressure as bison foraged more uniformly across the landscape because of low food availability during this growing season. Grazing activity reduced vegetation biomass and structure on grazed sites throughout the growing season, and habitat structure of the grass layer was not as differentiated among grazed sites as in other years. Consequently, the drought-grazing interaction reduced the differences in community assembly between early-summer and late-summer spider assemblages observed 2011 and 2013. Consequently, spider assemblages of the open grasslands reflected the sharp contrast of vegetation biomass/ structure availability between grazed and non-grazed habitats at the grass layer in early-summer, but towards the end of the growing season spider assembly of the open grassland were not differentiated like did in 2011 and 2013. Spider assemblages from the woody/ grasslands transitions remained distinguishable due to the unique profile of vegetation template and its associated spider assembly may have not been impacted drought-grazing interaction as the open grassland habitats.

Spider assembly responses to time since last burn

Disturbance from fire can play a critical role in maintaining grassland biomes by resetting vegetation growth and plant community succession, and heterogeneous dispersal of fire across the landscape coupled with variability in fire return intervals may promote species diversity among consumers. Recent and frequent burns are expected to have a negative effects on spider community complexity by reducing the availability of vegetation structural complexity, heterogeneity, and unique resources associated with increased plant richness, thus reducing spider opportunities for niche partitioning and species coexistence (Podgaiski et al. 2013). My results showed that in the year of burning, the taxonomic composition of spider assemblies from sites burned every 4 years were similar to sites burned frequently (1 & 2 yr). However, spider assemblages from sites burned at 4-year frequencies were separated from frequently-burned watersheds in ordination space as the time form last burn increased. Spider responses likely reflected differences in the availability of vegetation structure and spatial heterogeneity driven by variable plant succession patterns among watersheds subjected to different burn frequencies. Intermediate- burn disturbances promote an increase in abundance of novel habitat resources vegetation resources, particularly those provided by non-disturbance prone plant species, when compared to frequently burn watersheds. Further study of this pattern is required as I monitored spiders for only a period of three years, and a long-term study is needed to fully address spider assembly dynamics in response to increases in time since last burn.

At the other end of the spectrum, fire suppression for long periods allows the establishment and expansion of non-fire prone woody vegetation. Woody dominated plant communities have more permanent vertical structure that supports different spider taxa, especially web-forming species. The unique vegetation profile, characterized by rapid increases in vegetation structure and canopy heterogeneity beyond the grass-layer, promotes the assembly of unique spider communities with different taxonomic composition. Woody/grassland transition sites occupied a distinct position in the ordination space of spider assemblages regardless of fire and grazing disturbance regimes. Even in a year when these habitats burned, spider assemblages remained distinct within the ordination space and remained close to other not-burned sites as predicted. Further study of this pattern is required as I only examined a small number of woody habitat sites.

Spider community responses to grazing

Not-grazed habitat is dominated by warm season grasses and is characterized by a dense, homogeneous closed canopy. I previously documented that increased vegetation canopy closure (LAIM) negatively affected spider diversity, species evenness and richness of hunting strategies throughout the growing season (Chapter 2). Nevertheless, such vegetation structure favors some taxa characterized by active hunting styles that move constantly throughout the vegetation canopy in search of prey (e.g., stem-runner). For example, spiders from the family Philodromidae were found in all KPBS habitats, but their abundances were higher in not-grazed/ open grassland habitats. These species have relatively slender bodies, are well-suited to hide among grass leaf blades, and increases in grass canopy connectivity allows these species to cover more area and readily locate patches of food in the landscape. Species richness of web-builders in open/not-grazed habitats was lower than in any other habitat due to the absence of appropriate vegetation for web-placement. Still, some species reached high density when the appropriate structure for web-placement was available, including *A. stellata* (Araneidae) and *D. bostonensis* (Dyctinidae) during the flowering period of big bluestem in late summer. Thus, the proportional density contribution of the medium-orb-web (MOW) and mesh-web (MW) functional groups to the functional composition of spider assemblages is greater in not-grazed/ open grasslands than in grazed/ open grassland.

Grazing positively influenced consumer composition by promoting vegetation heterogeneity at multiple spatial and temporal scales along important habitat dimensions (Moran 2014): canopy openness, variability in vegetation height, increases in plant species richness, increases in cover and mixture among plant groups (grasses, forbs, shrubs and trees). Greater structure improves opportunities for habitat partitioning throughout the growing season, even when aboveground vegetation structure is lower than in not-grazed grassland; 1.4x more spider species were documented in grazed than non-grazed open grasslands at KPBS. Both wandering and web-building spider groups benefited from increased opportunities for habitat partitioning on grazed habitat in response to the higher abundance of forbs and other flowering plants, and increased spatial heterogeneity of plant architecture and habitat structure promoted by fire-grazing interactions. The web-builder component of the spider community was a minor component of the spider assemblages on open-grassland habitats due to the lack of vegetation structure on which to anchor webs (Baldissera et al. 2004; Podgaiski et al. 2013). Grazing effects on vegetation structure and heterogeneity support the formation of spider assemblages that are taxonomically and functionally more complex than seen in not-grazed /open grassland, but less complex than that of woody/ grassland transition habitats. Woody/ grassland transition habitats supported 1.6x more species than not-grazed/ open grassland. Grazed/ open grassland habitats are dominated in diversity and abundance by wandering spiders that exploit vegetation with complex architecture and spatial heterogeneity. A characteristic of the spider assemblages of complex habitats is the dominance of spiders with stout bodies compared to the slender body morphology found in non-grazed /open grassland. As spiders with slender body morphology are better suited to move across denser-closed and homogenous vegetation cover characteristic of non-grazed open grasslands.

Grassland spider community hot spots

Ecotonal transition habitats like the woodland-grassland transition can be hot spots for consumer diversity (Kitahara & Watanabe 2003, Rubio et al. 2008), including spiders, due to the higher diversity of structure/vegetation resources. Vegetation in transitional habitat includes a mixture of plant species adapted to fire and those that escaped the regulatory effect of fire, bringing unique combinations of habitat over a relatively narrow spatial scale. This increases opportunities for coexistence through increasing opportunities for niche partitioning at fine scales for both wandering and web-building spiders (Michalko & Pekar 2015, Michalko et al. 2016).

Web builders are a diverse group of predators representing ~60% of the North American spider fauna (Young & Edwards 1990), and web builders in US agricultural fields accounted for ~45% of the arachnid species richness found in these ecosystems. However, web-building spider guilds are uncommon in North American open grassland, seemingly because of the paucity of structure on which to anchor webs (Baldissera et al. 2004; Podgaiski et al. 2013). In contrast to open-grassland habitat, where overall abundance, species richness and richness of hunting strategies of spider assemblages is dominated by wandering spiders, habitats from woody-grassland transitions were characterized by the dominance of web-building spider species; 4 of the 6 most commonly found spider families were web-builders. The most commonly found web-building families were Araneidae (6 species), Dyctinidae (1 species), Agelenidae (1 species) and Theridiidae (1 species); while the commonly found wandering spider families are Anyphaenidae (2 species), Thomisidae (1 species) and Salticidae (3 species). Web-building spiders partition their habitat at fine spatial scales both vertically and horizontally (Colebourn 1974, Enders 1974, Brown 1981, Baldissera et al. 2004, Balmires et al. 2007, Richardson & Hanks 2009), the distribution of spider web-types/ web-building species at KPBS reflects increased vertical and horizontal complexity of plant architecture that serves as web-anchoring structures (Colebourn 1974, Brown 1981, Baldissera et al. 2004, Richardson & Hanks 2009). In addition to the high diversity of web-building spiders, woodland-grassland transitions supported diverse assemblages of wandering spiders that were as speciose and functionally diverse as those found in grazed /open-grassland habitats, although composed of slightly smaller sized species. For example, even though salticid spiders reached high abundances in both habitats, the species composition and abundances of these species in woody-grassland transition habitats tended to be dominated by small sized species from the genera *Pelegrina* and *Zygoballus* instead of species of the genera *Phidippus*, *Hentzia* and *Thiodina* which dominate grazed/open grassland. Similarly, thomisid *(Tmarus angulatus)* commonly found at woody-grassland transition site is a relatively small species that as a fully grown adult is comparable in size to juvenile individuals from species of the genera *Mecaphesa*, *Xysticus* or *Misumenoides* commonly found in open-grassland, and especially grazed habitats.

Conclusions

Overall, I documented the responsive and malleable nature of spider community assembly to spatial and temporal changes the structure of the vegetation driven by interactions among fire, grazing and climate that resulted in a shifting mosaic of local spider assemblages. The management plan at KPBS experimentally varies disturbances typical of grasslands and promotes habitat heterogeneity by burning only a fraction of the site each year in a prescribed rotational faction. Time since fire in turn influences bison grazing intensity. As shown in this study, spider assemblies track the resulting shifting mosaic pattern of habitat in a very dynamic fashion, with groups of species preferentially using different habitat types. Thus, a landscape subjected to multiple fire and grazing disturbance regimes can accommodate both species that prefer more frequently disturbed habitat as well as those that benefit from lower disturbance regimes. Shifting mosaics of habitat types ultimately lead to increased β-diversity and altered species distributions in time and space over the landscape. From a conservation and management perspective, results highlight the importance of maintaining a shifting mosaic of vegetation states across the landscape to promote increased β-diversity at the taxonomic and functional levels (Isaia et al. 2006, Rubio et al. 2008, Perović et al. 2015, Podgaiski et al. 2013). Habitat diversity ultimately promotes increases in the beneficial aspects of arthropod predators such as prey population regulation for herbivore and pest species that in turn trigger trophic cascades that could affect habitat productivity with positive feedbacks on diversity (Lang et al. 1999, Laws & Joern 2013) Although not studied here, such trophic responses have positive consequences for human economic endeavors/activity via rangeland control of pest insect outbreaks or perhaps they may indirectly contribute to non-monetary benefits as the structure and function of natural communities are supported.

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Figures and Tables

Table 3-1. Species rank for most common spider on vacuum samples from 2011-2013 at KPBS.

Common spider of KPBS			**Spider Density**		**Spider presence/absence**	
Species Name	**Hunting strategy**	**Code**	**Rank**	**Density**	**Rank**	**Detection**
Oxyopes salticus	Foliage Stalker	X54	1	12.2	1	123/131
Mecaphesa dubia	Foliage Sit &Wait	X117	2	10	2	110/131
Tibellus gracilis	Stem Runner	X57	3	6	4	85/131
Thanatus vulgaris	Stem Runner	X61	4	4.9	8	67/131
Hibana velox/gracilis	Stem Runner	X3	5	3.7	5	80/131
Mecaphesa celer	Foliage Sit &Wait	X116	6	3.2	7	72/131
Argiope trifasciata	Medium-Orb Web	X10	7	2.6	3	88/131
Wulfila saltabundus	Stem Runner	X6	8	2.5	20	37/131
Xysticus triguttatus	Foliage-Ground Sit&Wait	X124	9	2.3	10	60/131
Phidippus clarus	Foliage Stalker	X83	10	2	6	73/131
Pelegrina galathea	Foliage Stalker	X75	11	1.8	11	57/131
Salticidae morpho 2	Foliage Stalker	X66	12	1.5	13	52/131
Marpissa pikei	Foliage Stalker	X77	13	1.5	9	60/131
Tmarus angulatus	Foliage Sit &Wait	X114	14	1.3	23	32/131
Thiodina purpurea	Foliage Stalker	X72	15	1.2	19	37/131

Table 3-2. Species rank for most common web-builder and wandering spiders collected using on vacuum sampling from 2011-2013 at KPBS.

Web-Building Spiders

Species Name	**Hunting strategy**	**Code**	**Rank**	**Presence/ absence**	**Habitat association**
Argiope trifasciata	Medium-Orb Web	X10	1	88/131	Open grassland
Araneus pratensis	Small-Orb Web	X14	2	44/131	Woody
Dictynia bostonensis	Irregular-Mesh Web	X38	3	43/131	Woody
Acanthepeira stellata	Medium-Orb Web	X7	4	42/131	Open grassland
Larinia directa	Medium-Orb Web	X20	5	34/131	Woody
Agyneta spp.	Doily-Sheet Web	X37	6	32/131	Open grassland
Theridion rabuni/varians	Irregular-All-Directions Web	X105	7	31/131	Woody
Mangora gibberosa	Medium-Orb Web	X23	8	22/131	Woody
Tetragnatha laboriosa	Medium-Orb Web	X109	9	17/131	Woody
Euryopis spp.	Irregular-All-Directions Web	X107	10	16/131	Woody

Wandering Spiders

Species Name	**Hunting strategy**	**Code**	**Rank**	**Presence/ absence**	**Habitat association**
Oxyopes salticus	Foliage Stalker	X54	1	123/131	Open grassland
Mecaphesa dubia	Foliage Sit &Wait	X117	2	110/131	Open grassland
Tibellus gracilis	Stem Runner	X57	3	85/131	Open grassland
Hibana velox/gracilis	Stem Runner	X3	4	80/131	Generalist Generalist
Phidippus clarus	Foliage Stalker	X83	5	73/131	Generalist
Mecaphesa celer	Foliage Sit &Wait	X116	6	72/131	Generalist

Thanatus vulgaris	Stem Runner	X61	7	67/131	Open grassland
Marpissa pikei	Foliage Stalker	X77	8	60/131	Generalist
Xysticus triguttatus	Foliage-Ground Sit&Wait	X124	9	60/131	Generalist
Pelegrina galathea	Foliage Stalker	X75	10	60/131	Woody

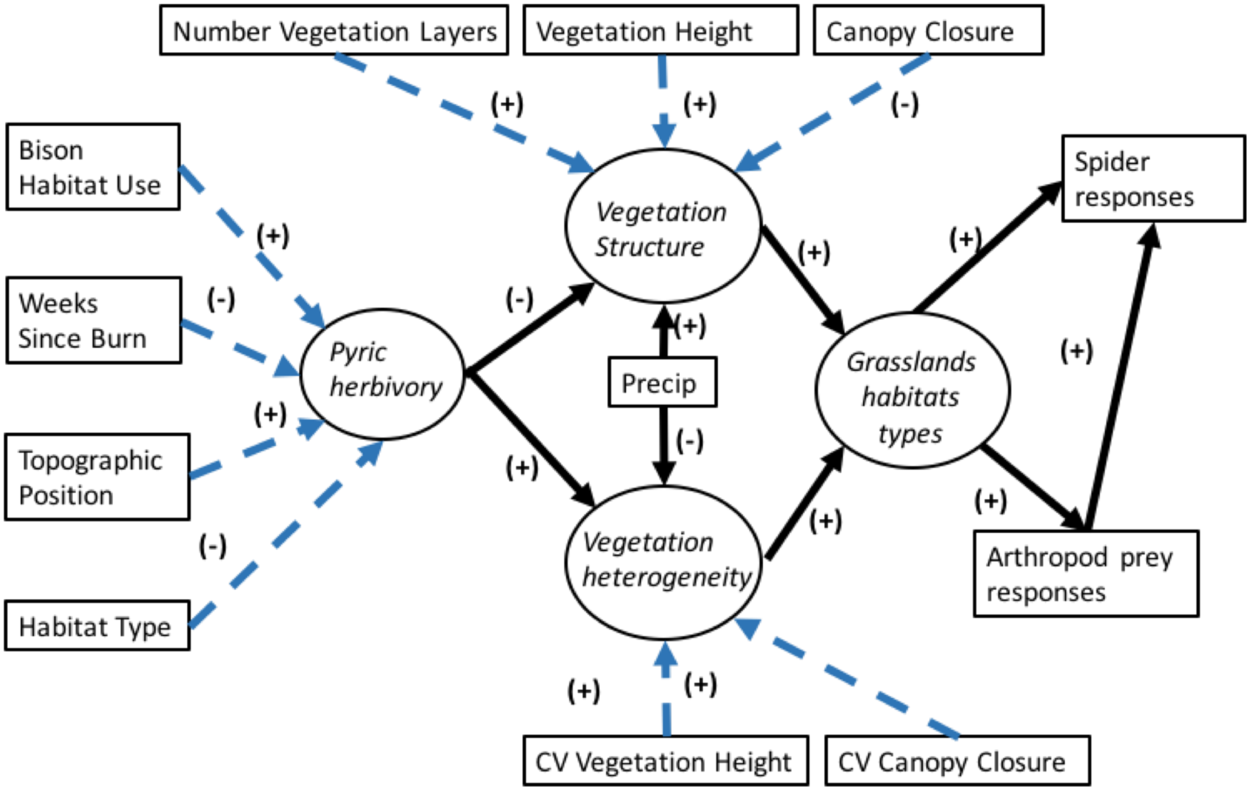


Figure 3-1. Conceptual framework showing predictions of how the ecological driver *pyric herbivory* indirectly structures the richness of local spider assemblages within a spider grassland community through its direct effects on vegetation structure and vegetation spatial heterogeneity. Vegetation attributes determine the diversity of grassland habitat types used by consumers. The conceptual framework was evaluated using the Structural Equation Modeling approach (SEM) and Redundancy Analysis. Boxes represent loading factors: responses and predictor variables for which I have empirical measurements. Ellipses represent latent variables (SEM), variables inferred from other measured variables that describe the synergistic effects of loading factors on a ecological process/interaction. Dashed arrows show which predictor variables were used to infer each latent variable. +/- symbols indicate the expected relation among the loading factor and latent variable. Solid arrows show the interactions of interest. +/- symbols show the expected interaction among predictor and responses interactions of interest in this model.

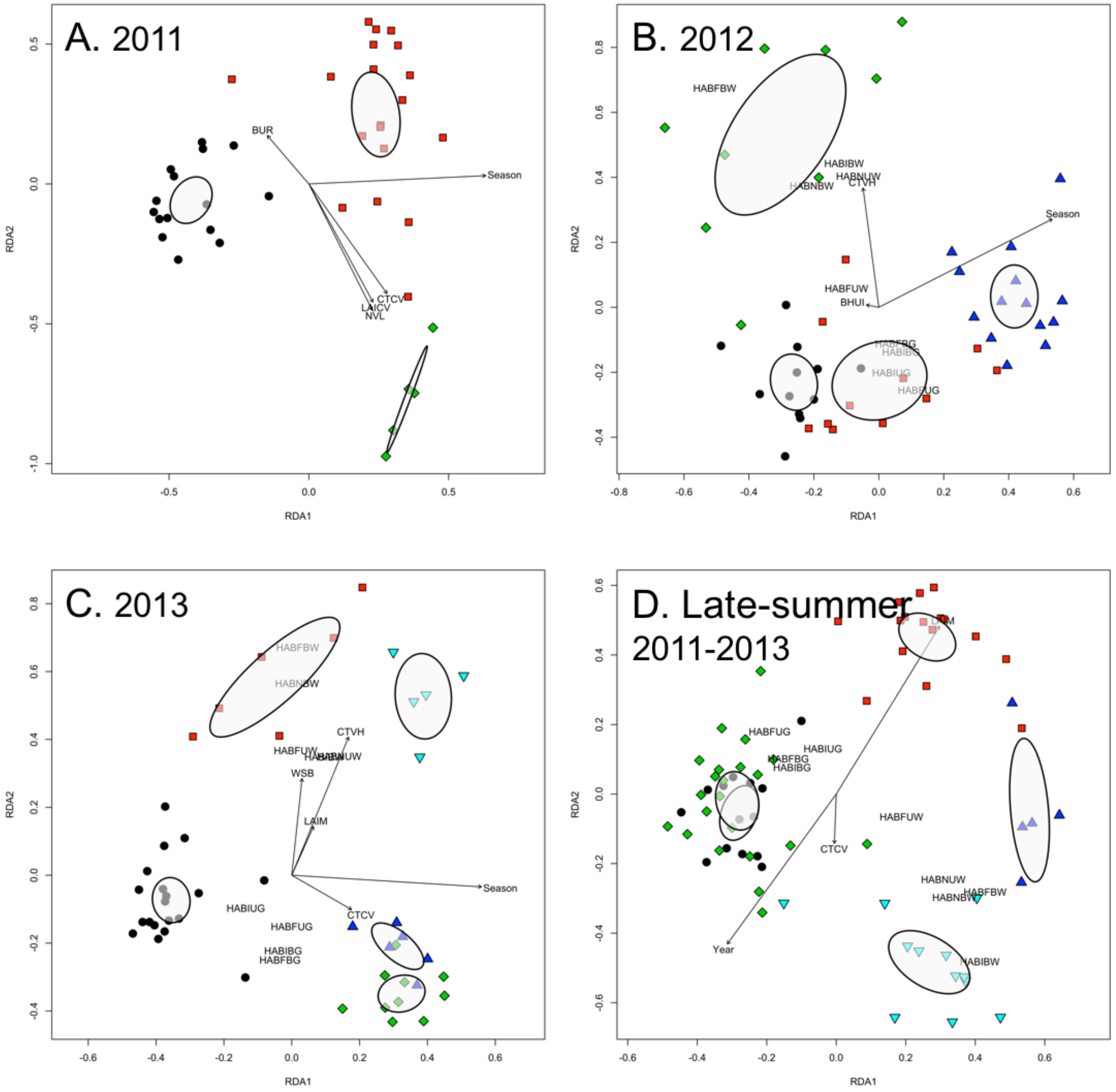


Figure 3-2. Results of redundancy analysis thatshows how sites are positioned in RDA-ordination space: sites are plotted in RDA space based on color cluster that were assigned using a hierarchical cluster analysis using Ward's distance criteria. Ellipses represent the centroid for each of the cluster in the ordination plot. (a) Three distinct spider assemblages were detected in the 2011 growing season (*black circles*: open grasslands in early-summer, *red squares*: open grasslands in late-summer and *green diamond*: woody-grassland transitions in late-summer). (b) In 2012, four distinct spider assemblages were detected based on local spider species composition (*black circles*: grazed/ open grasslands in early-summer, *red squares*: non-grazed/ open grasslands in early-summer, *green diamond*: woody-grassland transitions both in early- and late-summer, and *blue triangle*: open

grasslands in late-summer). (c) In 2013, a total of 5 spider assemblages was observed across KPBS (*black circles*: open grasslands in late-summer, *red squares*: woody-grassland transitions in early-summer, *green diamond*: grazed/ open grasslands in early-summer, *blue triangle*: non-grazed/ open grasslands in late-summer, and *light blue downward triangle*: woody-grassland transitions in late-summer). (d) For late-summer samples between 2011 and 2013, a total of 4 distinct spider assemblages was observed within the KPBS spider community (*black circles*: grazed/ open grasslands, *red squares*: sites sampled in 2011, *green diamond*: non-grazed/ open grasslands, *blue triangle*: woody-grassland transitions sampled in 2011, and *light blue downward triangle*: woody-grassland transitions sampled in 2012 & 2013).

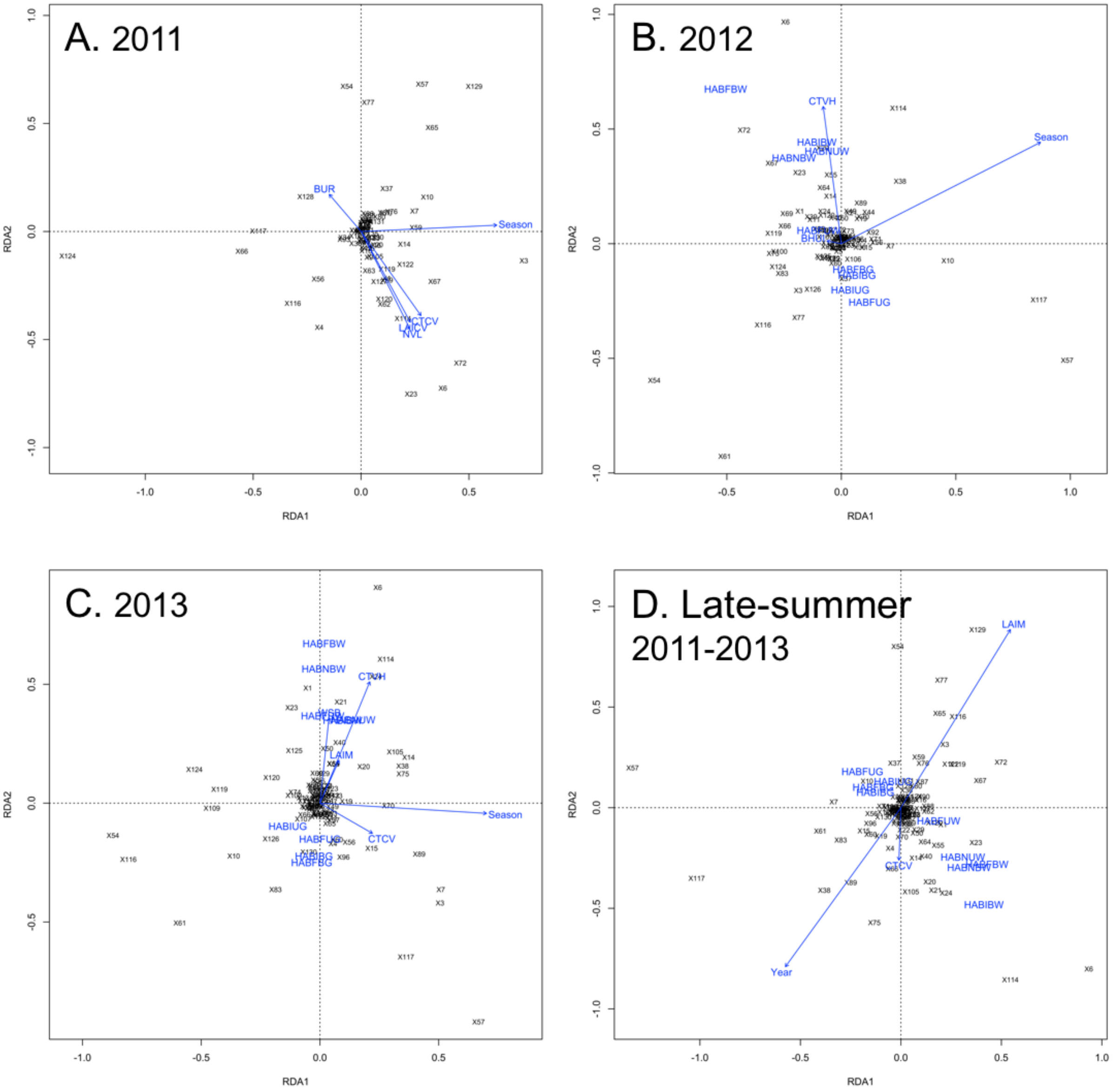


Figure 3-3. Results of redundancy analysis that shows spider species distributions in ordination space based on their site occurrence and respective density across those sites. Species located far from the centroid of the RDA-ordination space show affinity to certain habitat types and vegetation attributes associated to those habitats. Species near the centroid of the ordination space include all the species that occurred at low density, but also include the habitat generalists that can be commonly detected across KPBS but do not exhibit clear difference in density among habitat types. Plots represent spider species distributions within ordination space: (a) 2011, (b) 2012, (c) 2013 and (d) late-summer 2011-2013.

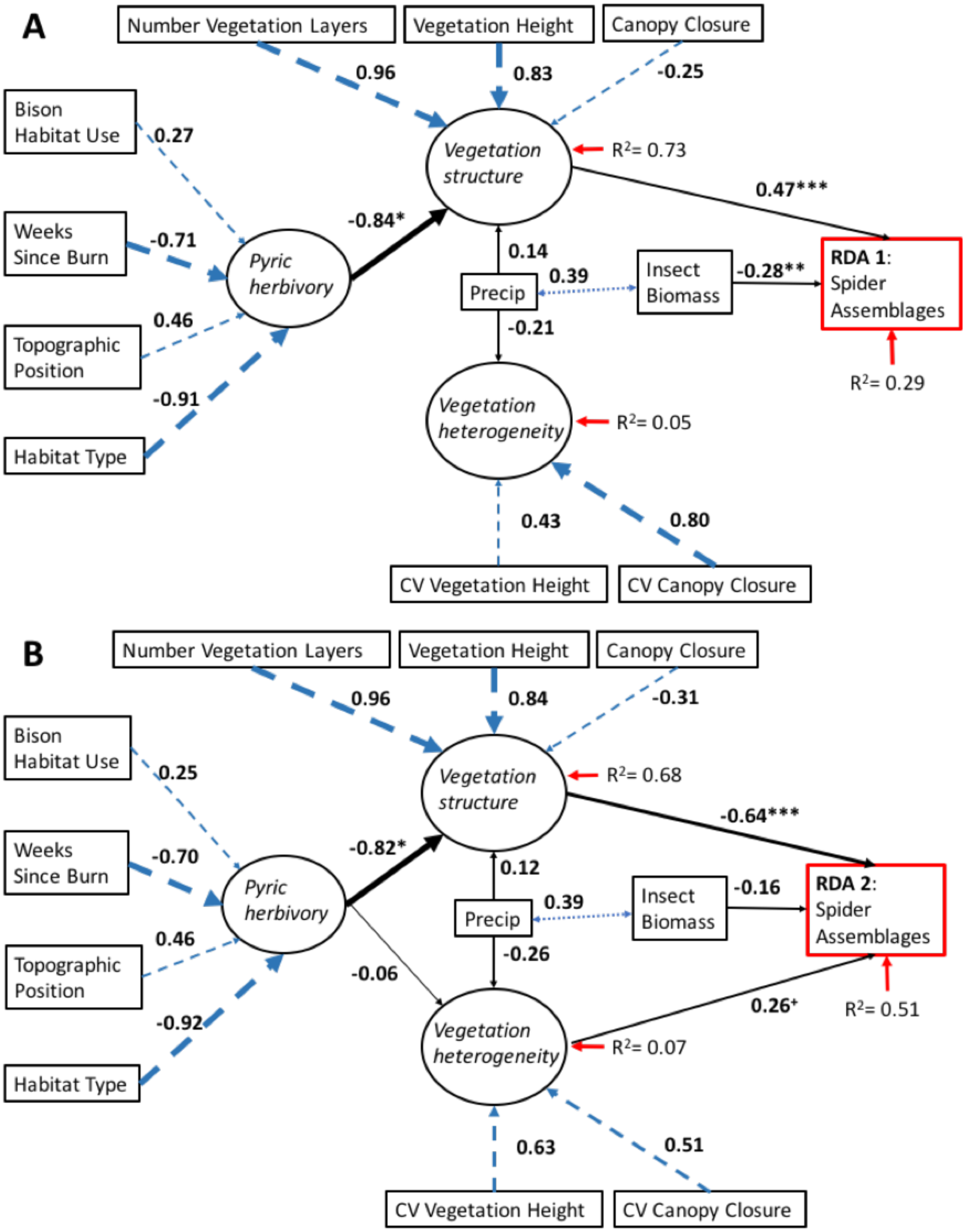


Figure 3-4. Structural equation model shows how fire and grazing interactions (Pyr) indirectly structure the richness of local spider assemblages within a grassland spider community complex through its direct effects on vegetation structure (HbS) and vegetation

heterogeneity (HbH) in the early-summer. Spider responses measured are RDA 1 (left) and RDA 2 (right). Arrow thickness is scaled to illustrate the relative strength of effects and significant coefficients are indicated with plus sign ($^{+}$ $p < 0.1$) asterisks (* $p < 0.05$, ** $p<0.01$ and *** $p<0.001$). The coefficient of determination (R^2) are shown for the spider response variables (RDA-1 and RDA-2) and latent variables: vegetation structure and vegetation heterogeneity.

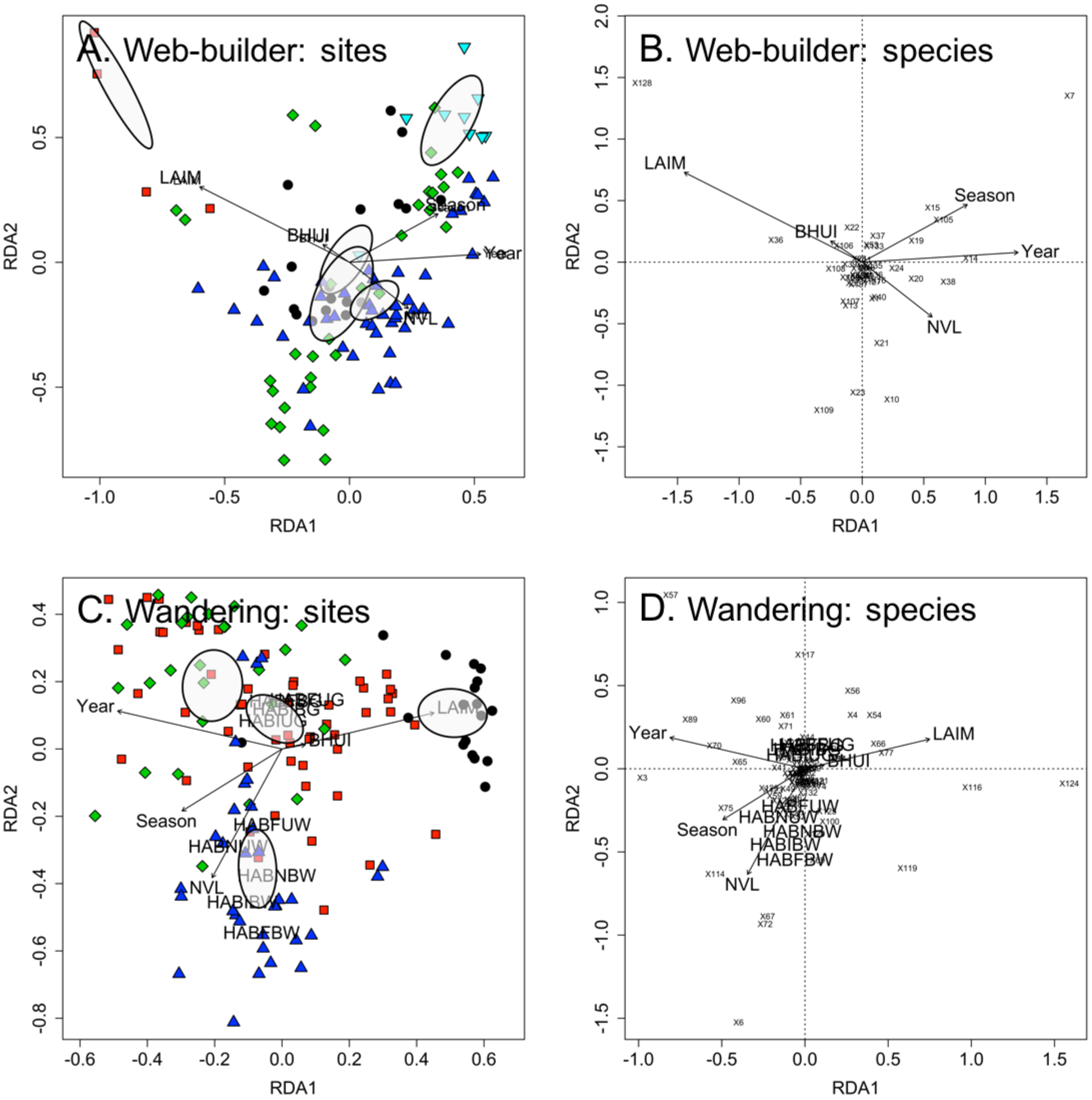


Figure 3-5. Presence-absence of web-builder and wandering spider ordinations show how major components of spider community complexity respond to changes in vegetation structure and heterogeneity. (a) Web-builder ordination shows that over 3 years, web-builders formed 5 clusters (*black circles*: open grasslands sampled in 2012 & 2013, *red squares*: open grasslands sampled in 2011, *green diamond*: grazed/ open grasslands sampled in 2011 & 2013, *blue triangle*: woody-grassland transitions both in early- and late-summer, and *light blue downward triangle*: late-summer grazed and non-grazed sites marked difference in vegetation height among vegetation patches within site scale). b) Web-builder ordination with scaling factors adjusted to show the species distribution in ordination space show that species associated with open grassland were positively associated along axis 2, while species from woody sitse were

negatively associated wtih axis 2. (c) Wandering spider ordination showing that wandering spider formed 4 distinct assemblages over three years (*black circles*: open grasslands sampled in early-summer 2011, *red squares*: open grasslands sampled in early-summer of 2012 & 2013, *green diamond*: open grasslands sampled in late-summer of 2012 & 2013, *blue triangle*: woody-grassland transitions and open grasslands with marked differences in vegetation height among vegetation patches within sites scaled in both in early- and late-summer). (d) Wandering spider ordination with scaling factors adjusted to show the species distributions in ordination space to show that species associated with open grassland had a positive association along axis 2 while species of woody sites were negatively associated with axis-2.

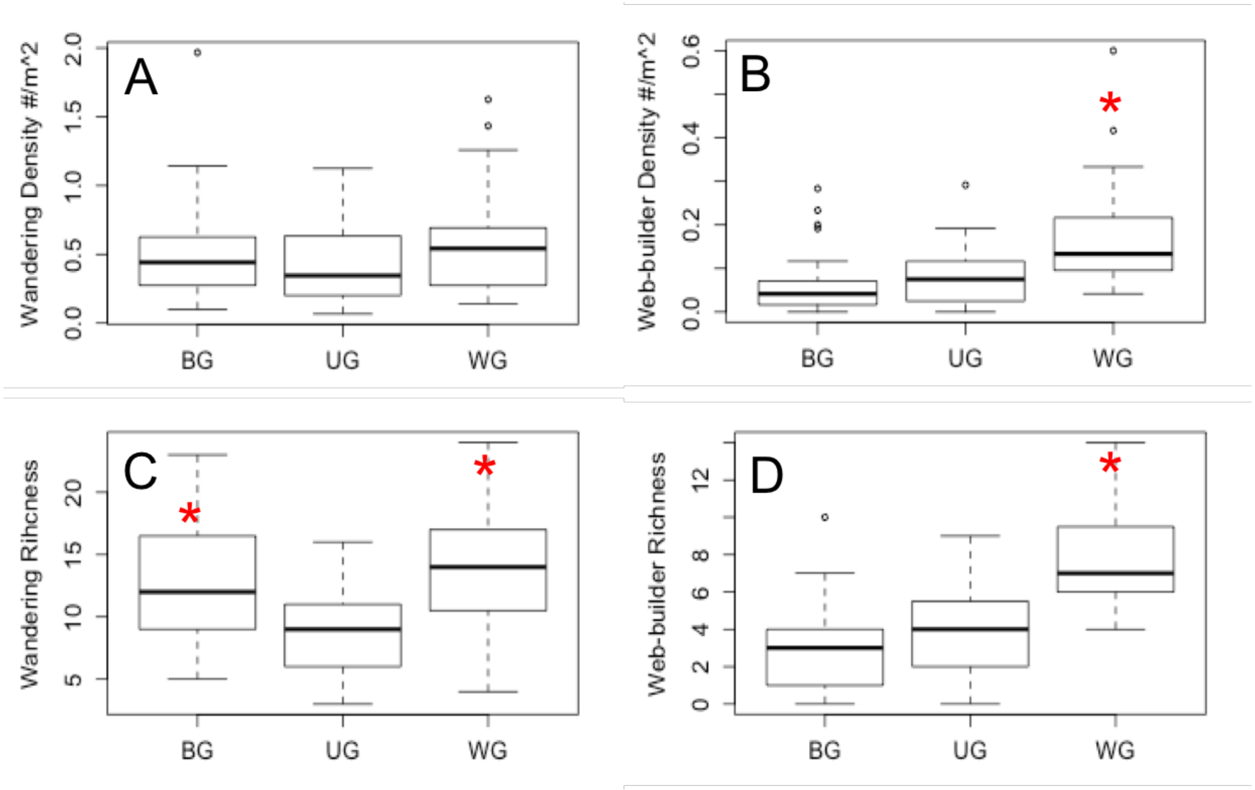
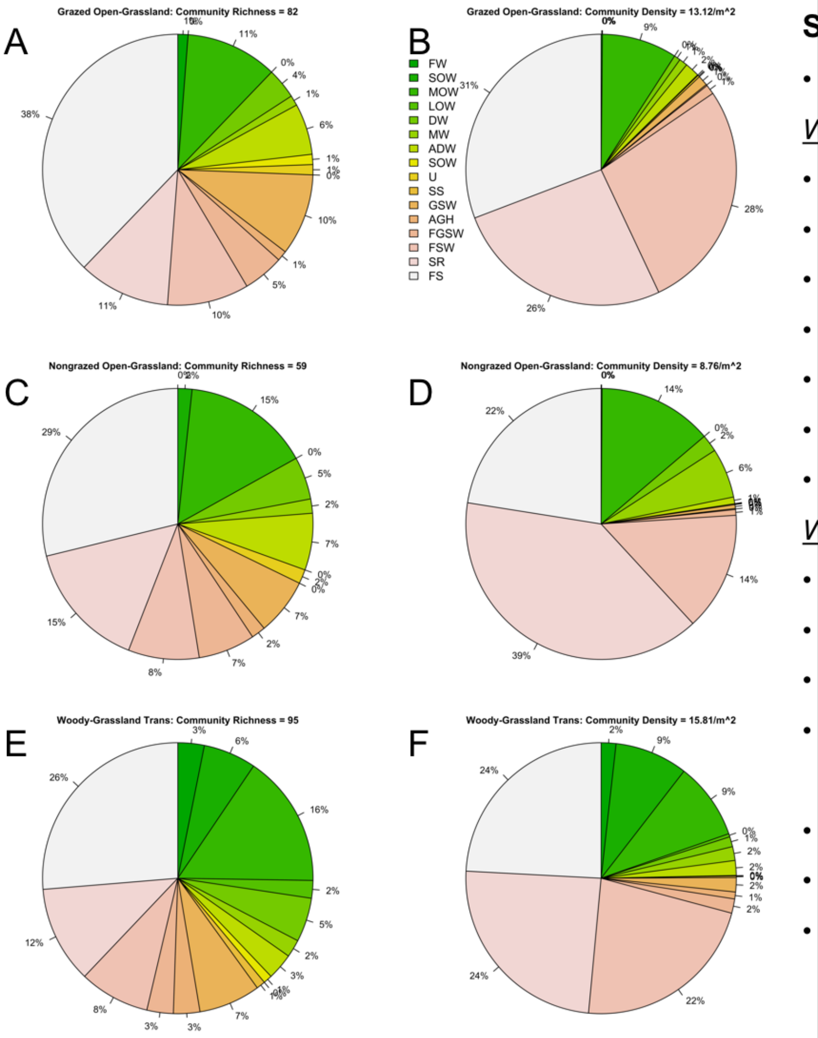


Figure 3-6. Web-builder and wandering spider density and species richness comparisons among three habitat types: grazed/ open grasslands (BG), non-grazed/ open grasslands (UG) and woody-grasslands transition habitats (WG) across Konza Prairie Biological Station, Kansas. Spider responses are: (a) wandering spider density, (b) web-builder density, (c) wandering species richness and (d) web-builder species richness. The box plot elements represent the following: box vertical dimension 5 interquartile range; horizontal line 5 median; whiskers 5 minimum and maximum values; circular points 5 maximum observations 1.5 (IQR) above the 75th percentile.



Spider Hunting Strategies

- U: Unkwon

Web-Building Spiders

- FW: Funnel Web
- SOW: Small Orb-Web
- MOW: Medium Orb-Web
- LOW: Large Orb-Web
- DW: Doily-Web
- MW: Mesh Web
- ADW: All Direction Web

Wandering Spiders

- SS: Spider Specialist'
- GSW: Ground Sit & Wait
- AGH: Active Ground Hunter
- FGSW: Foliage-Ground Sit & Wait
- FSW: Foliage Sit & Wait
- SR: Stem Runner
- FS: Foliage Stalker

Figure 3-7. Functional composition of grassland spider communities across three habitat types. A total of 16 spider functional groups were defined at KPBS. The left column shows the proportional species richness per functional groups found at each habitat type; the observed species richness for all functional groups combined at each of the habitat type is indicated next to each habitat type name. The right column shows the proportional spider density per functional group found for each habitat type; the observed spider density for all functional groups combined for each of the habitat types is indicated next to each habitat type name. Panels a & b represent the proportional species richness and proportional spider density per functional groups on grazed/ open grasslands; panels c & d show results for Nongrazed/ open grasslands, and panels e & f illustrate responses in woody-grasslands transition habitats, respectively.

Chapter 4 - Importance of vegetation structure of an aerial web-building spider community in North American open grassland

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Abstract

Spatial and temporal heterogeneity of suitable habitat in grasslands can promote species and functional diversity in arthropods, including responses by ubiquitous web-building spiders. A field experiment in tallgrass prairie habitat was performed to examine the response in abundance and web-type richness of aerial web-building spiders to changes in the availability of structure for web placement (vegetation architecture). To test the hypothesis that vegetation structure contributes directly to the web-builder abundance and web-type richness in open grasslands, we increased vegetation structure by adding dead woody stems of a common shrub along transects in each of three watersheds that differed in burn histories and existing habitat structure. Aerial web-building spiders were visually censused before and after the manipulations, at which time we recorded web-orientation, height, web-type, and the presence/absence of the spider associated with a web. Over the duration of the study, a total of seven web-type groups were encountered, of which medium-sized orb weavers were the most abundant web-building group across all watersheds. In general, higher spider abundances of orb-building spiders were observed in sections with added structure compared to the non-manipulated sections. However, reduced richness of web types was found on the manipulated sections of transects, suggesting that the architecture provided by woody stems does not provide sufficient and appropriate web-anchoring

structure for the full range of web-building spider groups in tallgrass prairie.

Introduction

Spiders are ubiquitous, generalist and functionally important arthropod predators in terrestrial ecosystems, including grasslands, where they can reach high levels of local species richness and abundance (Diehl et al. 2013; Malumbres-Olarte et al. 2013). In grasslands, interactions among fire, ungulate grazing, plant species diversity, and climate are key drivers determining habitat structure. In turn, consumers respond to bottom-up processes that promote significant spatial and temporal heterogeneity of habitat structure (Bonte et al. 2000; Fuhlendorf & Engle 2001, 2004; Joern 2005). An overarching hypothesis here is that the overall abundance and species diversity of consumer communities increases with increasing spatial heterogeneity of critical habitat attributes, including the overall variability in vegetation architecture and plant species diversity (Dennis et al. 1998; Fuhlendorf & Engle 2001; Fuhlendorf et al. 2006; Jimenez-Valverde & Lobo 2007; Allouche et al. 2012).

Habitat structure affects species interactions in spider communities in multiple ways (Jones & Syms 1998). More precisely, vegetation complexity has been recognized as an important factor influencing species presence, richness and composition of spider communities (Jimenez-Valverde & Lobo 2007). Spiders can partition habitat at fine scales, facilitating the presence of different hunting strategies, where different prey species are susceptible to different hunting strategies (Schmitz & Suttle 2001; Wise 2006; Malumbres-Olarte et al. 2013). Microhabitat partitioning has been documented in web-building spiders where webs differ in placement height, orientation, or type depending on vegetation structure (Enders 1974; Brown 1981; Schmitz & Suttle 2001; Wise 2006). Structural complexity of the habitat can also lead to reduced spider mortality by providing refuges from predation or by influencing intraguild interactions (Finke & Denno 2002; Malumbres-Olarte et al. 2013). Thus, understanding habitat characteristics that affect web placement can reveal whether and how the structural complexity of the habitat can modulate spider community assembly, species abundance and overall functional diversity (Robinson 1981; Bultman & Uetz 1982; Jimenez-Valverde & Lobo 2007; Diehl et al. 2013). In this sense, non-trophic effects on spider communities associated with habitat heterogeneity in plant architecture act as a “bottom-up template” for structuring spider assemblages (Halaj et al. 2000).

Open grasslands are dominated by non-woody vegetation, where graminoids comprise about 80% of the above ground vegetation biomass, while forbs often comprise about 80% of the plant species diversity (Knapp & Seastedt 1998; Joern & Laws 2013). Variation in vegetation architecture among habitats could result in different spider assemblages across the landscape. Web builders are a diverse group of predators representing, 60% of the North American spider fauna (Young & Edwards 1990), and web builders in US agricultural fields accounted for, 44% of the arachnid species richness associated to these ecosystems. Web-building spiders are mainly represented by the families Tetragnathidae, Araneidae, Linyphiidae, Theridiidae, and Dictynidae (Nyffeler & Sunderland 2003). However, web-building spider guilds are uncommon in North American open grasslands, seemingly because of a paucity of structure on which to anchor webs (Baldissera et al. 2004; Podgaiski et al. 2013). Grassland ecotones with woody vegetation along waterways or woodlots often exhibit sharp boundaries characterized by rapid changes in habitat structural complexity, vegetation height, and dominant plant cover. The functional composition of spider communities also changes routinely along this structural gradient, where guilds of web builders are common at the woody end of the gradient but nearly absent in open grasslands

(Baldissera et al. 2004).

We experimentally added woody structures in open grassland habitat to examine how changes in structural complexity affected aerial-web-builder abundance and the richness of web types. Our primary hypothesis states that the availability of structure for web placement limits density, richness of both species and web types, and the distribution of web-building spider guilds in open grassland. We focused first on how web density and web-type richness responded to the newly added structures for web anchoring (woody vegetation: manipulation) in open grasslands. Second, we asked how increasing the distance at which structures for web anchoring are available relative to riparian woodland edges affects web density and web-type richness. If the availability of structures for web placement limits web-building spiders in open grassland, we predicted: (a) a greater density of web-building spiders and web-type richness will be found in areas with increased diversity and availability of web-anchoring structure, regardless of burn history at a local scale (300 m^2 transects) and distance from grassland-woodland edge; (b) the density of web-building spiders will be higher in watersheds with a history of lower burn frequency because the availability of structures for web placement increase with increasing time since the last burn; c) the distance from a riparian wood stand edge is expected to negatively influence the abundances or web densities of web-building spiders along transects to which we added structure for web placement due to web-builder dispersal limitations or limitations in prey availability; and (d) aerial web-builder abundances within manipulated sections will be higher than those in non-manipulated sections of these transects regardless of distance from edge. Web-type richness will be affected primarily by the availability of web-anchoring structures with lower richness on non-manipulated sections of the open grassland.

Methods

Study site

Our field study was conducted at the Konza Prairie Biological Station (KPBS) located in the Flint Hills grassland of north-eastern Kansas, 10 km south of Manhattan (39° 05’ N, 96° 35’ W). KPBS is a 3487 ha native tallgrass prairie preserve that experiences a highly variable US continental climate consisting of wet, hot summers and dry, cold winters (Knapp & Seastedt 1998; Joern 2005). KPBS is a protected research area with long-term, landscape-level treatments that manipulate prescribed fire (1, 2, 4 and 20 year frequencies) and large ungulate grazing (bison and domestic cattle). Mean annual precipitation is 835 mm, most of which falls during the growing season. Steep-sloped terrain overlain by shallow soils and limestone benches unsuitable for cultivation characterize the topography of the site. The KPBS flora includes a mixture of more than 600 species (Towne 2002), including warm-season and cool-season grasses, legumes, and other forbs. The vegetation cover of KPBS is dominated predominately by perennial warm-season C_4 grasses although forb species contribute more than 80% of the plant diversity (Towne 2002). Prescribed burns in the watershed used in this study were initiated in 1972 (Knapp & Seastedt 1998; Collins & Calabrese 2012). Vegetation structure and species diversity has diverged over time, resulting in watersheds that vary from largely open grassland habitat with little woody cover to those with extensive invasion from woody vegetation in watersheds subjected to low fire frequency treatments (Briggs et al. 2002; Ratajczak et al. 2012) and along the riparian areas (Knight et al. 1994; Collins & Calabrese 2012). Woody plant encroachment is characterized by increased woody and forb cover at the expense of grass cover (Wilcox & Huang 2010), providing an ideal structurally complex and spatially heterogeneous habitat for web-building spiders.

Our study was conducted on three nongrazed watersheds (K1A, 113.9 ha; K4A, 53.16 ha; K20A, 83.13 ha) with fire frequency histories of 1, 4 and 20 years' fire return intervals, respectively. All three watersheds were burned in spring 2013 just weeks prior to commencing this experiment, resulting in similar understory vegetation layers in all three watersheds. However, woody plant and forbs vegetation cover still differed among watersheds (ANOVA, $F_{2,18} = 25.3$, $p < 0.0001$; Fig.1A). Vegetation height differed among watersheds (ANOVA, $F_{2,18} = 16.2$, $p < 0.0001$) and among the early (June) and late (August) part of the growing season (ANOVA, $F_{2,18} = 28.1$, $p < 0.0001$; Fig.1B), reflecting the legacies of burn history. Vegetation in these watersheds ranged from an open grass canopy in K1A with little woody vegetation to abundant woody shrub islands (a mixture of *Prunus* species, *Cornus drummondii*, and other shrub species) in watershed K20A; watershed K4A was intermediate in woody structure and consists primarily of open grass canopy with incursions of shrub islands.

Study design

To test the hypothesis that available structure for web placement limited the abundance and richness of web types in open grassland, woody structure was added along sections of the transects. In each of the three watersheds (K1A, K4A and K20A), we established four transects (100 m long by 3 m wide) beginning at the transition edge between a riparian woody stand near King's Creek and open grassland. We placed one end of all transects at the edge of woody riparian vegetation because we expected this transition zone to serve as a source of web-building spiders for recruitment into open grasslands if a response occurred. Our sampling scheme also allowed us to determine whether distance from the edge of a woody stand affected aerial-web-builder recruitment into open grass- lands when woody structure is added at different distances from this transition zone.

We manipulated habitat structure by adding dead woody stems of *Cornus* (dogwood) (experimental treatment) to randomly selected, 25 m sections for each 100 m long transect during July 1–4. The rest of each transect (75 m) served as a control. Two aluminum wires were stretched along five, evenly distributed fence posts (top and bottom) along the 25 m spans to serve as support structure for the dead *Cornus* stems. Stems that ranged in height between 1.5–2 m were collected nearby. To obtain a canopy diameter of approximately 60 cm, groups of two to three stems were tied to the wires approximately every 2.5 meters. Upon installation, the *Cornus* stems were immediately and carefully examined for the presence of spiders; none were detected during the installation phase. Transects were left unchecked for eight days to allow naturally dispersing spiders to colonize the structures before the first of three post manipulation censuses was conducted in the second week of July.

Sampling the spider community

Web builders are a diverse group of predators representing 60% of the North American spider fauna (Young & Edwards 1990). Web-builders are uncommon in North American open grasslands relative to other spider groups, seemingly because of a paucity of structure on which to anchor webs (Baldissera et al. 2004; Podgaiski et al. 2013). Aerial web-building spiders were visually censused up to 1.5 m away on each side of the 100 m long transects; each transect was spaced 50 meters from the neighboring transects and censused five times during a three-month period – two times in June before the habitat structure manipulation, and three times after the addition of woody structure (second and fourth week of July and third week of August). Visual censuses are effective for counting spiders with conspicuous webs, and spiders remain undisturbed in the study area and can be found repeatedly throughout the study period (Lubin 1978). Reference samples for each species were taken during our last survey in August to identify families and species, and to define their respective web types. For each web, we recorded the orientation (vertical, diagonal, horizontal or no clear orientation), height above the ground, web type (orb, bowl, sheet, funnel, threads without a clear structure), two measurements of web diameter to estimate area for prey capture in the web, and the presence or absence of the spider.

In the field, we used web structure to identify webs to family if spiders were not present on the web (Halaj et al. 1998; Uetz et al. 1999; Eisman et al. 2010). Family identity was confirmed on site for webs with resident spiders. Irregular, hackled silk around the heads of flowers, branches and dead stalks were classified as Dictynidae and sheet webs as Linyphiidae. Even though Linyphiidae is a very diverse family of sheet web builders in the US, representatives of this family tend to be less common (usually, 25% of total spider individuals) (Nyffeler & Sunderland 2003). Because we sampled only aerial webs in this study while most linyphiids build their webs near the ground, we only found individuals of the genus *Frontinella* (F.O. Pickard-Cambridge, 1902) as representatives of this family. Thus, the linyphiids are likely underrepresented in our surveys. All funnel webs were considered Agelenidae, and irregular cobwebs were classified as members of Theridiidae. Vertical and diagonally oriented orb webs were classified as Araneidae if the web had a closed center hub whereas webs with an open center hub were designated as Tetragnathidae.

We measured 740 webs from six families and 12 genera over a three-month period. Following Uetz et al. (1999) and Eiseman et al. (2010), we divided the web-builder spider community into five web-type groups: Orb web builders, Funnel web builders, Doily-sheet web builders, Irregular-all-directions web builders and Irregular-mesh web builders. Because of the large variation in orb-web diameters, we further divided this web-type group into three size classes, small (< 50 cm^2), medium (> 50–740 cm^2,) and large (> 740 cm^2), using as a reference a subset of data from those orb-weaving spiders that were consistently identified to genus, species or morpho-species (Table 4.1).

Habitat structure

Vegetation along the transects was measured twice during this study, once in early July before manipulating habitat structure and once in late August during the last spider survey. Habitat structural complexity (canopy structure: vegetation median height, mean height and number of vegetation layers) was measured using a modified point sampling technique (Joern 1979). A modified Robel pole was constructed using a 1.85 m copper tube (diameter 1.25 cm) demarcated with a scale of 5 cm increments. Canopy structure (habitat structural complexity) along transects was measured by taking measurements every 5 m along these transects (21 points per transect). At each point, the pole was placed within the vegetation perpendicular to the ground and the number of vegetation hits touching the pole in each 5 cm segment was recorded. "Vegetation median height" per transect was estimated as the average of the median for 21 sampling points along each transect. The "number of vegetation layers" at each site was based on vegetation touches in each 5 cm increment interval on the Robel pole. Values for the number of vegetation layers ranged from 1 to 37 layers per site, and at least two hits in a layer were required for a height interval to be considered a layer. "Vegetation cover composition" was estimated using a 0.1 m^2 quadrat, where cover was classified as open soil, litter, grass, forbs, or woody plant. Following the Daubenmire cover class method, the percentage of each vegetation cover class was scored as: 0 = 0%, 1= 1–5%, 2 = 6–25%, 3 = 26–50%, 4 = 51–75%, 5 = 75– 95%, 6 = 96–100% within each quadrat. Vegetation structure was scored three times in each 5-meter transect segment for a total of 60 estimates for each transect during each of the two vegetation sampling periods. Midpoints of cover classes were used in quantitative comparisons of samples and subsequent analyses (Daubenmire 1959). Because we were interested in how aerial-web-building spider abundance and the richness of web types responded to the availability of vegetation with complex architecture, we combined the values of forb and woody vegetation to obtain a better estimate of cover of plants with complex architecture.

Statistical analyses

Because watersheds differed in the percentage cover of plants with complex architecture and complexity of habitat structure, linear regression analyses were performed separately for July and August to assess whether web density increased as habitat complexity increased from open grassland to habitats with extensive invasion from woody vegetation in the non-manipulated sections of the transects. For these analyses, we used vegetation surveys from July and August, the first of the two July spider surveys, and the August spider survey. We only used the web density values from the non-manipulated sections of these transects to avoid web density bias effects driven by the addition of woody vegetation in the manipulated sections of these transects. Predictor variables to assess web density responses were: percentage of plants with complex architecture, Robel median, vegetation height, and number of vegetation layers.

We performed a 3-way analysis of variance (ANOVA) with repeated measures to determine the effects of adding habitat structure to aerial-web-builder density and richness of web types with respect to distance from riparian woodland edge. The response variables measured were: web density and richness of web types. We also explored the individual responses of the small-orb weaver and medium-orb weaver groups to our habitat manipulation as these were the numerically dominant groups in our samples and commonly found in the experimental structures. The predictor variables were: stem manipulation (addition of woody vegetation vs.

control), distance of 25 m experimental sections of these transects from the woodland edge (four levels: 0, 25, 50, 75 m) and survey (1–5) corrected for repeated measures per transects. Transects were treated as independent experimental units and the location of manipulated sections (0–25, 25–50, 50–75, 75–100 m) along transects were assigned randomly. Spider density and richness were calculated for each 25 m section of these transects for each survey period. Statistical analyses were performed using R 3.1.2 (R Core Team 2013) package vegan (Oksanen et al. 2011).

Results

Spider responses to gradients in vegetation structure.

Web density was positively related to an increase in percentage cover of plants with complex architecture, forbs and woody vegetation, both in July and August (linear regression, $F_{1,10} = 7.82$, $R^2 = 0.38$, $p = 0.02$; $F_{1,10} = 5.53$, $R^2 = 0.29$, $p = 0.04$, respectively; Fig. 4.2a, b). The density of aerial web builders increased with increased vegetation height (linear regression, $F_{1,10} = 15.51$, $R^2 = 0.57$, $p = 0.003$; Fig. 4.2c), and with an increase in the number of vegetation layers (linear regression, $F_{1,10} = 9.76$, $R^2 = 0.44$, $p = 0.01$; Fig. 4.2d) in early July. But these relationships were not significant in the late August survey (linear regression, $F_{1,10} = 0.5$, $R^2 = 0.05$, $p = 0.49$; $F_{1,10} = 2.72$, $R^2 = 0.14$, $p = 0.13$, respectively). These predictor variables suggest that web-builder density increased along a gradient of habitat structural complexity and web-anchoring availability driven by forbs and woody vegetation. No significant response was seen between web density and vegetation median height in either July or August surveys (linear regression, $F_{1,10} = 1.71$, $R^2 = 0.06$, $p = 0.22$; $F_{1,10} = 0.67$, $R^2 = 0.06$, $p = 0.43$, respectively). Results are consistent with the hypothesis that a greater abundance of aerial web-building spiders is found in areas with greater availability of web-anchoring structure associated with increased structural complexity.

The richness of web types varied among the watersheds with K20A showing the greatest response in abundance and richness of web-anchoring structures. For example, Funnel-web-builder groups were more abundant than expected because of the abundance of web-anchoring structure close to the ground (dead woody stems), which was lacking in the other two watersheds. Due to the woody vegetation type selected for the manipulation, we did not influence the abundance and/or distribution of this group. Our results also showed that the Irregular-mesh-web builders (Dictynidae) were only present during the early part of this study, disappearing in late June, just prior to habitat manipulation. Thus, our habitat manipulation potentially influenced density and distribution of five out of seven web types groups of web-building spider found at KPBS.

Web-building spider responses to increases in availability of web anchors in open grasslands.

In general, we found that web density was higher on the manipulated sections of the transects. We found that distance from riparian-woodland edge affected aerial-web-builder density, where web density decreased with increased distance from riparian woodland edge (ANOVA, $F_{1,219} = 5.3$, $p = 0.02$). Even though the manipulated section of these transects generally had higher web density, we found a strong interaction for manipulation-by-distance from the woodland edge (ANOVA, $F_{1,219} = 4.0$, $p = 0.048$; Fig. 4.3c). Web density in the manipulated sections decreased as the distance from the riparian-woodland edge increased, even though they still showed higher web densities than those seen in the non-manipulated sections of the transects. Results indicate that woody vegetation is a limiting resource for aerial web-building spiders in open grasslands systems. Of the five groups of web builders, only the density of the small-orb and medium-orb weaver groups (Fig. 4.3a, b) responded positively to the addition of woody web-anchoring structure (*Cornus* stems) in open grasslands (ANOVA, $F_{1,221} = 8.0$, $p = 0.005$; $F_{1,221} = 6.0$, $p = 0.015$, respectively) regardless of distance from woodland edge or sampling period after manipulation.

To determine whether aerial web-building spider density responded quickly to structure availability, we compared densities from our second pre-manipulation (late June) survey to our first survey after manipulation (early July), which was conducted eight days later. Habitat manipulation led to a quick positive effect on Small-orb weaver density (ANOVA, $F_{1,77} = 5.2$, $p = 0.026$); higher densities of this spider were observed in manipulated sections of transects when compared to non- manipulated sections, regardless of distance from wood stand edge. Results showed differences in web-type richness among manipulated and non-manipulated sections of these transects (ANOVA, $F_{1,221} = 5.5$, $p = 0.02$). Web-type richness increased in the manipulated sections of these transects as the growing season progressed (ANOVA, $F_{1,221} = 5.4$, $p = 0.02$; Fig. 4.4) compared to the non-manipulated sections.

Discussion

The habitat heterogeneity hypothesis posits that the abundance and diversity of arthropod species will respond positively to increases in the spatial heterogeneity of plant species richness and vegetation architecture (Dennis et al. 1998; Fuhlendorf & Engle 2001; Fuhlendorf et al. 2006; Jimenez-Valverde & Lobo 2007; Allouche et al. 2012). It is well recognized that fire-grazing interactions in grasslands modulate habitat heterogeneity with great effects on the abundance, diversity and trophic complexity of consumer assemblages through bottom-up regulation mediated by plants (Joern 2005; Joern & Laws 2013). Thus, habitat structural complexity and local plant architecture diversity in particular are important factors influencing terrestrial arthropod diversity (Dennis et al. 1998; Halaj et al. 2000; Joern 2005; Cobbold & MacMahon 2012; Joern & Laws 2013), abundance, and community dynamics at multiple levels (Langelloto & Denno 2004). For example, intensive grazing by sheep in a Hungarian grassland led to the loss of spider species sensitive to habitat disturbance and increased the representation of common and disturbance-tolerant species (Szinetár & Samu 2012).

In this study, we experimentally tested the proposition that availability of physical structure for web placement can limit aerial web-building spider communities in open grassland. We did so by increasing woody structure in the herbaceous-shrub layer at various distances from riparian woodland edge in three watersheds. Distributions of web-building spiders are directly linked to the spatial configuration of woody vegetation in their habitat due to web-anchoring requirements; both experimental and observational studies indicate the tight relationship between spider abundance and habitat structure (Halaj et al. 1998; Rypstra et al. 1999; Diehl et al. 2013). Vegetation examined among the three watersheds in this study ranged from an open grass canopy with little woody vegetation to watersheds with significant levels of woody vegetation encroachment and thus a significant gradient of habitat complexity. Indeed, our results for both July and August show that web-builder density increased as the percentage cover of forbs and woody vegetation increased from open grassland to grassland encroached by woody vegetation. In July, web-builder density increased with increasing number of vegetation layers as vegetation height increased, thus increasing the possibility of habitat partitioning by web-building spiders.

The highest web densities along this habitat structure gradient were observed on watershed K20A, a watershed with a history of low burn frequency and a high accumulation of woody vegetation.

Several lines of evidence from our experiment suggest that the availability of web-anchoring structure limits web-building spiders in open tallgrass prairie. We found critical responses by aerial-web-building spiders to regions where web-anchoring structures were added. (a) There was a greater density of aerial-web-building spiders and richness of web types in manipulated areas at the transect scale (300 m^2 transect) towards the end of the growing season. (b) Web density on the manipulated section decreased with increasing distance from the riparian woodland edge, even though it was higher overall than in non-manipulated sections. (c) After *Cornus* stems were added, web-type richness increased over time until, by the end of the study, it was higher than in the control sections. Similar results were found by Toti et al. (2000), where species richness of aerial web builders increased from spring to fall in grass habitat at the Great Smoky Mountains National Park. However, some transects in that study had control sections that consistently maintained high web types richness over the entire duration of the study, and the response was driven mostly by naturally high abundances and richness of web anchoring structures. (d) Finally, the addition of web-anchoring structure led to an increased density of small-orb and medium-orb web-builder groups in a watershed under frequent burn treatments, watersheds characterized by the paucity of woody vegetation cover. Even though small-orb and medium-orb densities were higher at the manipulated section than on the control sections at all distances from the riparian woodland edge as predicted, we also observed a decrease in the density of these two groups of web builders overall. Such results suggest that other factors such as species dispersal ability could affect their distribution on the habitat.

Web-building spider species differ in how webs are positioned within the vegetation, outcomes driven by differences in web type and web structure (e.g., spacing of mesh, web size, height of web placement, and the sizes of prey captured). Such variability in web placement constraints facilitates the assembly of web-builder diversity in habitats that are architecturally and floristically diverse (Richardson & Hanks 2009). Differences in the richness of web types seen among watersheds were associated with differences in habitat structural complexity and underlying variation in cover with complex architecture. Generally, we observed that web-type richness was higher in the manipulated sections of these transects even with exceptions from a few control sections from regions associated with dense, woody stands (e.g., *Cornus* shrub islands and/or diverse mixture of woody plant and forbs). Such sample sites with high overall structure could maintain high levels of web-type richness through the entire duration of the study. Such hotspots of web-type richness were found on all four transects of K20A watershed and one transect of K4A. We note that these hotspots not only supported diverse web-type richness but they also showed a higher diversity of web-building spiders species per web-type group than in samples from non-hotspot points along the same transect. Unfortunately, we could not directly analyze species richness in this study due to difficulty in identifying all species in the field and the lack of watershed replication in this study.

Habitat structure and vegetation architecture affect the spatial distribution of spiders with different web types (Colebourn 1974). For example, while our habitat manipulation using *Cornus* stems positively affected small-orb and medium-orb density at various distances from the riparian woodland edge, it did not influence the funnel-weavers, a common group of web builders at KPBS. The experimental design did not provide the appropriate web-anchoring structure close to the ground for assessing responses by funnel-weavers (Agelenidae) that were only found in open grasslands in zones with accumulation of woody stems near the ground in K20 and one transect in the K1A watershed. Even though, they were the most abundant web-building spiders found along the King's Creek basin in KPBS during the summer of 2012, Agelenidae densities dropped dramatically at the transition zone from riparian woodlands into open grassland (J. E. Gómez, unpublished data). Also, we could not address responses of the Mesh-weaver group (Dictynidae) to increases of web-anchoring structure in open grasslands as this group was only active early in the growing season and their abundance dropped by the end of June before our manipulation was conducted.

Even though vegetation structure is widely recognized as a key determinant resource of spider community composition, the exact mechanism for its influence is unknown and other indirect effects such as microclimate and prey availability may play important roles (Jimenez-Valverde & Lobo 2007). Initial colonization by spiders may be relatively quick because even large web spinners are capable of aerial dispersal at immature stages (Gibson et al. 1992). Our experiment demonstrates that spider density responded quickly to an increase in the availability of woody structure as new *Cornus* stems were colonized by multiple types of web-building spiders within a period of only eight days, and spider density was consistently higher on the manipulated sections when compared to the non-manipulated sections of these transects from mid- to late summer. We found that overall density responses of aerial-web builders to increased availability of web-anchoring structures were largely driven by the small-orb weavers and to a lesser extent by the medium- orb weavers. It makes sense that orb-weavers were the first colonizers (Blamires et al. 2007) as orb weavers occupy a wide range of habitats and accordingly there is a great diversity in both web architecture and behaviors among genera. For example, *Nephila* (Leach, 1815) and *Tetragnatha* (Latreille, 1804) build large webs in open habitats while *Argiope* Audouin, 1826 builds smaller webs among low, dense (closed) vegetation (Blamires et al. 2007). Variation in web-architecture and web-size increases the possibility that at least one species within an orb weaver web-type group could benefit from the architecture of *Cornus* stems. We conclude that the abundance and architecture of web anchoring structures limit aerial-web- builder density, distribution and richness of web type in the open grassland studied here.

Results from this study offer further support for the notion that structurally complex habitats provide a wider selection of web-attachment sites and thus increased habitat suitability for web-builder spiders in open grasslands in North America. Responses are facilitated by increased opportunities for spatial partitioning as the architectural complexity of the habitat increases (Robinson 1981), and responses likely operate at multiple scales.

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FIGURES & TABLES

Table 4-1. Web-building spider functional groups at KPBS and diversity associated with each functional group. Sample specimens were collected on August 2013 and identified to genus with the exception of the Dictynidae, which were no longer active in the field at this time of the year.

Web-morphology	**Family**	**Genus**	**Web size** (cm^2)	
			Minimum	**Maximum**
Small-Orb	Araneidae	*Micrathena*	4	< 50
Medium-Orb	Tetragnathidae, Araneidae	*Tetragnatha, Argiope, Cyclosa, Acanthepeira, Mangora, Larinioides*	> 50	740
Large-Orb	Araneidae	*Neoscona*	> 740	3239
Funnel-Web	Agelenidae	*Agelenopsis*	9.43	2842
Doily-Sheet-Web	Linyphiidae	*Frontinella*	5	506
Irregular-All-Direction-Web	Theridiidae	*Theridion, Euryopis*	55	566
Irregular-Mesh-Web	Dictynidae		4	12

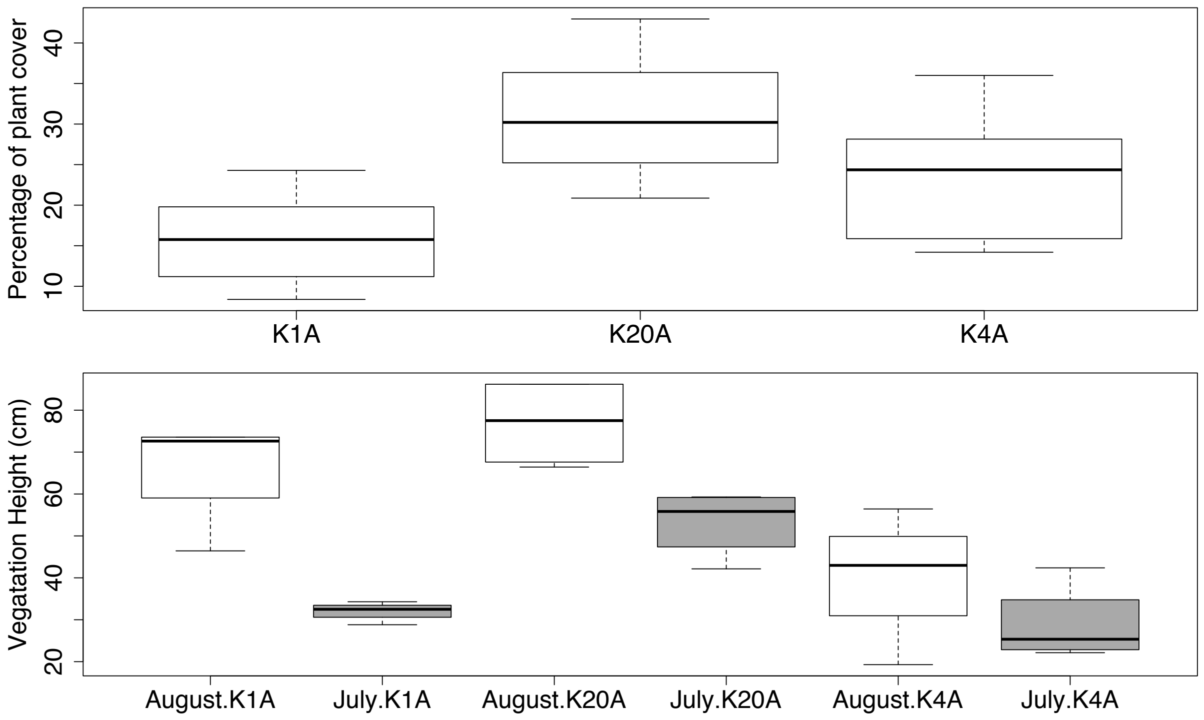

Figure 4-1. (A) Comparison of the percent cover of plants with complex architecture (forbs and woody vegetation) among watersheds at Kings Creek basin. (B) Comparison of the vegetation height of the grass layers between early July (shaded) and mid-August (open). The box plot elements represent the following: box vertical dimension 5 interquartile range; horizontal line 5 median; whiskers 5 the minimum and maximum values.

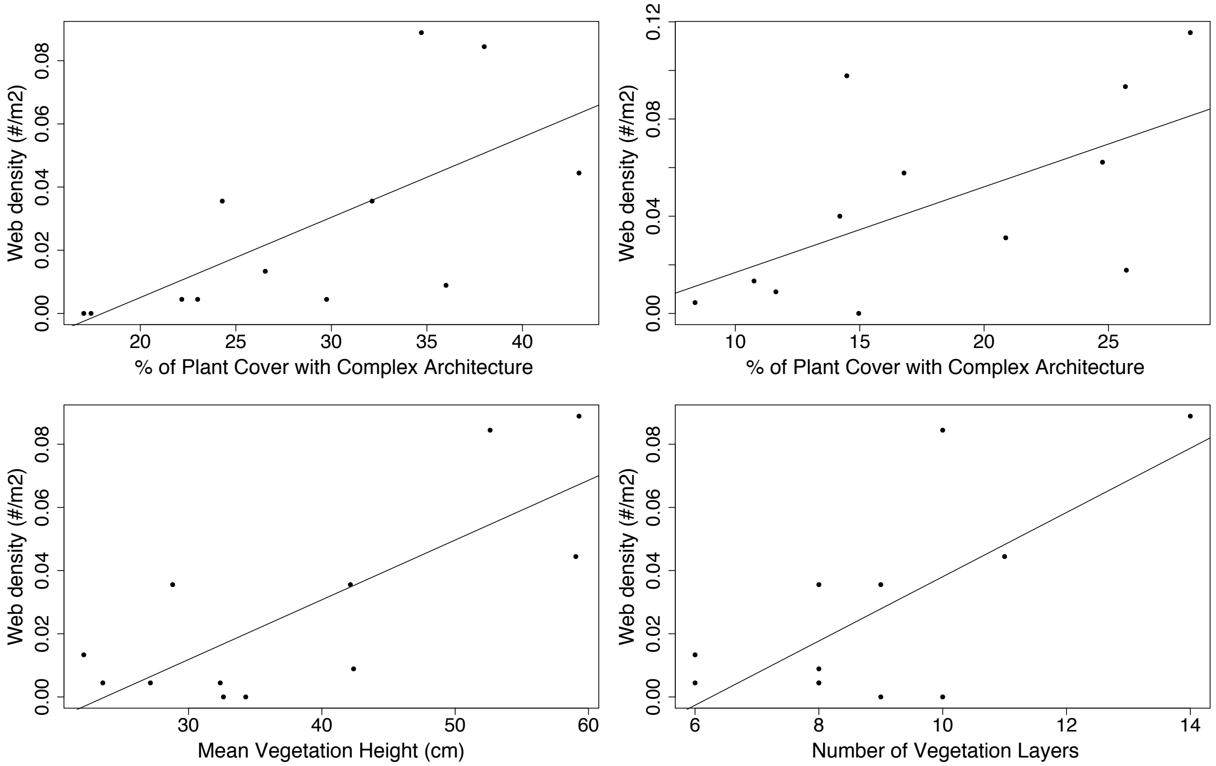

Figure 4-2. Relationships between web density and percent plant cover in July (A) and in August (B). Relationships between web density and mean vegetation height (C) or number of vegetation layers (D) in July.

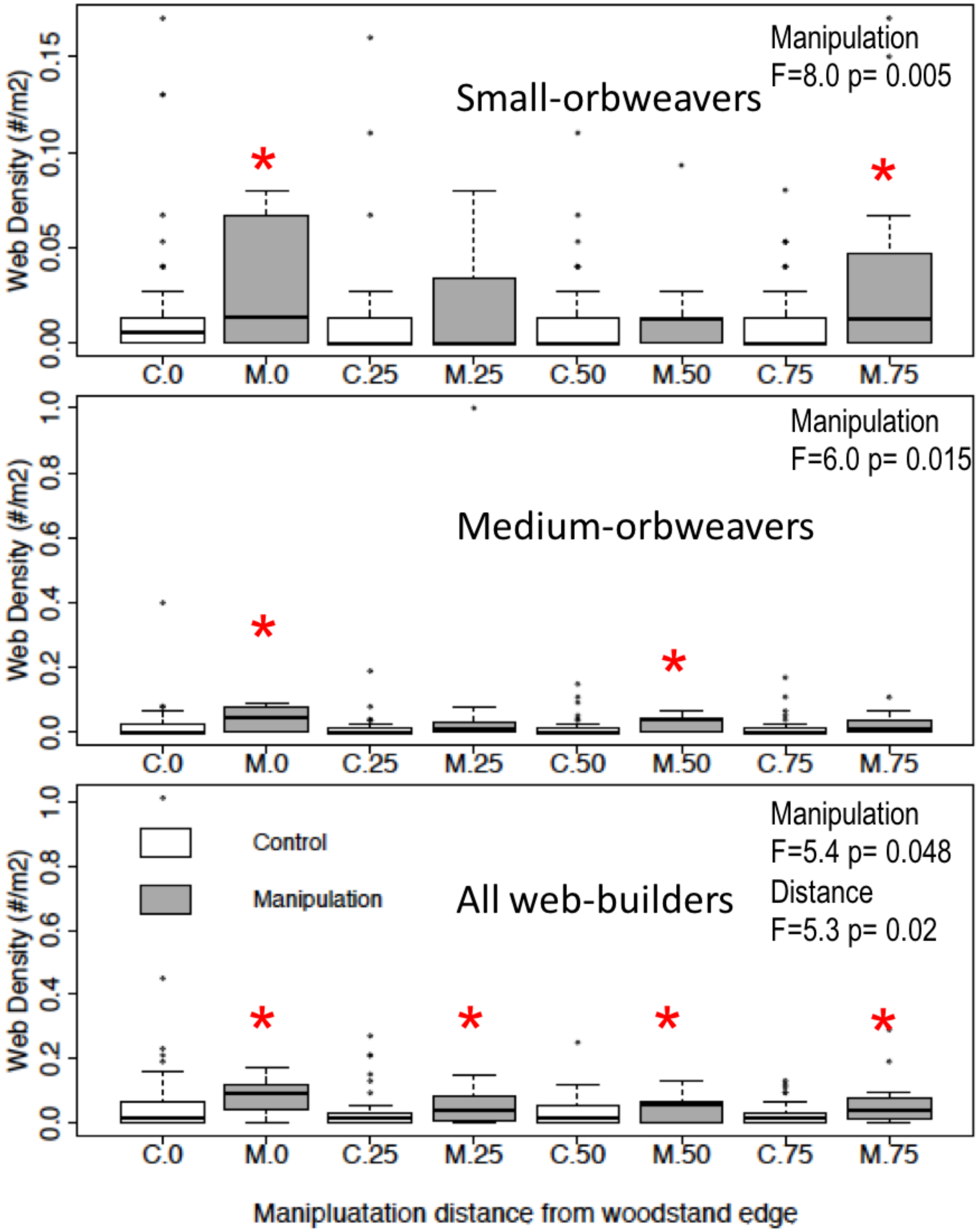

Figure 4-3. Comparison of open grassland web-builder spider density among various distances from a riparian woodland edge at Konza Prairie Biological Station, Kansas. (A) Small-orb weavers, (B) medium-orb weavers, (C) total web density (all web types groups

combined). The box plot elements represent the following: box vertical dimension 5 interquartile range; horizontal line 5 median; whiskers 5 minimum and maximum values; circular points 5 maximum observations 1.5 (IQR) above the 75th percentile.

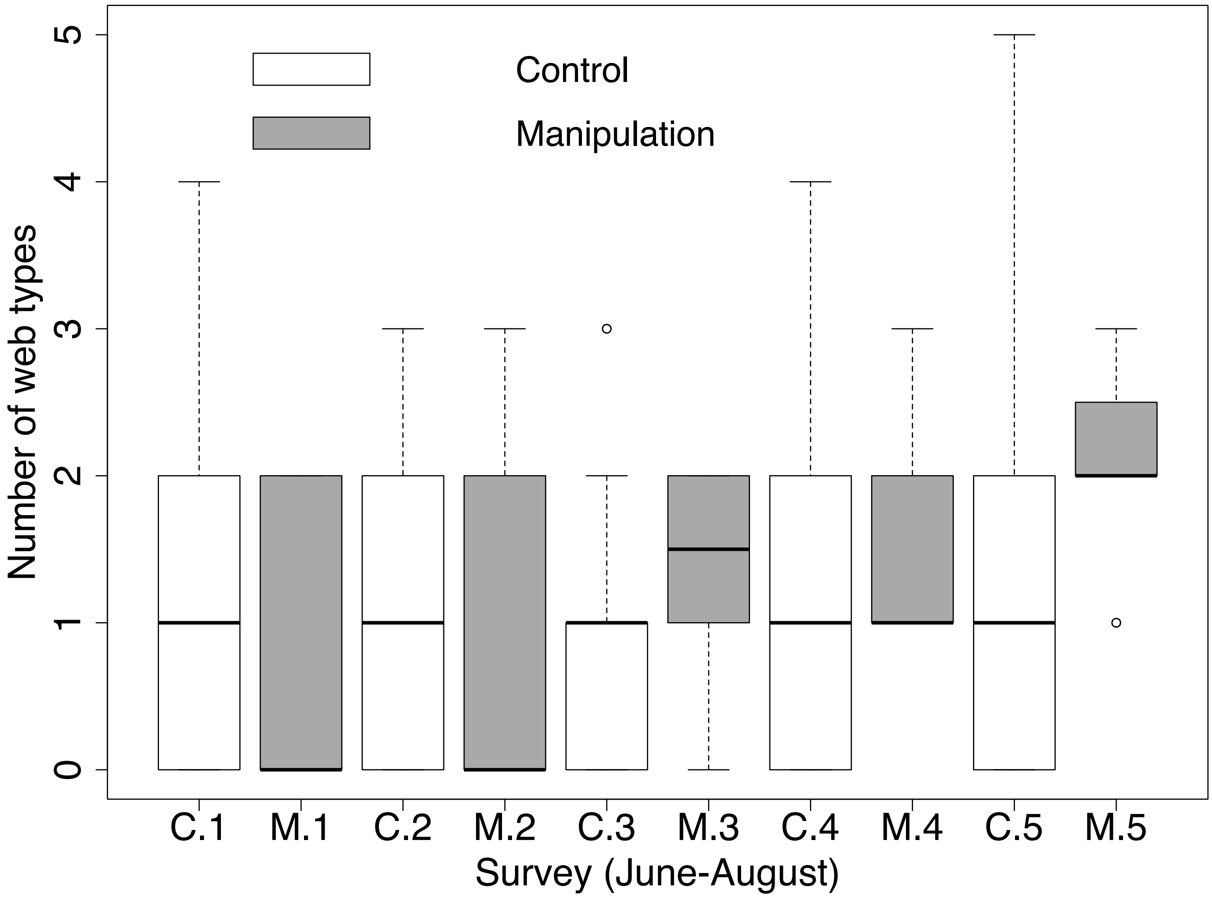

Figure 4-4. Comparison of richness of web types among various distances from riparian woodland edge. The box plot elements represent the following: box vertical dimension 5 interquartile range; horizontal line 5 median; whiskers 5 minimum and maximum values; circular points 5 maximum observations 1.5(IQR) above the 75th percentile.

Chapter 5 - Lessons from a spider community

Results from this study contribute new evidence to the view that spatial and temporal habitat heterogeneity increases diversity for many terrestrial communities (Dennis et al. 1998, Tews et al. 2004, Fuhlendorf et al. 2009, 2010, Allouche et al. 2012, Moran 2014). The study adds a critical element by focusing on spider communities, important arthropod predators that dominate in most natural and agricultural systems. Particularly in grasslands, fire-ungulate grazing interactions (pyric herbivory) lead to the formation of a spatially and temporally heterogeneous mosaic of vegetation communities and associated habitat richness. Habitat variability in turn supports increased β– and γ–diversity of consumers through its effects on vegetation structure and heterogeneity (Enders 1974, Robinson 1981, Halaj et al. 1998, 2000; Heikkinen et al. 2004, Diehl et al. 2013). Ubiquitous, taxonomically and functionally diverse terrestrial predators like spiders rely on the vegetation structure as critical habitat, and spatial heterogeneity of habitat adds important new opportunities for more species to coexist, including expanding the diversity of trophic positions in arthropod food webs (primary-, secondary- to top-predators) while simultaneously influencing the susceptibility of spiders as prey to other spiders. Architectural complexity of vegetation and habitat spatial heterogeneity is key for understanding coexistence of spider species as they contribute to habitat partitioning at fine spatial scales. Complexity expands the range of suitable hunting grounds, mediates species interactions to decrease competition with other spiders, and serves as a broad refuge allowing spiders to avoid their predators including other spiders. To address knowledge gaps for these issues, I combined observational and experimental approaches to evaluate how fire and grazing interactions coupled to variable weather and topography, critical drivers of grassland origin and maintenance, influence community structure of spiders (a) along gradients of vegetation structure and heterogeneity (Chapter 2), and (b) for understanding the taxonomic assembly of spider communities with respect to a shifting mosaic of habitat arising from vegetation structure that varies in time and space (Chapter 3). I also (c) experimentally increased web-building species abundance and diversity by adding woody stems to open grassland (Chapter 4) mediated through vegetation structure and heterogeneity.

First, I evaluated how fire and grazing interactions structured gradients of vegetation and its spatial heterogeneity across the KPBS landscape (Chapter 2). My results showed that habitat structure and heterogeneity gradients varied in time and space across KPBS, reflecting elapsed time since the last disturbance from pyric herbivory. As such, the habitat template that underlies spider community assembly is constantly changing across the landscape. As predicted by the habitat complexity and heterogeneity hypothesis, increases in key habitat resources (vegetation structural complexity and spatial heterogeneity) lead to increased density, species diversity, species evenness, and richness of hunting strategies of a grassland spider community. Similarly, increased spider species diversity showed a strong association with increased insect biomass through the growing season, which in turn also responded to habitat structure and its heterogeneity. The richness of hunting strategies and species evenness was positively associated with increased insect biomass. The results from this chapter show that elements in spider community complexity (species diversity, species evenness, and richness of hunting) are mediated through synergistic effects of fire and grazing disturbances leading to heterogeneous habitat attributes.

Next, I studied how the taxonomic assembly of local spider communities changed as habitats varied across the landscape in response to the effects of fire/ bison-grazing interactions on vegetation structure (Chapter 3). I examined the hypothesis that consumer meta-communities potentially track dynamic systems of interconnected habitat patches, where the abundance and distribution of species changes over time across the landscape (Sousa 1984; Levin and Paine 1974, Carmona et al. 2012). I documented the malleable nature of spider assemblages at a local scale by this grassland spider community, where the observed total number of spider assemblages within KPBS landscape varied each year as they tracked changes inherent in local vegetation communities. Spider assemblages varied in such a way that habitats resulting from similar management treatments supported spider assemblages that clustered together in ordination space. At least three distinct regional spider assemblages were typically evident, reflecting major trends in vegetation structure and heterogeneity in response to long term fire-grazing interactions at KPBS, including: grazed/ open-grassland, non-grazed/ open-grassland, and woody-grassland transition habitat. Moreover, additional clusters were observed as the diversity of vegetation states increased. Results of this study showed that the transition zone between grassland and woody vegetation (riparian woodlands and shrub islands) is a hot spot of spider diversity at the taxonomic and functional level for both wandering and web-building spiders. Moreover, this study revealed that habitat type not only differed in the total richness of species and hunting strategies/ functional groups, but the actual species richness within each functional group also differed among habitat types. The proportional density of each functional group also varies among habitat types, again reflecting the availability of important vegetation structure and heterogeneity. Last, this study documented how a shifting mosaic of vegetation communities, driven by pyric herbivory, led to increased β–diversity for spiders by sustaining a shifting mosaic of spider assemblages over the growing season and across multiple years

Even though web builders are a diverse group of predators representing 60% of the North American spider fauna (Young & Edwards 1990), web-building spider guilds are uncommon in

North American open grasslands such as KPBS, seemingly because of a lack of structures on which to anchor webs (Baldissera et al. 2004; Podgaiski et al. 2013). To test this hypothesis, I evaluated how the availability of vegetation structure for web anchoring limits the distribution of web-building spider into open grasslands that are typically depauperate in web building species or total number of aerial webs (Chapter 4). Here, I manipulated the abundance of dead woody-vegetation structure at different distances from the edge of riparian woody stands. Woody stems used in the experiment are appropriate for anchoring webs. In general, higher spider abundances of orb-building spiders were observed in grassland areas where I added woody structure compared to the non-manipulated sections. However, reduced richness of web types was found on the manipulated sections of the grasslands compared to what was possible based on data from chapters 2 and 3. Thus, the architecture provided by experimental woody stems does not provide sufficient and appropriate web-anchoring structure or the needed microhabitat for the full range of web-building spiders groups in found across KPBS tallgrass prairie.

Overall, the results of this dissertation show that spatial and temporal heterogeneity of key environmental factors leads to a shifting mosaic of key resources that then serves as the habitat template for spiders and likely consumers more generally. A shifting mosaic of vegetation structure and heterogeneity is critical for understanding β–diversity at the taxonomic and functional level. The lessons from my dissertation research, especially the need to promote habitat heterogeneity can be extended and generalized to improve habitat availability for other species as they cope with human impacted environments (Tews et al. 2004, Pacheco & Vasconcelos 2012). For example, results of my dissertation offer further support for grassland management programs that have as a core goal the promotion of habitat heterogeneity that varies in time and space to improve habitat diversity and biological diversity, while retaining the desired human profit derived from the exploitation of these systems. As an example, patch-burn grazing management plans are scientifically sound, and act as a shifting mosaic of habitat type driven by fire frequency and large herbivore grazing interactions. Fire-grazing interactions in my study resulted in a landscape that supported ~4.4 times more spider species than found the single most diverse site sampled. This finding is quite remarkable. Results from my dissertation research will be helpful in guiding management decisions for grassland habitat restoration, and for cultivated crop systems, especially small-scale grain operations where spiders are critically important arthropod predators (Wise 1995, Weibull et al. 2000, Wise 2006, Benton et al. 2012). At a broader scale, the findings of my study add support from scientific conclusions that promoting habitat heterogeneity may be a key management goal to preserve our terrestrial communities, particularly if we can enhance habitat availability on human dominated landscapes surrounding the "islands of native habitat preserves" were other species are trying to survive. It is our duty as a dominant species to find a way to coexist with other species that provide no economic gain, and to provide sufficient habitat for the survival of diverse communities of native wildlife with whom we share the planet we call home.

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Appendix A - Supplementary Material

Table 5-1. GPS coordinates, watershed management treatments and habitat classification for the 23 sites sampled in this study and used in chapters 2 & 3. Habitat classification was based on burn frequency, grazing treatments and dominant vegetation cover.

Site Original Numeric Label	Site Letter Label in Data	Watershed	Latitude + Longitude	Fire Freq.	Year of Burning	Bison grazed	Topography	Habitat
1	A	N1A	N39^{0}05.307’ + W096^{0}35.577’	1	2011, 2012, 2013	1	upland	Freq. Burn Grazed Grassland
2	B	N4C	N39^{0}05.284’ + W096^{0}35.735’	4		1	lowland	Inter. Burn Grazed Grassland
3	C	N2A	N39^{0}05.756’ + W096^{0}36.289’	2	2012	1	upland	Freq. Burn Grazed Grassland
4	D	N4A	N39^{0}05.014’ + W096^{0}36.399’	4	2012	1	slope	Inter. Burn Grazed Grassland
5	E	N4A	N39^{0}04.817’ + W096^{0}36.614’	4	2012	1	lowland	Inter. Burn Grazed Grassland
6	F	N1B	N39^{0}04.767’ + W096^{0}33.917’	1	2011, 2012, 2013	1	slope	Freq. Burn Grazed Grassland
7	G	N4B	N39^{0}05.606’ + W096^{0}34.530’	4	2011	1	upland	Inter. Burn Grazed Grassland
8	H	N4B	N39^{0}05.728’ + W096^{0}34.903’	4	2011	1	upland	Inter. Burn Grazed Grassland
9	I	N1B	N39^{0}05.100’ +	1	2011, 2012,	1	upland	Freq. Burn

			W096^{0}34.346’		2013			Grazed Grassland
10	J	N1A	N39^{0}05.801’ + W096^{0}35.653’	1	2011, 2012, 2013	1	lowland	Inter. Burn Grazed Grassland
11	K	4B	N39^{0}0 + W096^{0}3	4	2013	0	lowland	Inter. Burn Ungrazed Grassland
12	L	2A	N39^{0}0 + W096^{0}3	2	2012	0	lowland	Freq. Burn Ungrazed Grassland
13	M	2C	N39^{0}04.166’ + W096^{0}35.050’	2	2011, 2013	0	upland	Freq. Burn Ungrazed Grassland
14	N	SpB	N39^{0}04.084’ + W096^{0}35.177’	1	2011, 2012, 2013	0	upland	Freq. Burn Ungrazed Grassland
15	O	SuA	N39^{0}04.072’ + W096^{0}34.389’	1	2011, 2012, 2013	0	slope	Freq. Burn Ungrazed Grassland
16	P	1D	N39^{0}0 + W096^{0}3	1	2011, 2012, 2013	0	lowland	Freq. Burn Ungrazed Grassland
17	Q	N1A	N39^{0}05.740’ + W096^{0}35.355’	1	2011, 2012, 2013	1	lowland	Freq. Burn Grazed Woody-Grassland
18	R	N20 B	N39^{0}05.087’ + W096^{0}33.906’	20		1	slope	Infreq. Burn Grazed Woody-Grassland
19	S	20C	N39^{0}0 + W096^{0}3	20	2012	0	lowland	Infreq. Burn Ungrazed Woody-

								Grassland
20	T	20C	N39^{0}0 + W096^{0}3	20	2012	0	lowland	Infreq. Burn Ungrazed Woody-Grassland
22	U	N4A	N39^{0}04.866’ + W096^{0}36.568’	4	2012	1	lowland	Inter. Burn Grazed Woody-Grassland
23	V	R1A	N39^{0}0 + W096^{0}3	1	2011, 2012, 2013	0	slope	Freq. Burn Ungrazed Woody-Grassland
25	W	N20B	N39^{0}05.298’ + W096^{0}34.648’	20		1	lowland	Infreq. Burn Grazed Woody-Grassland

Table 5-2. Konza Prairie Biological Station spider community species list collected between summers 2011-2014. Spider species were described to the lowest taxonomic level possible (Family to species); specimens classified as unknown were either not well developed specimens tore were damaged during collection so they could not be properly identified. Each spider species received a unique numeric code (X##). Spider species were assigned to a hunting strategy based on general strategies used to capture prey known at the family level, or at the genus level if it diverged from the general strategy of the respective family. Furthermore. hunting strategy assignment was refined using literature references and field notes based on where in the vegetation a spider species was observed hunting. The Rank and Detection columns reflect the spider species collected across 23 sites using vacuum sampling from 2011-2013 at KPBS. Rank reflects how common a species was within the data sets used for Chapter 2 and Chapter 3 based or detection, not their density. The detection column shows how many times a spider species was present in a sample out of 131 samples collected across the 23 sites between 2011-2013. Since each species was counted as 0 or 1 for each sample, the maximum number of possible detections for a species was 131.

Mygalomorphae					
Family					
Genus	**Species**	**Hunting strategy**	**Code**	**Rank**	**Detection**
Atypidae					
Sphodros	*fitchi*	Purse Web	X31		
Araneomorphae					
Family					
Genus	**Species**	**Hunting strategy**	**Code**	**Rank**	**Detection**
Agelenidae					
Agelenopsis	*spp.*	Funnel Web	X1	48	11/131
Amphnectidae					
Metaltela		Funnel Web	X2	119	1/131
Anyphaenidae					
Hibana	*gracilis*	*Stem Runner*	X3*	5*	80/131*
Hibana	*velox*	*Stem Runner*	X3*	5*	80/131*
Anyphaena	*celer*	*Stem Runner*	X4*	16*	42/131*

Anyphaena	*pectorosa*	*Stem Runner*	X4*	16*	42/131*
Anyphaena	*spp.*	*Stem Runner*	X5	115	2/131
Wulfila	*saltabundus*	*Stem Runner*	X6	20	37/131
Araneidae					
Acanthepeira	*stellata*	Medium Orb-Web	X7	17	42/131
Acacesia	*hamata*	Medium Orb-Web	X11	80	5/131
Araneus	*spp.*	Medium Orb-Web	X12		
Araneus	*diadematus*	Large Orb-Web	X13	81	5/131
Araneus	*pratensis*	Medium Orb-Web	X14	14	44/131
Araniella	*displicata*	Medium Orb-Web	X16	73	6/131
Argiope	*aurantia*	Medium Orb-Web	X9	95	3/131
Argiope	*lobata*	Medium Orb-Web	X134	129	1/131
Argiope	*trifasciata*	Medium Orb-Web	X10	3	88/131
Cyclosa	*conica*	Medium Orb-Web	X135	68*	7/131*
Cyclosa	*turbinata*	Medium Orb-Web	X135	68*	7/131*
Eustala		Medium Orb-Web	X17	116	2/131
Gea		Medium Orb-Web	X18	130	1/131
Hypsosinga	*funebris*	Medium Orb-	X15	42	14/131

		Web			
Hypsosinga	*rubens*	Medium Orb-Web	X22	41	14/131
Kaira	*alba?*	Medium Orb-Web	X19	45	13/131
Larinia	*directa*	Medium Orb-Web	X20	21	34/131
Larinioides	*patagiatus?*	Small Orb-Web	X21	39	16/131
Mangora	*gibberosa*	Small Orb-Web	X23	33	22/131
Mangora	*placida*	Small Orb-Web	X24	43	14/131
Metazygia		Medioum Orb Web	X7	17	42/131
Metepeira	*labyrinthea*	Medioum Orb Web	X25	96	3/131
Micrathena	*gracilis*	Small Orb-Web	X26	117	2/131
Micrathena	*mitrata*	Small Orb-Web	X27	131	1/131
Micrathena	*sagittata*	Small Orb-Web	X28		
Neoscona	*crucifera*	Large Orb-Web	X29	47	12/131
Neoscona	*pratensis*	Large Orb-Web	X30	132	1/131
Corinnidae					
	spp.	Active Ground Hunter	X146		
Cybaeidae					
	spp.	Funnel Web	X32	122	1/131
Clubionidae					
Clubiona	spp.	Active Ground Hunter	X147		
Dictynidae					
Dyctina	bostoniensis	Mesh Web	X38	15	43/131
	spp.	Mesh Web	X33	100	2/131

Gnaphosidae					
Sergiolus	capulatus	Active Ground Hunter	X34	79	5/131
Sergiolus	spp.	Active Ground Hunter	X141	125	1/131
Hahniidae					
Neoantistea	agilis	Doily Web	X136	72	6/131
Linyphiidae					
Erigoninae (subfamily)		Doily Web	X35	55	9/131
Linyphiinae (subfamily)		Doily Web	X36	52	10/131
Agyneta	*spp.*	Doily Web	X37	22	32/131
Frontinella	*communis*	Doily Web	X40	46	12/131
Neriene	*litigiosa*	Doily Web	X39	83	4/131
Lycosidae					
	juveniles spp.	Ground Sit & Wait	X41	49	11/131
Gladicosa	*spp.*	Ground Sit & Wait	X142	114	2/131
Hogna	*carolinensis*	Ground Sit & Wait	X42	113	2/131
Pardosa	*spp.*	Ground Sit & Wait	X49	59	8/131
Piratula/Pirata?	*spp.*	Ground Sit & Wait	X50	75	5/131
Rabidosa	*rabida*	Ground-Veg. hunter	X46	97	3/131
Rabidosa	*punctulata*	Ground-Veg. hunter	X47		

Schizocosa	*avida*	Ground Sit & Wait	X44*	51*	11/131*
Schizocosa	*mccooki*	Ground Sit & Wait	X44*	51*	11/131*
Schizocosa	*retrosa*	Ground Sit & Wait	X45	94	3/131
Schizocosa/Gladicosa	*spp.*	Ground Sit & Wait	X43	101	2/131
Trabeops	*spp.*	Ground Sit & Wait	X48		
Trochosa	*terricola*	Ground Sit & Wait	X51	89	3/131
Mimetidae					
Mimetus	*notius*	Spider-specialized hunter	X52	69	6/131
Mysmenidae					
Microdipoena	*guttata?*	All-Directions Web	X53	90	3/131
Nesticidae					
Nesticus	*spp.*	All-Directions Web	X137	98	2/131
Oxyopidae					
Oxyopes	*salticus*	Foliage Stalker	X54	1	123/131
Oxyopes	*scalaris*	Foliage Stalker	X55	63	7/131
Philodromidae					
Ebo		Stem Runner	X59		
Philodromus	*rufus*	Stem Runner	X58	82	4/131
Philodromus	*spp.*	Stem Runner	X129	37	16/131
Philodromus	*vulgaris*	Stem Runner	X61*	8*	67/131*

Tibellus	*duttoni*	Stem Runner	X56	32	22/131
Tibellus	*oblongus*	Stem Runner	X57	4	85/131
Titanebo	*spp.*	Stem Runner	X60	27	28/131
Thanatus	*vulgaris*	Stem Runner	X61*	8*	67/131*
Pisuaridae					
Pissuarina	*dubia*	Foliage Sit & Wait	X64	70	6/131
Pissuarina	*mira*	Foliage Sit & Wait	X62	74	5/131
Tinus	*peregrinus*	Foliage Sit & Wait	X63	102	2/131
Salticidae					
	immature light color	Foliage Stalker	X65	18	39/131
	immature dark color	Foliage Stalker	X66	13	52/131
Bredana	*spp.*	Foliage Stalker	X99	99	2/131
Colonus	*puerperus*	Foliage Stalker	X72	19	37/131
Colonus	*sylvanus*	Foliage Stalker	X71	62	7/131
Cyllodania	*spp.*	Foliage Stalker	X87	86	4/131
Eris	*flava*	Foliage Stalker	X70	31	23/131
Habronattus	*calcaratus*	Foliage Stalker	X102	112	2/131
Habronattus	*coecatus*	Foliage Stalker	X100	29	25/131
Habronattus	*mexicanus*	Foliage Stalker	X101	111	2/131
Habronattus	tranquilus group	Foliage Stalker	X144&X140	126	1/131
Hassarius	*spp.*	Foliage Stalker	X98	124	1/131
Hentzia	*mitrata*	Foliage Stalker	X89*	26*	29/131*
Hentzia	*palmarum*	Foliage Stalker	X89*	26*	29/131*
Maevia	*inclemens*	Foliage Stalker	X139	118	1/131
Marchena	*spp.*	Foliage Stalker	X90	107	2/131

Marpissa	*formosa*	Foliage Stalker	X138	120	1/131
Marpissa	*lineata*	Foliage Stalker	X148		
Marpissa	*obtusa*	Foliage Stalker	X78	121	1/131
Marpissa	*pikei*	Foliage Stalker	X77	9	60/131
Messua	*spp.*	Foliage Stalker	X91	108	2/131
Myrmarachne	*formicaria*	Active Ground Hunter	X93	91	3/131
Neon	*spp.*	Foliage Stalker	X92	77	5/131
Paraphidippus	*aurantius?*	Foliage Stalker	X74	65	7/131
Pelegrina	*galathea*	Foliage Stalker	X75	11	57/131
Phanias	*spp.*	Foliage Stalker	X76	66	7/131
Phidippus	*apacheanus*	Foliage Stalker	X149		
Phidippus	*audax*	Foliage Stalker	X79	60	8/131
Phidippus	*carneus*	Foliage Stalker	X130	61	8/131
Phidippus	*cardinalis*	Foliage Stalker	X84	85	4/131
Phidippus	*clarus*	Foliage Stalker	X83	6	73/131
Phidippus	*johnsoni*	Foliage Stalker	X80	67	7/131
Phidippus	*purpuratus*	Foliage Stalker	X81	105	2/131
Phidippus	*texanus*	Foliage Stalker	X85		
Phidippus	*tux*	Foliage Stalker	X86	76	5/131
Phidippus	*spp. 1*	Foliage Stalker	X131	84	4/131
Phidippus	*spp. 2*	Foliage Stalker	X82	106	2/131
Rhetentor	*texanus*	Foliage Stalker	X94	123	1/131
Salticus	*scenicus*	Foliage Stalker	X95	109	2/131
Salticus	*spp.*	Foliage Stalker	X143		
Sarinda	*hentzi*	Active Ground Hunter	X97	110	2/131
Sassacus	*cyaneus*	Foliage Stalker	X73	64	7/131
Sassacus	*papenhoei*	Foliage Stalker	X96	34	20/131
Synageles	*noxiosus/*	Active Ground	X88	58	8/131

	bishopi?	Hunter			
Synemosyna	*formica*	Active Ground Hunter	X150		
Zygoballus	*iridescens*	Foliage Stalker	X68	103	2/131
Zygoballus	*rufipes*	Foliage Stalker	X67	25	30/131
Zygoballus	*sexpunctatus?*	Foliage Stalker	X69	40	14/131
Zygoballus	*spp.*	Foliage Stalker	X132	104	2/131
Theridiidae					
	spp.	All-Directions Web	X103	92	3/131
Euryopis	*funebris*	All-Directions Web	X133	87	4/131
Euryopis	*spp.*	All-Directions Web	X107	38	16/131
Latrodectus	*variolus*	All-Directions Web	X104	127	1/131
Theridion	*frondeum*	All-Directions Web	X106	53	10/131
Theridium	*rabuni/ varians?*	All-Directions Web	X105	24	31/131
Theridiosomatidae					
Theridiosoma	*gemmosum/ savannum?*	Sling-shot Orb Web	X108	78	5/131
Tetragnathidae					
Glenognatha	*foxi*	Medium Orb-Web	X112		
Meta	*spp.*	Medium Orb-Web	X111		
Tetragnatha	*elongata*	Medium Orb-Web	X145		

Tetragnatha	*extensa*	Medium Orb-Web	X151		
Tetragnatha	*laboriosa*	Medium Orb-Web	X109	36	17/131
Tetragnatha	*spp.*	Medium Orb-Web	X110		
Thomisidae					
Mecaphesa	*celer*	Foliage Sit & Wait	X116	7	72/131
Mecaphesa	*dubia*	Foliage Sit & Wait	X117	2	110/131
Mecaphesa	*lepida*	Foliage Sit & Wait	X118	56	9/131
Misumenops	*spp.*	Foliage Sit & Wait	X115		
Misumenoides	*formosipes*	Foliage Sit & Wait	X119	12	54/131
Misumessus	*oblongus*	Foliage Sit & Wait	X121	71	6/131
Synema	*parvulum*	Foliage Sit & Wait	X120	35	20/131
Tmarus	*angulatus*	Foliage Sit & Wait	X114	23	32/131
Tmarus	*minutus*	Foliage Sit & Wait	X113	93	3/131
Xysticus	*elegans*	Foliage-Ground Sit & Wait	X122	128	1/131
Xysticus	*spp. Similar to elegans?*	Foliage-Ground Sit & Wait	X122.1	50	11/131
Xysticus	*ferox*	Foliage-Ground	X123	57	9/131

		Sit & Wait			
Xysticus	*gulosus*	Foliage-Ground Sit & Wait	X126	30	25/131
Xysticus	*luctans*	Foliage-Ground Sit & Wait	X125	54	10/131
Xysticus	*triguttatus*	Foliage-Ground Sit & Wait	X124	10	60/131
Uloboridae					
	spp.	Small Orb-Web	X127	88	4/131
Unknown			X128	44	13/131

Spider species were identified to the family or genus level using the Spider of North America an identification manual (reference: Ubick, D. P., & Cushing, P. 2005. Spiders of North Americaan identification manual. No. C/595.44097 S7.). Spiders were identified to species level by matching specimens to illustrations and /or pictures on the book Common spider of North Ammerica (reference: Bradley, R. A. 2012. Common Spiders of North America. Univ of California Press.), the Checklist of Kansas Orbweaving Spiders/ Jumping Spiders/ Crab Spiders/ and Ground Spiders by Hank Guarisco (references: Guarisco, H. (2005). Checklist of Kansas orb-weaving spiders Vol. 52(2). Emporia State University.; Guarisco, H., Cutler, B., & Kinman, K. E. (2001). Checklist of Kansas jumping spiders. Vol 47(1). Emporia State University.; Guarisco, H. (2007). Checklist of Kansas ground spiders. Emporia State University.; and Guarisco, H., Cutler, B., & Jennings, D. (2003). Checklist of Kansas crab spiders. Vol 49(1). Emporia State University.) and, using pictures from the web-site www.bugguide.net. Spider scientific names reported here have being revised and updated to the current nomenclature in the World Spider Catalog version 17.5 (www.wsc.nmbe.ch).

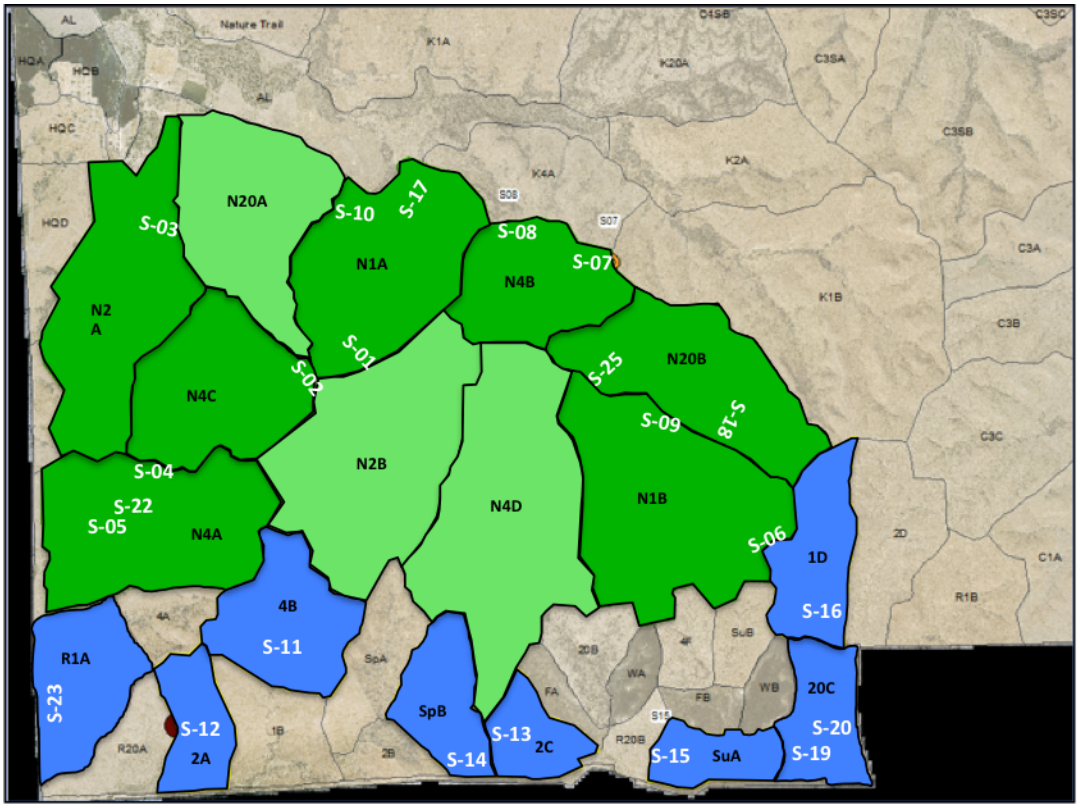

Figure 5-1. Map of the 23 sites sampled in this study for chapters 2 & 3 within the KPBS landscape. Bison unit watersheds are green, where bison-grazed watersheds actually sampled in this study are dark green. Not-grazed watersheds that were sampled in this study are blue. Site IDs are indicated on the map.

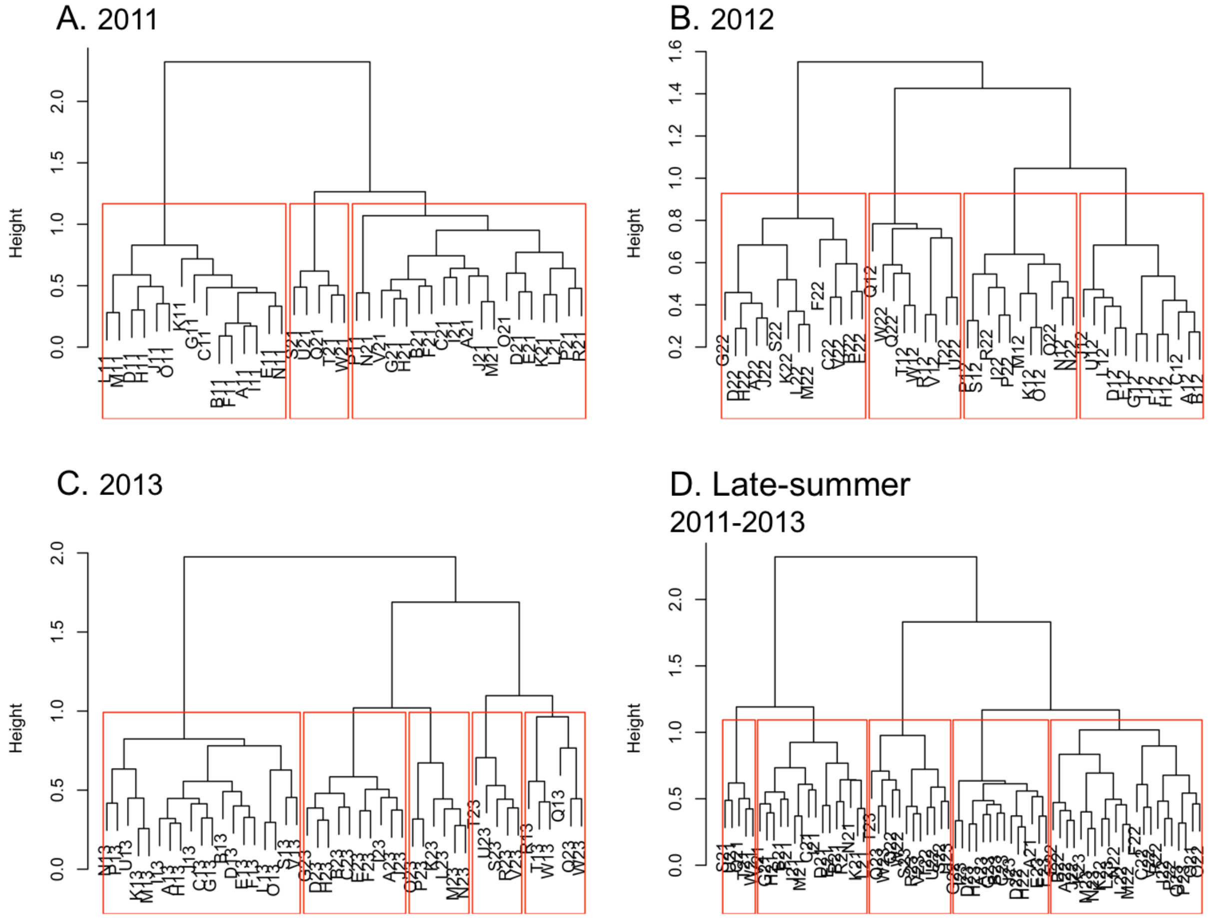

Figure 5-2. Site-clusters based on spider species composition by individual years: (a) 2011, (b) 2012, (c) 2013, and (d) late-summer sites between 2011-2013. For (a) 2011and (c) 2013, the first split in the dendrogram is driven by seasonal differences in spider assembly resulting in early-summer and late-summer spider assemblages. This pattern was lost during the 2012 drought.