DISSERTATION

INFLUENCE OF HABITAT COMPLEXITY ON DIVERSITY AND COMMUNITY STRUCTURE OF ARBOREAL SPIDERS IN GRASSLAND-SHRUB SYSTEMS

Submitted by

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ABSTRACT

INFLUENCE OF HABITAT COMPLEXITY ON COMMUNITY STRUCTURE OF ARBOREAL SPIDERS IN GRASSLAND-SHRUB SYSTEMS

Revealing the ecological drivers of species distribution is one of the central issues in ecology. The ecological niche concept recognizes that distribution of species is influenced by abiotic (e.g., temperature, landscape characteristics, and nutrients) and biotic (e.g., food availability) factors through both direct and indirect mechanisms. Many of these niche factors can influence the spatial position of plants in a landscape. Plant communities often determine the physical structure of the environment (microclimate, plant architecture) and therefore, have a considerable influence on the distribution of animal species, such as arthropods, and on local community structure. For instance, vegetation structure provides spatial complexity by creating microenvironments that may enable more interactions with other species that live on plants or allow resource partitioning. In grasslands, much of the arboreal habitat is in the form of shrubs, but the role and importance of shrubs in distribution and diversity of arthropods in grasslands is unknown. Spiders are a useful indicator for examining the role of shrubs in arthropod ecology because they are genetically and behaviorally diverse predators and prey that can be captured and counted with a single method.

Spiders are a key component of invertebrate communities of grasslands and arboreal spiders of grasslands provide a unique ecological system to study habitat association and community assemblage. However, most spider studies in prairie ecosystems have focused on ground dwelling taxa or those associated with agroecosystems. Only limited data exist for shrub-dwelling species and few studies have compared arboreal spider occupancy across different grassland shrub species. I endeavored to understand this system in more detail by investigating how arboreal spider community structure responds to native shrub species, plant community composition and landscape complexity. Since landscape complexity can be evaluated at multiple scales, landscape characteristics can be significant predictors of presence and abundance for a variety of taxa.

I collected and identified 3,053 specimens to family, genus or species level and found that presence of certain shrub species predicted spider species occurrence and suggested diversity community structure patterns. I found that habitat association to combinations on shrub species indicated habitat specific niche partitioning of arboreal spiders in two Colorado grassland systems. Because shrub species occurrence is largely dependent on elevation and moisture gradients, spider occupancy may also be tied to similar gradients correlated with these landscape factors. Changes in the topography of the sampling area affected the local plant communities of shrubs across a recognized elevational gradient, which correlated to habitat zones for arboreal spiders in the local area.

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CHAPTER 1: MAIN INTRODUCTION

BACKGROUND

Understanding the ecological drivers of species distribution and predicting the spatial dynamics of populations remain central goals in ecology (Hanski & Simberloff, 1997; Alexander et al., 2012). For instance, species distribution models (SDM), also known as ecological niche models, seek to identify the relationship between species occurrence and environmental variables. These models predict species ranges with climate data as predictors (Hijmans & Elith, 2016) or predict habitat suitability for conservation use (Liu et al., 2005; Chefaoui et al., 2005). The patterns explained by these models for species-habitat relationships are also sensitive to the spatial scales at which they are evaluated (Kumar et al., 2008; McGarigal et al., 2016, Chase et al., 2019).

The ecological niche concept recognizes that a species' distribution is influenced directly and indirectly by abiotic and biotic factors and their interactions (Hutchinson, 1957; Soininen, 2010; Hijmans & Elith, 2016). These patterns of distribution are associated with adaptations of a species to its environment (Hutchinson, 1957; Leibold et al., 2010). Biotic factors can include dispersal (Samu et al., 1999; Malumbres-Olarte et al., 2013), competition (Chase et al., 2005), and predation (Schmitz, 2008; Holt & Barfield, 2009; Pawar, 2009). Abiotic factors, such as temperature, moisture, and light (Pearson et al., 2002; Soberon & Peterson, 2005; Entling et al., 2007), can also influence a species' reproductive success in an area of physical space. Many of these abiotic factors can affect local plant distribution patterns, changing the complexity of habitat and altering the interaction and distribution of animal species occupying these plants (Lawton, 1983; McCoy & Bell, 1991). This pattern of heterogeneous habitats affecting diversity is central to biogeography (MacArthur & Wilson, 1967; Willig & Bloch, 2006) and other fields of landscape ecology. In biogeography, the spatial configurations of habitat influence ecological patterns, such as biodiversity (Pickett & Cadenasso, 1995; Turner, 1987), and results in species groups found across recognizable community types, such as in intertidal zones (Connell, 1961) or specifically in grassland systems (Knopf, 1996). Different plant communities should vary in habitat suitability for supporting varied species within because heterogenous habitats provide allow for greater biological complexity through available environmental resources (Tews et al., 2004). These may also increase species diversity along recognized ecological gradients (Hutchinson, 1957; MacArthur & Wilson, 1967; Futuyma & Moreno, 1988; Sexton et al., 2017).

In grassland ecoregions (Omernik & Griffith, 2014) vegetation structure within plant communities provides additional spatial complexity by creating microenvironments that enable more species interactions and allow resource partitioning. In shortgrass steppe, one of the more arid grassland regions, common shrubs include sand sagebrush (*Artemisia filifolia* Torr.), four-winged saltbush (*Atriplex canescens* (Pursh) Nutt.), rubber rabbitbrush (*Ericameria nauseosa* (Pall. Ex. Pursh)), greasewood (*Sarcobatus vermiculatus* Torr.), skunkbush sumac (*Rhus trilobata* Nutt.) and one-seed juniper (*Juniperus monosperma* (Engelm) Sarg.). Shrub occupancy may suggest long-term habitat configuration of an ecological system and allow detailed habitat association and habitat suitability estimates across a landscape.

Spiders play a vital role in the functioning of grassland ecosystems, occupying terrestrial food webs as both predators and prey (Uetz, 1991). They encompass a wide range of foraging strategies and different shrub species possess unique structural attributes, which may affect arboreal spider taxa. Structural features of plant height and density can influence spider habitat use (Uetz, 1992; Gibson et al., 1992). For instance, species diversity and local abundance of web-building spiders are usually greatest in plant communities that are architecturally complex because they provide greater variation in substrate for building webs (Robinson, 1981; Greenstone, 1984; Wise, 1993; Langellotto & Denno, 2004) and provide higher levels of resources for the spiders' prey. The type of vegetation within grasslands has been observed to influence the diversity of web-building spiders (Gibson et al., 1992; Borges & Brown, 2001) and abundance of Salticidae and Oxyopidae, which do not build webs, are often more abundant on one vegetation type than another (Cutler et al., 1977). In addition, some insects may feed on a specific plant's nectar, phloem, leaves, roots, or cambium while other insects act as predators and will be tied to a specific plant community as well, even if indirectly. Since spiders fill similar trophic parameters as these predatory insects, these insect-plant associations may also indirectly affect arboreal spiders.

Arboreal spider habitat use in grasslands makes a data-rich ecological system to study the effects of spatial heterogeneity on local diversity and community structure. Spider-plant associations may be determined since many of these plants (shrubs) are associated with specific landscape features (elevation, slope, etc.) and thus, combinations of biotic and abiotic thresholds can be used to predict habitat suitability for these spiders. In a restricted local space, shrub species in grassland landscapes may be numerous and dense in an area and then become more fragmented, intermixing with other plant species that will possess their own habitat restrictions. By measuring habitat heterogeneity effects (shrub composition) and topographic predictors for shrub occupancy, patterns of spider community assembly may be used to identify core habitat features (Forman, 1995; Broennimann et al., 2012) which may suggest specialization to habitat. Thus, examining arboreal spider habitat partitioning and community structure may allow us to test concepts of niche theory at multiple scales.

RESEARCH OVERVIEW

My overall goal was to improve habitat mapping for spiders in the Great Plains grassland region by investigating how arboreal spider community structure responds to native shrub species, plant community composition and habitat complexity. Spiders are behaviorally and genetically diverse. They are predators of arthropods, including other spiders, and are prey for arthropods, birds, reptiles, and mammals. Spiders inhabiting shrubs in grassland systems make excellent models for ecological research because they can be sensitive to specific habitat conditions while being isolated from the neighboring habitat of open grassland occupied by ground dwelling taxa, including ground dwelling spiders. Unlike many insects that fly long distances, spiders are in comparison more stationary. Whether by inhabiting webs or by stalking prey, spiders are more likely to reside in a local region. To determine arboreal spider habitat-use in grasslands more clearly, I needed to determine if there are associations between spider taxa and other environmental factors in grasslands.

My first research objective was to determine which environmental factors influence species diversity patterns for arboreal spiders in grasslands. I hypothesized that plant type (shrub species) will affect habitat availability of arboreal spiders. I predicted that differences in diversity of arboreal spiders will be observed among local shrub species. To test this hypothesis, I first compared variables that explained the diversity of spiders between Comanche and Pawnee National Grassland sites. These variables included seasonal factors (year, month) and two local area factors (shrub species). Araneae taxa lists are reported for both Colorado NG locations. My results demonstrated that shrub species was a significant factor for explaining spider diversity in two national grassland sites (Chapter Two: Knutson, 2022).

I found that for the Comanche National Grassland, significant differences in spider diversity existed between specific shrub species, especially for the spider families Salticidae, Philodromidae, Oxyopidae and Dictynidae. Diversity tests for Pawnee National Grassland were more limited due to overall sample data size, with low incidence of sandsage and rabbitbrush in the region. Spider diversity was highest in juniper (CNG) and big sagebrush at (PNG), which are taller than other shrubs in these systems and have a higher density of foliage compared to other shrub species.

My second objective was to determine the overall composition of insects collected on the native shrubs sampled, suggesting additional environmental factors influencing patterns for arboreal spiders (Chapter Three: Knutson et al., 2019).

I found that Chrysomelidae, Cicadellidae, Cleridae, Formicidae, Meloidae, and Miridae were abundant at Pawnee National Grassland, primarily from four-winged saltbush (*Atriplex canescens*). Acrididae, Aphididae, Chrysomelidae, Cleridae, Coccinellidae, Formicidae, Lygaeidae, Miridae, and Reduviidae collected from sandsage (*Artemisia filifolia*), four-winged saltbush, rabbitbrush (*Ericameria nauseosa*), greasewood (*Sarcobatus vermiculatus*), skunkbush (*Rhus trilobata*), and one-seed juniper (*Juniperus monosperma* (Engelm.) were abundant at Comanche National Grassland. These findings are useful for future steps in predator-prey analyses.

My third research objective was to test how different grassland shrub species affect arboreal spider community structure and to determine if shrubs are useful indicators to spiders in this environment (Chapter Four). I hypothesized that local plant community structure (vegetation composition) will affect arboreal spider community complexity in grasslands of eastern Colorado. To test how local plant community structure increases habitat availability for arboreal spiders, I used multilevel pattern and hierarchal clustering analysis that provide comparisons of spider families to shrub species and found associations between spider families and shrub species. Because some shrub species are limited to the sides and bottoms of canyons, I also inferred that some spider families were also limited in distribution.

The results of Random Forest (ex. Salticidae and Oxyopidae with juniper. Philodromidae with greasewood and sandsage) all indicated that shrub species can predict patterns of habitat association in local communities altering spider community structure. Community analyses suggested that Dictynidae was significantly associated with greasewood and rabbitbrush, Oxyopidae was significantly associated skunkbush, and Philodromidae, was significantly associated with rabbitbrush, greasewood and sandsage.

I also hypothesized that elevation change impacts shrub growth and presence and that this alters habitat availability for spider species associated with each shrub species, thereby altering arboreal spider diversity and community structure. I predicted that elevation would predict shrub occupancy. I also predicted that shrub habitat zones related to elevation [steppe, cliff region of canyon slope, lower canyon region] would be associated with different spider communities. Since the plant communities in these systems can be delineated across recognized gradients, shrub position in canyons may predict taxa-specific spider habitat and suggest transitions between habitat zones that may support species from neighboring communities or contain habitat specialists.

My results support that elevation, relative to each canyon, was correlated to shrub habitat zones, including the upper canyon steppe, cliff region, and canyon bottom. Since the elevation affected the overall pattern of shrubs presence and abundance and different spider species are associated with each different shrub species, elevation also affected the community structure of arboreal spiders. Juniper occurred across most of the elevational gradient, with the majority of juniper in uplands, skunkbush grew along canyon cliff sides, while greasewood, rabbitbrush, and sandsage were found at the canyon bottom. Although elevation above canyon floor predicted shrub species habitat, additional attributes such as slope and aspect would likely enhance predictions of local shrub species occupancy. Depending on the available shrubs present locally, spider communities varied in habitat use. This indicates that many shrub species are important to the overall community assembly of arboreal spiders and may also indicate critical thresholds for some spider groups at the genus and species level. Finally, I briefly outline potential directions for future spider research in grasslands and make recommendations for characterization of arboreal spider habitat and community structure in a spatially heterogeneous landscape.

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CHAPTER 2: ARBOREAL SPIDERS OF NATIVE SHRUBS IN GRASSLAND SYSTEMS OF EASTERN COLORADO

INTRODUCTION

Biological diversity is a major component for evaluating ecological systems for conservation efforts. Heterogeneous habitats provide a wide variety of niches (Finke & Snyder, 2008) and habitat complexity with varied resources (Stein et al., 2014) and might support an increase in biological diversity (MacArthur & Wilson, 1967; Pickett & Cadenasso, 1995; Tews et al., 2004) compared to ecological systems with less habitat complexity. Native grasslands are among the most imperiled ecosystems globally because of competition with urban development, agriculture, invasive species, and changes in fire frequency (Collins et al., 1998; Samson et al., 2004; Stevens et al., 2008; Ceballos et al., 2010). As a result, it is imperative that taxa in grassland regions that are intact are documented to detect patterns of habitat use and to aid in restoration. Such inventories can provide information about species identity, diversity, and abundance and are critical for making management decisions and determining if restoration efforts are effective.

In the United States, shortgrass steppe is a major grassland ecosystem found on the High Plains from Wyoming to Texas, east of the Rocky Mountains. The grasslands have minimal annual rainfall, with most plant biomass below ground (Stromberg, 2011). In Colorado, the Pawnee National Grassland (PNG) covers more than 193,000 acres in northeastern Colorado and the Comanche National Grassland (CNG) covers 463,000 acres in southeastern Colorado. The grasslands were established in 1960, in part to restore an ecosystem damaged by agriculture and drought that led to the Dust Bowl of the 1930s. Both grasslands are dominated by buffalo grass (*Bouteloua dactyloides* (Nutt.)) and blue grama grass (*Bouteloua gracilis* (Kunth)), as well as shrubs and forbs that evolved in the presence of large numbers of grazing animals. In the shortgrass steppe ecosystem, shrubs provide an overstory with species such as sagebrush (*Artemisia* sp. (Nutt.)) and rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh)). Shrub species in shortgrass steppe ecosystems vary in structure, flowering time, insect fauna, and microclimates in the shrubs. This plant heterogeneity might result in diversity in predators and prey, such as arthropods, in each shrub species (Mooney et al., 2010; Rzanny & Voigt, 2012).

Spiders (Araneae) are a diverse taxonomic group that fills many crucial niches in a grassland landscape. As predators and prey, they reflect a larger array of species above, adjacent to, and below their trophic levels (Nyffeler & Birkhofer, 2017). However, most studies involving spiders in grasslands are confined to ground-dwelling spider taxa or species associated with agricultural production (Sunderland & Samu, 2000; Weeks & Holtzer, 2000; Schmidt et al., 2005; Fourie et al., 2013). Diversity of spiders has been associated with vegetation structure (Abraham, 1983; Uetz et al., 1991; Vasconcellos-Neto et al., 2007), but few studies compared spider distribution across different shrubs in grassland systems. By comparing spider occupancy of native shrubs in grasslands, biodiversity patterns of arthropod predators might be improved in a threatened ecosystem with species impacted mostly because of change in land use requiring ongoing documentation of occurrence and changes in local communities.

This research studied arboreal grassland spiders in native shrubs in the Colorado grassland steppe ecoregion, and how they differ among native shrub species at two U.S. National Grassland locations. I hypothesized that plant type (shrub species) will affect habitat availability of arboreal spiders. I predicted that differences in diversity of arboreal spiders will be observed among local shrub species. To test this hypothesis, I compared variables (shrub, month, year) that explained the diversity of spiders between Comanche and Pawnee National Grassland sites. Araneae taxa lists are also reported for both Colorado NG locations. Considering that the distinct locations have different shrub species and that spiders might access native shrub species in various ways, differences in spider diversity patterns (Shannon index, abundance) were expected locally. In addition to providing a baseline inventory of spiders in the grasslands, this research can provide essential data for long-term ecological studies of future habitat use.

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METHODS

Study Locations

Field research was done at the Colorado semi-arid shortgrass steppe locations of Comanche National Grassland (CNG) and Pawnee National Grassland (PNG). CNG, which is in southeastern Colorado (N 40.7614588, W-104.0493284 (www.fs.usda.gov)), includes a large network of canyons on the Southern Great Plains (Hazlett, 2004). The plant communities are steppe and shortgrass prairie, with different assemblages of shrubs including sand sagebrush (*Artemisia filifolia* Torr.), four-winged saltbush (*Atriplex canescens* (Pursh) Nutt.), rabbitbrush (*Ericameria nauseosa* (Pall. Ex. Pursh)), greasewood (*Sarcobatus vermiculatus* Torr.), skunkbush sumac (*Rhus trilobata* Nutt.), and a juniper complex including Utah juniper (*Juniperus osteosperma* (Torr.) Little) and one-seed juniper (*Juniperus monosperma* (Engelm) Sarg.).

PNG, which is in northeastern Colorado (N 40.7614588, W -104.0493284 (www.fs.usda.gov)), has minimal variation in elevation and is in an exposed landscape (Hazlett, 1998). The plant community is dominated by four-winged saltbush (Hazlett, 1998), and also has rabbitbrush, sandsage, and big sagebrush (*Artemisia tridentata*) Nutt.

Sampling Method

Sampling in the field was done each month from May-September 2014-2017. On each sampling date, a target total of 40 individual shrubs of each taxon were sampled at each locality. A tally counter was used to count the number of replications of shrub species, which varied with the availability of each shrub species sampled along a transect at all sites. At CNG, sampling occurred in canyons in shortgrass steppe including Picture, Vogel, Withers, Minnie, No-Name, and Iron canyons and the mean sample size was 33 shrubs of each species. For CNG, an elevational gradient-based survey was used across wide transects encompassing the width of each canyon. At PNG, sampling occurred in areas in the Central

Plains Experimental Range (CPER), which is a shortgrass steppe with minimal variation in elevation and the mean sample size was 30 shrubs per species.

Spiders and other arthropods were extracted from each shrub by the beating method (Knutson, 2010). The funnel bucket had the dimensions of a 5-gallon (0.0189 cubic meter) container and contained a separate housing container to retain arthropods collected. To use a funnel bucket, a branch was held into the bucket cavity and briskly beaten. Arthropods in the funnel bucket were collected by hand, or the housing container attached to the funnel was removed, covered, and replaced for quick sampling. All arthropods were transferred from the collecting device and stored temporarily in Ziploc bags with leaf material to prevent damage or interaction of specimens. The specimens were transferred and processed in a laboratory at Colorado State University, Fort Collins. Samples were sorted by family groups and stored in 95% ethanol in vials.

Spider Identification

Adult spiders were identified to genus or species (Ubick et al., 2005 and primary literature) and immature spiders were identified to family or genus when possible. An Olympus SZX12 microscope was used to aid in sorting and identification of spiders. I used keys and species checklists by taxonomic authorities for the Rocky Mountain and Great Plains region. Immature spiders varied in ease of identification. For example, immature *Xysticus* (Thomisidae), *Salticus* (Salticidae), *Sassacus* (Salticidae), and *Ebo* (Philodromidae) had prominent adult characteristics. However, some immature spiders are especially difficult to identify to genus and species (Sackett et al., 2008).

Data Analysis

Spider family count data (samples grouped by locality, shrub species) was collected at the two national grasslands in Colorado from 2014-2017. A data matrix was prepared by incorporating count data of shrub localities (samples grouped by locality, shrub species). The combined National Grassland metadata had 388 samples (spiders collected from shrub species from specific local and sampling date).

Analysis of Variance (ANOVA) (Index: Shannon) was used to determine the abundance (number of individuals of spider family per shrub species) between locations.

A Generalized Linear Model was used to compare diversity patterns for CNG and PNG with a Poisson distribution for non-transformed count-based data with log link function. Generalized linear models in R (R Core Team, 2020) was used to compare abundance and distribution of spider families on shrub species. A diversity metric was fitted using shrub species as a categorical effect, with month as a random factor and with the intercept at zero, which allowed results to be interpreted as all positive numbers. Betas describe the relationship between the response (counts) and that covariate, reported as linear predictors. If $\beta > 0$, $\exp(\beta) > 1$ and the expected count $\mu = E(y)$ is $\exp(\beta)$ times larger than when $X = 0$. This provided the expected change in the response (count) for a unit change in the covariate of interest (shrub species). If $\beta < 0$, then $\exp(\beta) < 1$, and the expected count $\mu = E(y)$ is $\exp(\beta)$ times smaller than when $X = 0$.

To assess the response of spider diversity to potential drivers such as plant species, a trimmed set of explanatory variables was tested using ANOVA with normalized count data (Hellinger transformation) in R (R Core Team, 2020). A model was spider family (11) (categorical) count data (3,302) to shrub species (covariate) by date-location. Predictor variables were shrub species (four or five), national grassland location (two), month (five), and year (four).

RESULTS

Summary of Spider Captures

Spider genera and species are listed for CNG (Table 2.1) and PNG (Table 2.2). Sampling from 2014-2017 for CNG and PNG combined resulted in 3,052 adult and immature spiders in 21 genera in 11 families: Agelenidae, Araneidae, Dictynidae, Eutichuridae, Mimetidae, Oxyopidae, Philodromidae, Salticidae, Tetragnathidae, Theridiidae, and Thomisidae. The dominant families were Salticidae, Oxyopidae, Philodromidae, Thomisidae, Dictynidae, and Araneidae, with 36, 19, 14, 13, 11, and 4%, respectively, of total abundance (Figure S1-S3) in the grasslands. The same spider families were on most shrub species, but genera varied (Tables 2.1-2.2). Salticidae, Philodromidae, Oxyopidae, and Dictynidae were abundant at CNG, while Dictynidae, Oxyopidae, and Salticidae were abundant at PNG. Agelenidae, Eutichuridae, Mimetidae, and Theridiidae were less common at both locations.

At CNG, 2,658 individual spiders were collected from the families Salticidae (878 individuals), Oxyopidae (502), Philodromidae (394), Thomisidae (344), Dictynidae (312), Araneidae (119), Mimetidae (54), Eutichuridae (25), Theridiidae (14), Agelenidae (12) and Tetragnathidae (4). For PNG, 394 individuals were collected of Salticidae (217), Oxyopidae (82), Thomisidae (40), Philodromidae (35), Dictynidae (12), Araneidae (6), Eutichuridae (1), and Theridiidae (1).

Table 2.1. Spiders on Shrub Species at the Comanche National Grassland, Colorado from May-September 2014-2017 and Identified to Family, Genus, and/or Species.

			Shrub				
Family	**Genus**	**Species**	*Ericameria nauseosa*	*Sarcobatus vermiculatus*	*Rhus trilobata*	*Juniperus monosperma*	*Artemisia filifolia*
Agelenidae	*Agelenopsis*				●	●	
Araneidae	*Araneus*				●		
	Argiope			●			●
	Lariniodes			●			
	Mangora	*gibberosa*			●		
	Mangora				●		
	Metepeira			●			
	Neoscona	*crucifera*				●	
	Neoscona	*oaxacensis*			●		
	Neoscona		●	●	●	●	●
Dictynidae	*Dictyna*	cf. *abundans*		●			
	Dictyna	cf. *bellans*				●	
	Dictyna	cf. *bostoniensis*		●			
	Dictyna	cf. *volucripes*		●		●	
	Dictyna		●	●	●	●	●
Eutichuridae	*Cheiracanthium*	*inclusum*	●	●	●	●	
Mimetidae	*Ero*				●		
	Mimetus	*hesperus*			●	●	
	Mimetus		●	●	●	●	●
Oxyopidae	*Oxyopes*	*scalaris*	●	●	●	●	●
	Oxyopes		●	●	●	●	●
Philodromidae	*Ebo*		●	●	●	●	●
	Philodromus		●	●	●	●	●
	Philodromus	*marginellus*				●	
	Titanebo	*californicus*		●			
	Titanebo	*parabolis*		●			
	Thanatus					●	●
Salticidae	Dendryphantine			●		●	
	Metaphidippus	*chera*				●	
	Metaphidippus					●	
	Pelegrina	*galathea*			●		
	Pelegrina	*proterva*	●				
	Pelegrina				●		
	Phidippus	*apacheanus*		●		●	
	Phidippus	*audax*		●		●	●
	Phidippus	*cardinalis*				●	
	Phidippus	*carneus*				●	
	Phidippus	*johnsoni*	●	●	●	●	
	Phidippus	*octopunctatus*		●	●	●	
	Phidippus		●	●	●	●	●
	Salticus		●	●		●	●
	Sassacus	*papenhoei*	●	●			●
	Sassacus		●				●
Tetragnathidae	*Tetragnatha*				●		
Theridiidae	*Latrodectus*					●	
	Steatoda					●	
	Theridion				●		
Thomisidae	*Mecaphesa*	*asperata*		●	●	●	
	Mecaphesa	*celer*	●	●	●	●	
	Mecaphesa	*coloradensis*			●	●	
	Mecaphesa		●	●	●	●	●
	Misumena	*vatia*				●	
	Misumena						●
	Xysticus	*elegans*	●				
	Xysticus	*gosiutus*				●	
	Xysticus			●		●	●

Table 2.2. Spiders on Shrub Species at Pawnee National Grassland, Colorado from May-September 2014-2017 and Identified to Family, Genus, and/or Species.

			Shrub			
Family	Genus	Species	*Ericameria nauseosa*	*Atriplex canescens*	*Artemisia filifolia*	*Artemisia tridentata*
Araneidae	*Argiope*					●
	Neoscona			●		
Dictynidae	*Dictyna*		●	●		●
Eutichuridae	*Cheiracanthium*	*inclusum*		●		
Oxyopidae	*Oxyopes*	*scalaris*	●	●		
	Oxyopes					●
Philodromidae	*Ebo*			●		●
	Philodromus			●	●	●
	Philodromus	*marginellus*				●
Salticidae	Dendryphantine		●			●
	Marpissa					●
	Pelegrina	*arizonensis*		●		●
	Pelegrina			●		●
	Phidippus	*audax*		●		
	Phidippus	*octopunctatus*		●		
	Phidippus				●	
	Sassacus	*papenhoei*			●	
Theridiidae	*Latrodectus*					●
Thomisidae	*Mecaphesa*		●	●		●
	Misumenoides					●
	Xysticus			●		

Diversity of Spiders from Shrubs Sampled

Spider diversity on *Sarcobatus vermiculatus* and *Juniperus monosperma* at CNG was significantly greater than on *Ericameria nauseosa*, *Artemisia filifolia*, and *Rhus trilobata* (Figure 2.1a). More diversity was found in *Artemisia tridentata* than in *Atriplex canescens*, *Ericameria nauseosa*, and *Artemisia filifolia* at PNG (Figure 2.1b), but the differences were not significant.

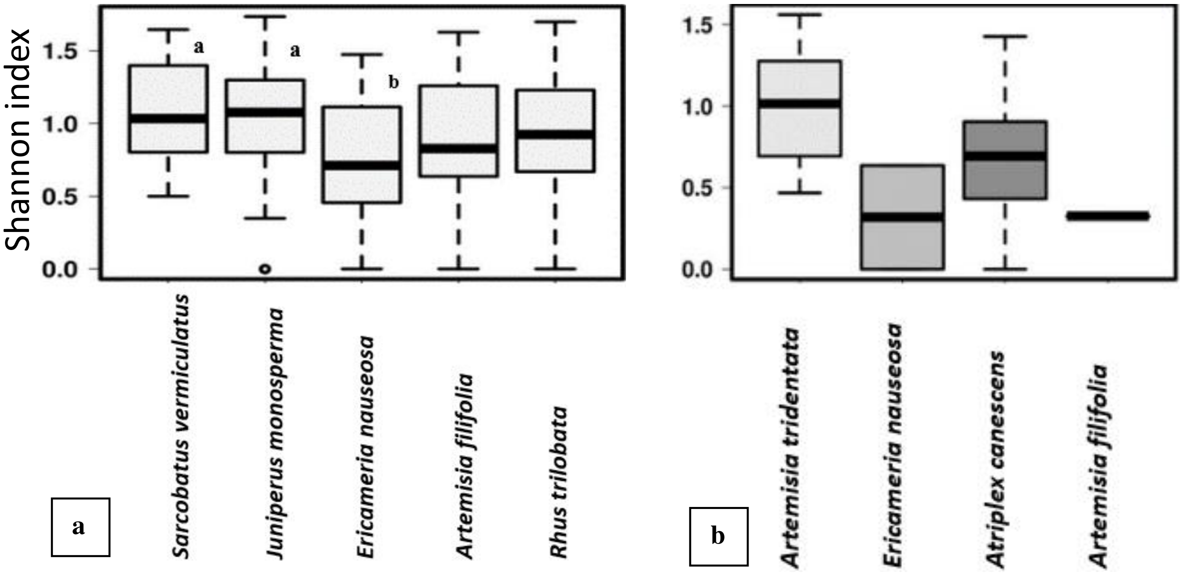

Figure 2.1. Shannon Index for diversity of spiders between shrub species. Spider family data grouped by shrub species represented by ANOVA boxplot at a) Comanche National Grassland ($P = 0.0081$) and b) Pawnee National Grassland ANOVA ($P = 0.052$). Pair-wise comparisons by *t*-test ($P < 0.05$).

Generalized Linear Models

Differences in spider abundance among shrub types were tested by generalized linear models (GLMs) with Poisson errors on numbers. Analyses indicated significant differences in abundance of many spider families by month at CNG (Table 2.3). No significant differences were detected for Araneidae. Significant differences were found in Dictynidae on *Sarcobatus vermiculatus* ($P = 0.0003$) and *Ericameria nauseosa* ($P = 0.007$). Numbers of Mimetidae differed between *Sarcobatus vermiculatus* and other shrubs. Mimetidae was negative relative to the intercept to juniper (intercept = -1.3098) and *Rhus trilobata*. Oxyopidae was significant on *Sarcobatus vermiculatus* ($P = 4.42\text{e-}06$), *Juniperus monosperma* ($P = 0.0002$), and *Rhus trilobata* ($P = 4.19\text{e-}07$). Philodromidae was significant on *Sarcobatus vermiculatus, Ericameria nauseosa*, and *Artemisia filifolia*. Salticidae was significantly more abundant on all shrub species, as was Thomisidae. The generalized linear model for PNG (Table 2.4) indicated significant differences in numbers of Thomisidae between *Artemisia tridentata* ($P = 1.52\text{e-}09$) and other shrubs. Results also indicated significant differences in Salticidae between *Artemisia tridentata* and other shrub species ($P = 0.00149$).

Table 2.3. Product of Generalized Linear Model with Poisson Distribution with Log Link Function for Comanche National Grassland.

Spider family and shrub species

Araneidae	**Estimate**	**Std. Error**	**z value**	***P* > z**
Sarcobatus vermiculatus	3.19E-01	2.13E-01	1.494	0.1353
Juniperus monosperma	7.06E-02	1.51E-01	0.468	0.6395
Ericameria nauseosa	6.93E-01	4.08E-01	1.698	0.0895.
Artemisia filifolia	9.69E-15	2.77E-01	0	1
Rhus trilobata	1.45E-01	1.64E-01	0.883	0.3772
Dictynidae				
Sarcobatus vermiculatus	1.01153	0.2831	3.573	0.000353 ***
Juniperus monosperma	0.08636	0.31203	0.277	0.781964
Ericameria nauseosa	0.78406	0.29385	2.668	0.007626 **
Artemisia filifolia	0.35274	0.32805	1.075	0.282267
Rhus trilobata	0.22319	0.35238	0.633	0.526496
Mimetidae				
Sarcobatus vermiculatus	1.48E+00	2.13E-01	6.949	3.67e-12 ***
Juniperus monosperma	1.72E-01	2.29E-01	0.749	0.454
Ericameria nauseosa	9.71E-17	1.00E+00	0	1
Artemisia filifolia	5.11E-01	4.47E-01	1.142	0.253
Rhus trilobata	1.54E-01	3.78E-01	0.408	0.683
Oxyopidae				
Sarcobatus vermiculatus	1.1236	0.2448	4.59	4.42e-06 ***
Juniperus monosperma	0.7933	0.2171	3.654	0.000258 ***
Ericameria nauseosa	0.1349	0.4305	0.313	0.753985
Artemisia filifolia	0.3435	0.2603	1.319	0.187079
Rhus trilobata	1.0974	0.2169	5.06	4.19e-07 ***
Philodromidae				
Sarcobatus vermiculatus	0.9182	0.111	8.273	< 2e-16 ***
Juniperus monosperma	0.2991	0.1606	1.862	0.06260.
Ericameria nauseosa	0.5296	0.1984	2.669	0.00761 **
Artemisia filifolia	0.5303	0.1121	4.728	2.26e-06 ***
Rhus trilobata	0.2245	0.2234	1.005	0.31498
Salticidae				
Sarcobatus vermiculatus	0.42019	0.09406	4.467	7.93e-06 ***
Juniperus monosperma	0.49198	0.06266	7.851	4.12e-15 ***
Ericameria nauseosa	0.4664	0.11637	4.008	6.13e-05 ***
Artemisia filifolia	0.43839	0.08419	5.207	1.92e-07 ***
Rhus trilobata	0.204	0.09809	2.08	0.0375 *
Thomisidae				
Sarcobatus vermiculatus	0.69315	0.11471	6.043	1.52e-09 ***
Juniperus monosperma	0.08224	0.11471	0.717	0.473414
Ericameria nauseosa	0.55118	0.13019	4.234	2.30e-05 ***
Artemisia filifolia	0.43672	0.12403	3.521	0.000430 ***
Rhus trilobata	0.42744	0.12039	3.551	0.000384 ***

Beta estimates for effect size for differences in abundance for spiders and *p*-values for each spider family to shrub species. Model fit by maximum likelihood (Laplace Approximation) with intercept set to zero and month a random effect.

Table 2.4. Product of Generalized Linear Model with Poisson Distribution with Log Link Function for Pawnee National Grassland.

Spider family and shrub species				
Oxyopidae	**Estimate**	**Std. Error**	**z value**	***P* > z**
Artemisia tridentata	1.1109	0.3276	3.391	0.000695***
Ericameria nauseosa	-0.4669	1.0762	-0.434	0.664393
Atriplex canescens	0.3407	0.8516	0.4	0.689098
Philodromidae				
Artemisia tridentata	3.63E-01	2.09E-01	1.74	0.0818.
Atriplex canescens	4.52E-01	3.02E-01	1.499	0.1339
Artemisia filifolia	6.94E-18	1.00E+00	0	1
Salticidae				
Artemisia tridentata	0.91942	0.28935	3.178	0.00149 **
Ericameria nauseosa	0.05564	1.03961	0.054	0.95732
Atriplex canescens	0.30596	0.2928	1.045	0.29605
Artemisia filifolia	0.86658	0.44298	1.956	0.05044.
Thomisidae				
Artemisia tridentata	6.90E-02	2.58E-01	0.267	0.789
Ericameria nauseosa	1.74E-17	7.07E-01	0	1
Atriplex canescens	1.18E-13	2.13E-01	0	1

Beta estimates for effect size for differences in abundance for spiders and *p*-values for each spider family to shrub species. Model fit by maximum likelihood (Laplace Approximation) with intercept set to zero and month a random effect.

Explanatory Variables

Multivariate analysis showed a significant effect from multiple factors on explaining variation in diversity of spider families for both national grassland sites (Tables 2.5-2.6). ANOVA showed that both shrub and month were significant drivers of spider diversity in CNG (Table 2.5). Shrub (P = 7.37e-05) explained the most variation followed by month (P = 2.00e-07). Year did not significantly influence spider diversity at CNG. ANOVA for diversity of spider families in PNG (Table 2.6) did not indicate significance of variables evaluated.

Table 2.5. Analysis of Variance for Explanatory Strength of Variables on Spider Composition Profiles of Comanche National Grassland.

Variable	Df	Sum square	Mean square	*F*-value	*P* > *F*
Shrub	4	86	21.43	6.087	7.37e-05 ***
Month	4	131	32.73	9.298	2.00e-07 ***
Year	1	5	4.69	1.331	0.249
Residuals	1,543	5,431	3.52		

P value: 0, '***' 0.001, '**' 0.01, '*' 0.05. Elevation, temperature (mean), and precipitation (mean) removed as confounding the model.

Table 2.6. Analysis of Variance for Explanatory Strength of Variables on Spider Composition Profiles of Pawnee National Grassland.

Variable	Df	Sum square	Mean square	*F*-value	*P* > *F*
Shrub	3	28.3	9.429	2.328	0.0755
Month	4	34.5	8.625	2.130	0.0782
Year	1	11.4	11.406	2.817	0.0948
Residuals	211	854.4	4.049		

P value: 0, '***' 0.001, '**' 0.01, '*' 0.05. Elevation, temperature (mean), and precipitation (mean) removed as confounding the model.

DISCUSSION

Analyses suggested spiders discriminate among shrub species in a shortgrass steppe ecosystem. Multivariate analyses demonstrated that shrub species was an important driver of diversity of spider families in the grasslands studied. At Comanche National Grassland, spider diversity, especially for families Salticidae, Philodromidae, Oxyopidae, and Dictynidae, differed significantly among shrub species. At Pawnee National Grassland, there was no significant difference in diversity of spiders among shrubs except for Oxyopidae and Salticidae on *Artemisia tridentata*. Greater environmental variation and increased habitat heterogeneity of shrub species at CNG were related to greater spider diversity compared to PNG. The research further supported that shrub species in shortgrass steppe ecosystems provide habitat for spiders at recognizable spatial amounts of heterogeneity for quantifying diversity. Changes in available shrub habitat might significantly impact spider abundance in the grassland ecosystems and there are various reasons that explain why shrubs are a major factor impacting spider diversity.

Patterns of local spider distribution and abundance might be because of effects of shrub architecture on foraging behavior (Robinson, 1981; Greenstone, 1984; Gunnarson, 1990; Rypstra et al., 1999; Whitmore et al., 2002). Because spiders that use webs require support structure, plant architecture might affect distribution of some spiders. For example, Dictynidae builds small mesh webs, often on small branch points, and Dictynids were abundant on *Sarcobatus vermiculatus* and *Ericameria nauseosa*, both of which have many terminal branches that support webs. Salticidae, Philodromidae, and Oxyopidae do not use webs but actively crawl across foliage and they are also sensitive to variation in plant structure (Abraham, 1983; Romero & Vasconellos-Neto, 2005; Cobbold & MacMahon, 2012). Spiders also can be affected by vertical stratification of habitat (Gunnarson, 1990; Floren, 2005; Jimenez-Valverde & Lobo, 2007; Pinzon et al., 2013). In agroecosystems, such as in orchards, structurally complex sites often support more web-building spiders than less complex sites (Borges & Brown, 2001; Haddad et al., 2005, Stenchly et al., 2011; Hajian-Forooshani et al., 2014). Spider diversity in foliage and canopies of distinct types of temperate forests suggest structural complexity enhances biodiversity (Brierton et al., 2003; De

Souza & Martins, 2005). This analysis may infer that larger shrubs might provide more microhabitat for arboreal spiders than do smaller shrubs. Spiders were most diverse in juniper and big sagebrush, which are taller and denser than other shrub species at CNG and PNG. The greater surface area of the shrubs could increase available microhabitats, providing greater ecological flexibility for co-existence of multiple spider species and increase habitat complexity, allowing different spiders to occupy different niches.

In many cases, multiple genera were observed in specific families and thus further details in habitat association and community assembly may be observed at the genus level. For example, the genera of Salticidae collected at CNG and PNG include *Marpissa*, *Metaphidippus*, *Pelegrina*, *Phidippus*, *Salticus*, and *Sassacus*. These spiders do not make webs but visually hunt prey. Multiple genera of Thomisidae including *Mecaphesa*, *Misumena*, *Misumenoides,* and *Xysticus* on shrubs at CNG and PNG were often flower dwelling and they are predators of pollinators and flower visitors (Dondale, 2005). Thomisidae was more common on *Ericameria nauseosa* than other shrubs at CNG and PNG. *Ebo*, *Philodromus*, *Thanatus*, and *Titanebo* genera in the family Philodromidae were collected at CNG and PNG. Each genus might require specific habitat to forage effectively and interact with preferred prey. Because spider hunting mode affects plant-spider mutualism (Kersch-Becker et al., 2018), DNA barcoding data on spiders and gut analysis might reveal which spiders are habitat generalists or specialists. Attaining such data would indicate patterns of local spider communities, indicate early and late-season phenology, and possibly show trophic systems (Persson, 1999) whether the spiders are preying on insects associated with specific shrubs or feeding types, such as phloem feeders or pollinators.

Diversity analyses provided support that arboreal spiders in these grasslands prioritize specific shrubs and suggested that changes in available shrub habitat might significantly impact spider diversity in grassland ecosystems, which is consistent with similar research with spiders in grasslands and related agricultural habitats (Siemann, 1998; Schmitz, 2009; Prieto-Benitez & Mendez, 2011). Spider family composition on shrubs seldom overlapped with the Colorado spider taxa identified in studies of ground-dwelling spiders from agricultural fields (Kerzicnik et al., 2013) or from PNG (Weeks & Holtzer, 2000), most likely because of differences in the habitat sampled.

Because much habitat in grasslands is composed of grass species, much of what we know of grassland spider ecology is from detection of ground-dwelling taxa. However, some shrub-dwelling spiders appear predominant to specific shrub species. For example, at the Comanche National Grassland, significant differences were found in Dictynidae on *Sarcobatus vermiculatus* and *Ericameria nauseosa*. Additionally, at CNG, Oxyopidae was significant on *Sarcobatus vermiculatus*, *Juniperus monosperma*, and *Rhus trilobata* while Philodromidae was significant on *Sarcobatus vermiculatus, Ericameria nauseosa*, and *Artemisia filifolia*. Shrubs provide potential habitat for spiders that otherwise might not successfully inhabit grasslands because suitable habitat for arboreal spiders in grasslands is restricted. This suggested that changes in available shrub habitat significantly impacted spider diversity in a shortgrass-steppe ecosystem. Without such sampling efforts, documenting changes in local communities will be limited and unable to represent local taxa adequately. Results emphasize the importance of continued surveys at native and altered grassland sites in shortgrass steppe to evaluate changes in grassland ecosystems for development of management strategies and conservation efforts.

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CHAPTER 3: POTENTIAL SPIDER PREY: INSECTS OF DOMINANT SHRUB COMMUNITIES AT PAWNEE AND COMANCHE NATIONAL GRASSLANDS, COLORADO

INTRODUCTION

The Great Plains of North America is historically, one of the largest grasslands worldwide (Knopf & Samson, 1995; Lauenroth et al., 1999; Lauenroth & Burke, 2008) and includes unique plant communities (Samson & Knopf, 1994). Many environmental factors such as seasonal precipitation, drought, fire, and grazing by large mammals affect plant communities in grasslands (Epstein et al., 1997; Stromberg, 2011), with faunal richness largely dependent on species composition, productivity, and habitat structure of plant communities (Lawton, 1983; Strong et al., 1984). A range of animals (Webb 1981) including a large diversity of insects (Ross, 1970) inhabit grasslands of the Great Plains. Examples are leafhoppers (Cicadellidae) (Whitcomb et al., 1986), grasshoppers (Capinera & Sechrist, 1982), and ants (Formicidae) (Whitford et al., 1995). Most insects in grasslands are herbivorous (Chew, 1974) and often-in areas with a mixture of plant species (Samways, 1994). Since European settlement, habitat loss and decrease in species have affected native grasslands of the Great Plains (Samson & Knopf, 1994). After the Homestead Act of 1862, thousands of settlers began plow-based agriculture that depleted topsoil to wind. By the early 1930s, the Midwest was in the Dust Bowl and Great Depression (Engle et al., 2008). The National Industrial Recovery Act of 1933 and Emergency Relief Appropriations Act of 1935 allowed the federal government to purchase and restore damaged land. National Grasslands were classified as managed lands under the Bankhead-Jones Farm Tenant Act of 1937, legislation to develop a program of land conservation and utilization to assist in controlling soil erosion and preserving natural resources (Duram 1995). U.S. National Grasslands played a significant role in grassland conservation and supporting numerous habitats for diversity of species including insects.

The USDA-ARS Central Plains Experimental Range site at the Pawnee National Grassland in northeastern Colorado was established in 1937 on land managed by the Forest Service after drought, overgrazing, and dust storms forced abandonment of ranches and farms (Shoop et al., 1989). The Agricultural Act of 1953 reorganized the USDA and transferred administration of Central Plains Experimental Range from the Forest Service to the ARS. Colorado State University collaborates on research with Central Plains Experimental Range in association with International Biosphere Program and Shortgrass Steppe Long-Term Ecological Research (SGS-LTER). The efforts support research to advance understanding of the structure and function of semiarid rangeland ecosystems. Information on insects at Pawnee National Grassland was from reports of the International Biological Program that coordinated large-scale ecological and environmental studies in separate continental regions. This included the Grassland Biome Project that resulted in some of the first recorded surveys at Pawnee National Grassland. The first report (Jameson, 1969) described numerous plant and animal species but did not list arthropods. Later reports studied insects pertaining to predator and parasite relationships (Lavigne & Rogers, 1970), arthropods below ground (Lloyd & Grow, 1971) and above ground (Dickinson & Leetham ,1971; Lavigne et al., 1972), and plant-insect interactions (Yount & Thatcher, 1972) with updated lists of insects at Pawnee National Grassland (Kumar et al., 1972, 1975, 1976).

The International Biological Program Grasslands Biome Project facilitated reports pertaining to insect orders. Pfadt (1971) provided a description of Orthoptera at Pawnee National Grassland, and other studies examined the effects of biomass for grasshoppers (Van Horn, 1969, 1972). Colorado State University facilitated ecological studies pertaining to Orthoptera such as grasshopper response to grazing and precipitation (Capinera & Sechrist, 1982; Welch et al., 1991) to above-ground plant biomass as a primary food source (Newbold et al., 2014) and how black-tailed prairie dogs affect abundance and diversity of short-horned grasshoppers (Acrididae) on shortgrass steppe (Kenney et al., 2016). For Hymenoptera, Lavigne et al. (1971) and Rogers (1972) investigated the western harvester ant (*Pogonomyrmex occidentalis* (Cresson, 1865) and arthropod predators and parasites including robber flies (Asilidae), spiders (Lycosidae, Salticidae), Carabidae (Cicindelinae), Mantidae, and Sphecidae (s.l). Studies of Coleoptera, included species of Carabidae at Pawnee National Grassland surveyed by Bell (1971), predation of the ground beetle *Pasimachus elongatus* LeConte, 1846 (Ebert & Kondratieff, 1992), and community structure of darkling beetles (*Eleodes* spp. and Tenebrionidae) (McIntyre, 2000). Surprisingly, there are no reports of pollinators at Pawnee National Grassland.

In southeastern Colorado, the Rocky Mountain Southwest Region of the U.S. Forest Service manages Comanche National Grassland that includes Purgatoire Canyon, the longest and deepest canyon in eastern Colorado (Pague et al., 1995). Ecological inventories described plant communities of Purgatoire Canyon including shortgrass prairie, riparian woodlands, and mixed shrublands (Shaw et al., 1989; Johnston & Reed, 1991). In a diversity assessment for the U.S. Army and U.S. Fish and Wildlife Service, Texas AgriLife Research reported a one-season insect survey of the area (Michels et al., 2007). Studies of grasshoppers at Comanche National Grassland included fire disturbance (Nadeau et al., 2006). Additional literature on insects collected at Comanche National Grassland is limited.

Few insects associated with shrub species of the Great Plains have been studied. Insects associated with dominant shrubs were sampled from Pawnee and Comanche National Grasslands in eastern Colorado. Insects were collected as part of a study investigating effects of shrub habitat on arboreal spider richness in Colorado shortgrass steppe. The objective here was to determine the overall composition of insects collected on the native shrubs sampled in order to identify potential prey of arboreal spiders on each shrub species.

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METHODS

Study Locations

Field sites were in Pawnee National Grassland (40.841922, -104.090663) in Weld County in northeastern Colorado and Comanche National Grassland (36.997242, -102.700475) in Baca, Las Animas, and Otero counties in southeastern Colorado that includes a large network of canyons on the High Plains. The dominant shrub sampled at Pawnee National Grassland was four-wing saltbush (*Atriplex canescens*) (Pursh.) Nutt) (Hazlett, 1998). The dominant shrubs sampled at Comanche National Grassland were sandsage (*Artemisia filifolia* Torr.), four-winged saltbush, rabbitbrush (*Ericameria nauseosa* (Pallas ex. Pursh), greasewood (*Sarcobatus vermiculatus* (Hook) Torr.), skunkbush (*Rhus trilobata* Nutt.), and one-seed juniper (*Juniperus monosperma* (Engelm.) (Hazlett, 2004).

Sampling Design

Samples of insects were collected at field sites each month from June to September 2014-2015 by funnel-bucket method (Knutson, 2010) and identified to family or genus, with some taxa identified to species. The sampling technique was especially useful for collecting arboreal spiders and other arthropods but might not effectively sample active fliers such as Diptera, Hymenoptera, and Lepidoptera. Voucher specimens were deposited in the C.P. Gillette Museum of Arthropod Diversity, Colorado State University. Lists of relative abundance of insect families and genera were compiled for Pawnee and Comanche National Grasslands.

Analysis

To isolate dominant insect groups, rank abundance plots for all taxa at a site was reviewed, ordered from least to greatest abundance, and a threshold was set to a ratio for insect families relative to order >0.087 relative abundance for the 20 most-abundant families at each grassland.

RESULTS AND DISCUSSION

At least 360 taxa of insects were collected from six shrub species at Pawnee and Comanche National Grasslands (Table S1). At Pawnee National Grassland, the dominant insects (relative to order) on shrubs (Table 3.1) were Coleoptera including Chrysomelidae, Cleridae, Coccinellidae, and Meloidae. Families of Diptera most commonly collected were Chironomidae, Scenopinidae, and Tephritidae. The most-abundant families of Hemiptera were Cicadellidae, Miridae, and Pentatomidae. Acrididae and Gryllidae were the most-abundant Orthoptera. Aeolothripidae and Thripidae also were common at Pawnee National Grassland. At Comanche National Grassland, the dominant insects on shrubs (Table 3.1) were Chrysomelidae, Cleridae, Coccinellidae, and Phalacridae families of Coleoptera. The most-abundant families of Diptera were Cecidomyiidae, Chloropidae, and Mycetophilidae. For Hemiptera, the most-abundant families were Issidae, Lygaeidae, Miridae, and Reduviidae. Acrididae was the most abundant orthopteran. Aeolothripidae and Thripidae also were common at Comanche National Grassland.

Hemiptera was the most abundant order on shrubs at Pawnee and Comanche National Grasslands. Leafhoppers (Cicadellidae), plant bugs (Miridae), and stink bugs (Pentatomidae) were the most-abundant families on four-winged saltbush at Pawnee National Grassland, with aphids (Aphididae), plant bugs, seed bugs (Lygaeidae), assassin and ambush bugs (Reduviidae), and plant hoppers at Comanche National Grassland. At Pawnee National Grassland, *Cuerna* spp. and other unidentified taxa of Cicadellidae were abundant on four-wing saltbush, a host reported by Nielson (1965). *Lygus* was the most abundant plant bug genus primarily represented by *L. elisus* Van Duzee, 1914, a species known from numerous hosts including chenopods (Fye, 1982). Red-shouldered stink bug, *Thyanta custator* (Fabricius, 1803), also was common on four-wing saltbush at Pawnee National Grassland. The species has a wide range of plant hosts (Oetting & Yonke, 1971).

Hemiptera at Comanche National Grassland were primarily unidentified aphids. The plant bug *Taedia deleticus* (Reuter, 1909) was common on *A. filifolia.* Seed bugs were represented by at least nine genera and Reduviidae by *Phymata* spp. and *Sinea* sp. Caliscelidae was represented by *Bruchomorpha* sp.. The cicada *Hadoa inauditus* (Davis, 1917) was commonly associated with one-seeded juniper at Comanche National Grassland and is widespread throughout southwestern U.S. (Kondratieff et al., 2002; Sanborn & Phillips, 2013). Nymphs are associated with xerophytic trees and shrubs.

Coleoptera was the next most abundant order of insects at Pawnee and Comanche National Grasslands. Chrysomelidae leaf beetles were most diverse and abundant. At Pawnee National Grassland, *Spintherophyta globosa* (Olivier, 1808) was the most abundant leaf beetle and especially on saltbush and rabbitbrush. The genus *Monoxia* was often collected at both grasslands. Riley et al. (2003) listed several species of *Monoxia* in Colorado, but identification to species is difficult. Adults chew leaves and larvae mine leaf tissue (Haws et al., 1988). Other beetle families collected at both grasslands were Cleridae, Coccinellidae, and Meloidae. The predaceous checkered beetle *Phyllobaenus* and blister beetle *Epicauta ferruginea* Say, 1824 were abundant on four-wing saltbush. *Epicauta ferruginea* is considered a common species in Colorado (Schmidt, 2008). At Comanche National Grassland, two common coccinellids in Colorado, *Hippodamia convergens* Guérin-Méneville, 1842 and *H. parenthensis* (Say, 1824) (Gordon 1985) were abundant, associated with aphids on the five shrub species sampled.

Formicidae was collected at Pawnee and Comanche National Grasslands from all shrubs sampled, especially four-wing saltbush and rabbitbrush but also in moderate numbers from other shrubs. Ants were represented primarily by the genus *Formica*, well-known foragers on shrubs of the region (Gregg, 1963). Eight species were identified by Kumar et al. (1976) from Pawnee National Grassland. At Comanche National Grassland, Orthoptera were well represented by Acrididae, primarily *Melanoplus* on the five shrub species, while fewer grasshoppers were on four-wing saltbush at Pawnee National Grassland. The juniper grasshopper, *M. splendidus* Hebard, 1920, was collected on juniper at Comanche National Grassland.

Table 3.1. Dominant Insects Collected at Pawnee and Comanche National Grasslands, Colorado. Based on Insect Rank Abundance Set to a Ratio for Order >0.087.

		Pawnee National Grassland		Comanche National Grassland	
Order	Family	Frequency	Ratio for Order	Frequency	Ratio for Order
Coleoptera	Chrysomelidae	178	0.408	39	0.235
Coleoptera	Cleridae	82	0.188	16	0.096
Coleoptera	Coccinellidae	42	0.096	61	0.367
Coleoptera	Meloidae	75	0.172		
Coleoptera	Phalacridae			15	0.09
Diptera	Cecidomyiidae			2	0.143
Diptera	Chironomidae	4	0.16		
Diptera	Chloropidae			4	0.286
Diptera	Mycetophilidae			2	0.143
Diptera	Scenopinidae	3	0.12		
Diptera	Tephritidae	6	0.24		
Hemiptera	Aphididae			67	0.215
Hemiptera	Cicadellidae	363	0.551		
Hemiptera	Issidae			29	0.093
Hemiptera	Lygaeidae			29	0.093
Hemiptera	Miridae	124	0.188	38	0.122
Hemiptera	Pentatomidae	72	0.109		
Hemiptera	Reduviidae			52	0.167
Hymenoptera	Formicidae	203	0.879	110	0.846
Lepidoptera	Gelechiidae	4	0.091		
Lepidoptera	Geometridae	21	0.477	5	0.278
Lepidoptera	Noctuidae	17	0.386	5	0.278
Lepidoptera	Pyralidae			4	0.222
Lepidoptera	Tortricidae			3	0.167
Mantodea	Mantidae	1	1	10	1
Neuroptera	Chrysopidae	1	1	1	1
Orthoptera	Acrididae	20	0.8	118	0.952
Orthoptera	Gryllidae	5	0.2		
Thysanoptera	Aeolothripidae	1	0.143	2	0.1
Thysanoptera	Thripidae	6	0.857	18	0.9

Insect surveys of grasslands usually include taxa associated with grasses and forbs but not species of shrubs. This is the first study reporting insects from six grassland shrubs at Pawnee and Comanche National Grasslands in northeastern and southeastern Colorado. At both study sites, local species collected suggested that insect diversity differed depending on shrub habitat. However, more trapping methods would need to be used and insects would need to be identified to species level to effectively assess insect diversity. Regardless, this analysis shows that insect diversity and abundance differed between the two grasslands. I found that Chrysomelidae, Cicadellidae, Cleridae, Formicidae, Meloidae, and Miridae were abundant at Pawnee National Grassland, primarily from four-winged saltbush (*Atriplex canescens*) (Pursh.) Nutt). Acrididae, Aphididae, Chrysomelidae, Cleridae, Coccinellidae, Formicidae, Lygaeidae, Miridae, and Reduviidae collected from sandsage (*Artemisia filifolia* Torr.), four-winged saltbush, rabbitbrush (*Ericameria nauseosa* (Pallas ex. Pursh), greasewood (*Sarcobatus vermiculatus* (Hook) Torr.), skunkbush (*Rhus trilobata* Nutt.), and one-seed juniper (*Juniperus monosperma* (Engelm.) were abundant at Comanche National Grassland.

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CHAPTER 4: HABITAT PARTITIONING OF ARBOREAL SPIDERS OF NATIVE SHRUBS AT COMANCHE NATIONAL GRASSLAND

INTRODUCTION

Ecological communities are often measured though interactions of species and their environment. Communities can be measured in how diversity changes within a local habitat (alpha) or by changes in composition between different habitats (beta) and suggest species coexistence and persistence of certain species in an area (Whittaker, 1972; Leibold et al., 2010). Habitat partitioning (niche segregation) of species to local habitat can also suggest broader community structure in an ecological system. For example, variation of local vegetation can provide increased habitat complexity since a greater amount of structure will provide more resources, habitats and niches (McCoy & Bell, 1991), thus altering communities within a local area, and allowing us to understand niche parameterization from community assembly patterns (Hutchinson, 1957; Futuyma & Moreno, 1988) and suggesting environmental thresholds for species (Oviedo et al, 2018; Villanueva-Bonilla et al, 2019). In this way, the different environments and habitats a species is able to occupy reflect the conditions the species can tolerate across both abiotic and biotic gradients. This variation in habitat use across environmental gradients can be measured in how habitat heterogeneity increases species diversity across recognized environmental gradients (Riesch et al., 2018) and across spatial scales (Tews et al., 2004; Tamme et al., 2010). In contrast, species specialization (Gaston, 1997) can indicate limited niche breadth, which often affects species more at risk of local extinction than generalist species (Sexton et al., 2017; Carscadden et al., 2020). Understanding these environmental tolerances and thresholds can be used to determine how species coexist in communities and indicate the spatial configuration of habitat for local species and retention of community complexity.

The semi-arid shortgrass steppe lies on the western edge of the central grassland region of North America and includes drought tolerant grasses and occasional woody species (Lauenroth et al., 1999;

Gibson, 2009). The Colorado shortgrass steppe consists of a mosaic of plant communities that include shortgrass, mixed grass prairie, riparian woodlands and shrublands (Stevens et al., 2008). A unique, but critically important habitat component of grassland ecosystems are the native shrubs, which provide additional habitat complexity in the shortgrass steppe. and the primary woody shrubs found there are sandsage (*Artemisia filifolia* Torr.), rubber rabbitbrush (*Ericameria nauseosa* Pall. ex. Pursh) and greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.). Fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.), which is highly tolerant to drought and salinity, is also common (Tilley & John, 2013).

Grassland shrubs, which are limited in landscape location by environmental factors such as soil type, temperature, and moisture gradients, may serve as ecological indicators. Ecological indicators are biological assemblages or taxa that, by their presence or condition, indicate something about the environment. They are often used for environmental monitoring and can reflect changes in ecosystems such as capacity of populations or density of land-use change. Indicators make it possible to reduce ecological factors to a small number of estimated parameters. Due to their niche preferences, they are often used to suggest how species are associated with habitats or ecological community types (Dufrene & Legendre, 1997; Carignan & Villard, 2002) to study how species are associated with habitats.

Arthropods occupy specific microhabitats within an ecological community, including on shrubs, and perform diverse ecological roles (Burger et al., 2003). In particular, spiders are excellent models for ecological study as they are generalist predators, are prey for arthropods and vertebrates, and they are highly abundant in many ecosystems. They are also a highly diverse taxonomic group, with a deep evolutionary history (Garrison et al., 2016) allowing for specialization in hunting, foraging, and defense strategies (Uetz, 1992; Richardson & Hanks, 2009). Unlike insects, which can quickly disperse by flying and so require multiple trapping methods, most spiders in an ecosystem can be collected with basic pitfall or bucket sampling methods.

Spiders in grasslands have shown a high degree of species overlap among habitats which can be further tracked and spatially separated (Uetz & Unzicker, 1976; Robinson, 1981). This overlap may be due to their response to the habitat complexity and to specific spider habitat requirements through their life stages. Due to this specialization, the presence of certain spiders may suggest associations with their physical habitat, interactions with other arthropods, temperature tolerances, or other habitat features. Previous studies have shown that spider abundance changes with habitat configuration, such as in the sagebrush steppe in Utah (Abraham, 1983; Cobbold & MacMahon, 2012). However, the effect different shrub species have on local spider community assembly processes is little studied. Given the extensive time that North American grasslands have developed along temperature and moisture gradients, native plants would presumably harbor endemic spider species that can serve as indicators for grassland ecosystems.

Spider distribution may vary with topographic variation because resource conditions vary along such gradients. (Ayyad & Dix, 1964; Svenning, 1999; Harms et al., 2001; Gunatilleke et al., 2006). Thus, habitat complexity of shrubs in grasslands may allow spiders to segregate in the grassland habitats. To understand how local plant community complexity affects spider communities, I addressed two main objectives. First, I evaluated whether shrub species were associated with certain elevations within canyons. I predicted that elevation within each canyon would delineate vegetation into habitat regions, specifically, the steppe, cliff, and lower canyon regions. Then I tested whether spider communities differed by local shrub species or community. I predicted that if local plant community structure increases habitat complexity, then greater variation in spider community composition would be observed through specific spider-shrub habitat associations.

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[11] For submission to Ecological Indicators

METHODS

Study Area

The Comanche National Grassland (CNG) is in southeastern Colorado and includes a large network of canyons imbedded within the shortgrass steppe region. The study area was selected due to its limited disturbance either by public access or by use for cattle grazing. Due to the availability of multiple adjacent canyons in close proximity, the study area also allowed for replicated survey with a high number of individuals of different shrub species available for sampling. Picture (Chorizo Unit), Vogel, Withers, Minnie, No-Name, and Iron canyons (Timpas Unit) were used for the study (Figure 4.1).

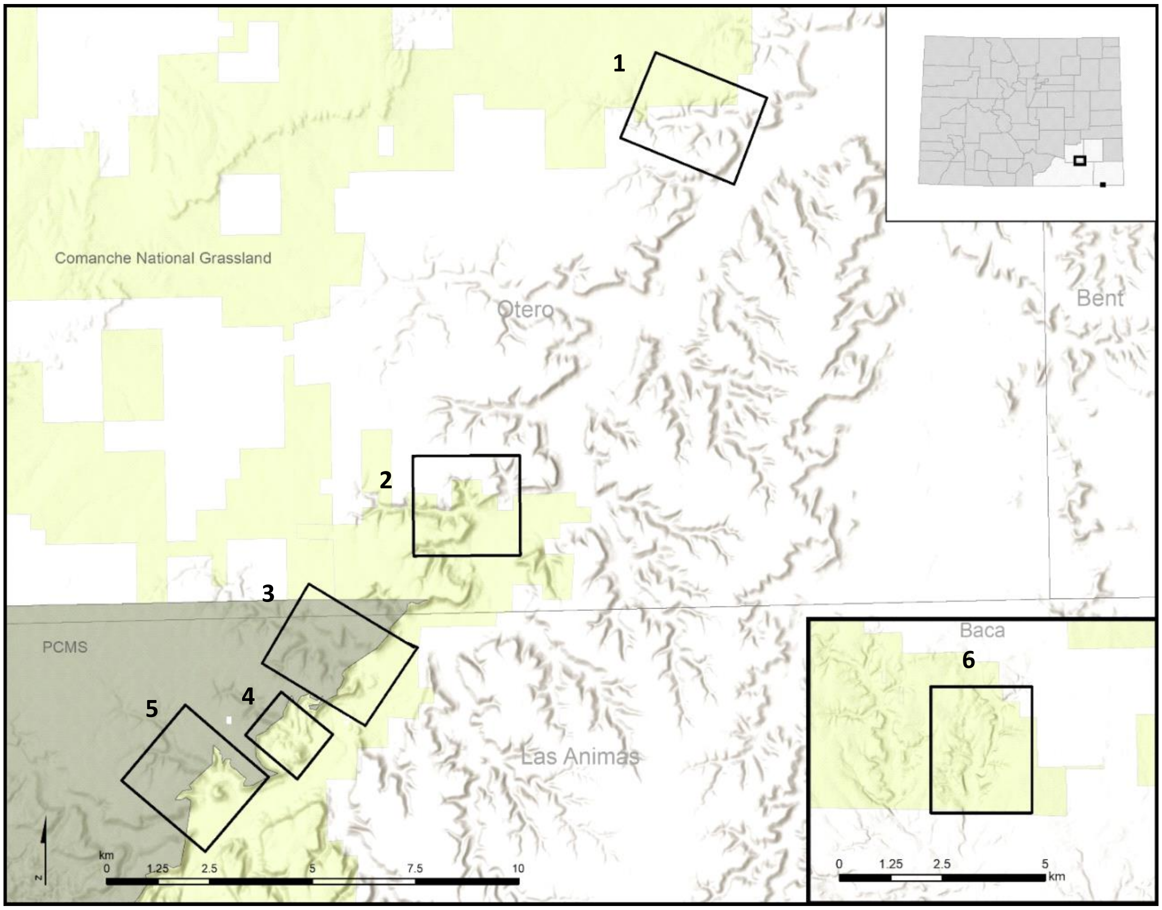

Figure 4.1. Comanche National Grassland study areas (locator map upper right). Vogel (1), Withers (2), Minnie (3), No-Name (4) and Iron (5) canyons with Picture canyon (6) displayed in insert map.

In the Comanche National Grassland, the plant communities include the native shrubs sand sagebrush (*Artemisia filifolia* Torr.), rabbitbrush (*Ericameria nauseosa* (Pall. Ex. Pursh)), greasewood (*Sarcobatus vermiculatus* Torr.) skunkbush sumac (*Rhus trilobata* Nutt.) and a juniper complex composed of Utah juniper (*Juniperus monosperma* (Torr.) Little) and one-seed juniper (*Juniperus monosperma* (Engelm) Sarg.) (Hazlett, 2004).

Sampling Design

Monthly sampling of shrubs occurred May-August of 2014-2017 by funnel-bucket method (Knutson, 2010). On each sampling date, a target of 40 individual shrubs of each plant taxon were sampled at each sampling site. Shrub species were selected based on their abundance in each canyon. An elevation gradient-based survey method was selected across wide transects encompassing the width of each canyon. There was no evidence of excessive grazing or motor vehicle activity in canyons selected for sampling. Sampling occurred on United States Forest Service (USFS) lands for all canyons, as well on Piñon Canyon Maneuver Site (PCMS) property for parts of Minnie, No Name and Iron canyons.

Canyon Parameterization

To collect data on the variation of elevation for individual canyons of CNG, 10-meter Digital Elevation Models (DEMs) of the CNG study areas were constructed in Geographic Information System (GIS to derive slope rasters in ArcGIS 10.5 (Figure 4.2a). A Topographic Position Index (TPI) algorithm (Jenness, 2005) was then used to compare the elevation of each cell in a DEM to the mean elevation of a specified neighborhood around that cell. This further isolated individual canyon topography from the canyon floor bottom to the upper canyon regions as three landform categories (upper canyon steppe, cliff region, bottom canyon region) (Figure 4.2b). Thresholds were selected to remove small areas of isolated variation in elevation that were not directly connected to the individual canyons. Individual canyon data were then extracted for analysis of individual canyon DEMs in ArcGIS 10.5 (Figure 4.2c).

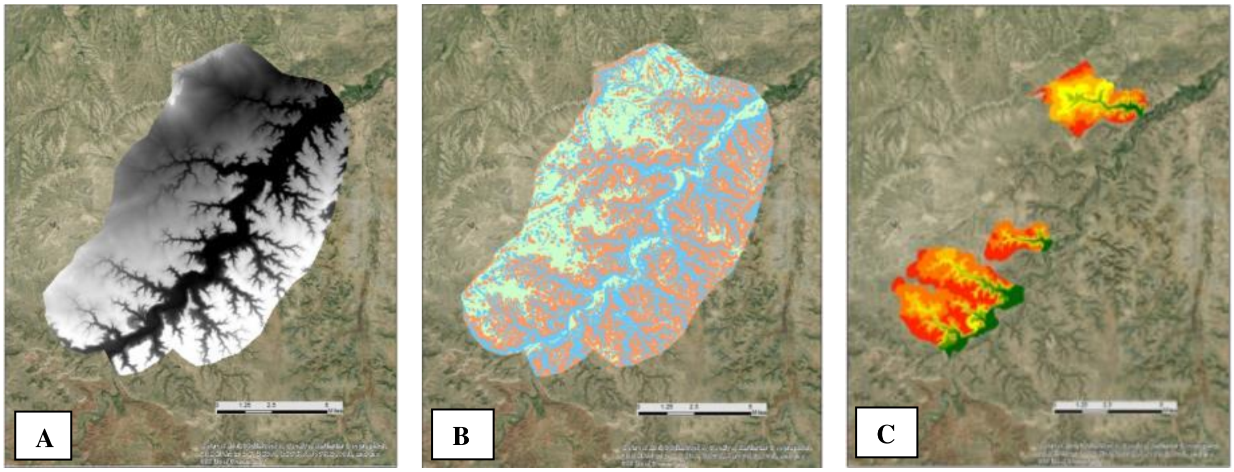

Figure 4.2. Intermediate steps for quantifying the elevation in individual canyons of Comanche National Grassland, Colorado, Timpas Unit. A. Digital Elevation Model (DEM) subset. B. Topographic Position Index for three landform classes: to define canyon regions. C. Separate canyons DEM (restricted to 15 elevation classes).

Spider Identification

Adult spiders were identified to genus or species (Ubick et al., 2005 and primary literature); immatures were identified to family or genus when possible. An Olympus SZX12 microscope was used for sorting and identification.

Data Analysis

Since different analyses function to highlight rarity in samples more while other methods function better for commonness, and because the data structure for this research was confined to spider family level, multiple methods for testing how local CNG plant communities affect spider communities are compared. I selected the *multipatt* function (multilevel pattern analysis) in the R package *indicspecies* to examine group combinations to indicate which spiders were more associated with groups of sites or habitats. Spider families were assigned to the groups of shrubs for which they achieved the highest Indicator Value (IndVal); this method therefore provides a measure of exclusiveness (Dufrene and Legendre, 1997; De Cáceres et al., 2012; De Caceres, 2020). Significance of the relationship between taxa and habitat was based on permutation tests to estimate p-values. Currently, the default of *multipatt* uses an extension of the original Indicator Value method by selecting for both individual site groups and combinations of site groups (De Cáceres et al, 2012). ISA is also sensitive to rare taxa groupings, estimates strength of associations with a priori groups of interest and a randomization test to evaluate the probability of association.

I selected the R package *vegan* (Oksanen et al., 2016) and used Hierarchical Clustering Analysis (HCA) with a Spearman correlation coefficient to examine group combinations (Torondel et al., 2016) of the spider family data grouped by shrub species, which creates a tree based on the similarities of pairwise distance between all data points. For the purposes of my research, I used spider family level data and shrub species group combinations. For HCA, a correlation coefficient measures the extent to which two variables tend to change together. The coefficient describes both the strength and the direction of the relationship. I used the Spearman correlation coefficient, which is based on the ranked values for each variable instead of the raw data. The resulting output was displayed with a dendrogram instead of cluster assignments. The data matrix was clustered by Spearman correlation distances and hierarchical clustering produced a nested sequence of clusters. A dendrogram was created where branches in the dendrogram represent the similarities in Spearman correlation distances. HCA builds a hierarchy of clusters without having fixed number of clusters. It is also effective in comparing spider-shrub habitat association for all spider families and a better option for common species groups.

I also compared habitat use among spider families to local shrubs through Random Forest (RF) (Breiman, 2001) with a Mean Decrease in Accuracy (MDA) (Breiman, 2001; Strobl et al., 2007) which constructs and combines multiple decision trees to make predictions through a non-linear classification algorithm. The MDA measures the decrease of accuracy when the values of a given covariate are permuted, thus breaking its relation to the response variable and to the other covariates. Variable importance according to Mean Decrease Accuracy of the Random Forest classifier was set for the top predictor spider families associated with shrub species for Comanche National Grassland, Colorado This means a high decrease of accuracy indicates that the considered covariate has a strong influence on the prediction. I also used a Discriminant Analysis of Principal Components (DAPC) a multivariate method to identify and describe clusters of related individuals (Pritchard et al., 2000; Jombart et al., 2010).

Finally, I examined the spider genera to shrub species and compared the variation in spider genera at each canyon of Comanche National Grassland.

RESULTS

Shrub-Elevation Gradient

Different shrub species occupied distinct regions of the canyons. The elevation range and shrub species sampled are shown in Figure 4.3 (see also Figure S10). Juniper was present across the entire elevation range for each canyon, although was not common at the canyon bottom. Skunkbush (*R. trilobata*), occupied an intermediate elevation range, common in high slope areas and often near steep canyon walls. Greasewood (*S. vermiculatus*), rabbitbrush (*E. nauseosa*) and sandsage (*A. filifolia*) were present almost exclusively at the bottom of the canyons. Picture and Vogel canyons have the least variation in elevation while No Name and Iron canyons have the most variation in elevation.

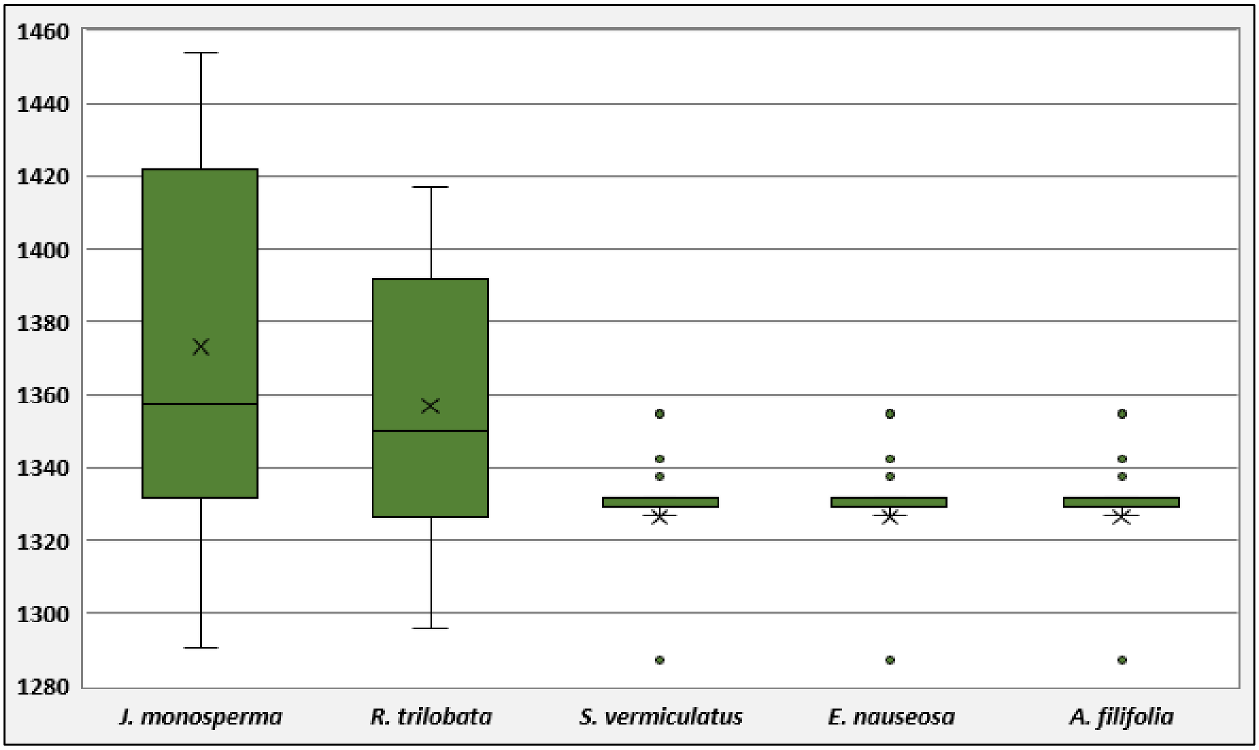

Figure 4.3. Boxplot for mean elevation range (meters a.s.l. on y axis) for shrub species sampled at Comanche National Grassland: juniper (*J. monosperma*), skunkbush (*R. trilobata*), greasewood (*S. vermiculatus*), rabbitbrush (*E. nauseosa)*, sandsage (*A. filifolia)*. The box plots represent data spread for shrub species. Bars represent median value, x represents the mean, and the error bars and dots display the minimum and maximum of data.

Multilevel Pattern Analysis

Multilevel Pattern Analysis showing spider habitat association for CNG is presented in Table 4.1. The analysis indicated specific spider families responded to combinations of local shrub communities differently. Dictynidae and Philodromidae were highly associated with greasewood (*S. vermiculatus*), rabbitbrush (*E. nauseosa*), and sandsage (*A. filifolia)*. These shrubs were typically found only at the bottom of canyons. A notable lack of association was found with skunkbush, which is found primarily on the steep sides of the canyons. Additional information for individual canyons is available in Tables S2.

Table 4.1. Multilevel Pattern Analysis showing the habitat association of spider families with native shrubs in Comanche National Grassland, Colorado. Spiders were assigned to the groups of shrubs for which they achieved the Indicator Value (IndVal) as described in Dufrêne & Legendre (1997), De Caceres et al., (2012) and De Caceres (2020). The statistical significance of this relationship was tested using permutation tests to estimate p-values. Significance of the relationship between species and habitat was based on permutation tests using 999 random permutations to estimate p-values.

Group	**IndVal**	**p value**
juniper		
Agelenidae	0.185	0.101
rabbitbrush+ skunkbush		
Eutichuridae	0.229	0.076
greasewood+ rabbitbrush		
Dictynidae	0.456	0.005
greasewood+ rabbitbrush+ sandsage		
Philodromidae	0.476	0.002
greasewood+ juniper+ skunkbush+ sandsage		
Oxyopidae	0.471	0.038

Hierarchical Clustering Analysis

Hierarchical clustering analysis revealed habitat association to shrub taxa for many spider families for CNG (Figure 4.5). For example, Dictynidae was associated with greasewood and rabbitbrush and Philodromidae was associated with sandsage. Similarly, some were associated with shrubs found at higher canyon elevations, such as with Salticidae and Agelenidae, which were highly associated with Juniper, while Oxyopidae was highly associated with skunkbush. The tree above the heatmap indicates that Dictynidae and Philodromidae habitat use was similar and that Salticidae and Agelenidae habitat use were similar. The tree on the left of the figure indicates a separation of habitat use for spider families associated with shrubs found at higher canyon elevations compared to those that are found in the canyon bottom area. Based on the HCA, there were at least two recognizable communities of arboreal spiders in the sampling areas of CNG. One region was with juniper and skunkbush, while the other habitat region was confined to the canyon bottom.

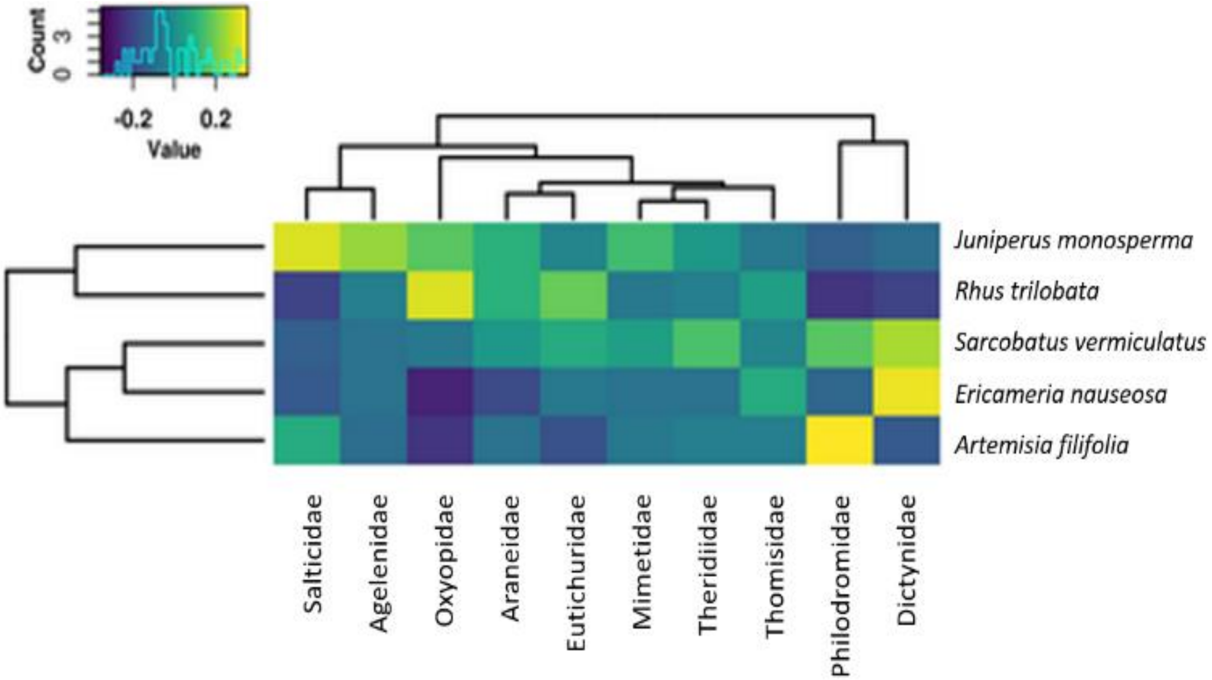

Figure 4.5. Correlation heatmap (Index: Spearman) with dendrograms generated from hierarchical clustering analysis for spider family-shrub association for Comanche National Grassland, Colorado. Color bar indicates level of standardized value. Matrix of eigenvalues with brightest colors (yellow) indicating highest abundance between all combinations in local plant community. The data matrix is clustered by Spearman correlation distances. Hierarchical clustering produces a nested sequence of clusters. Branches in the dendrogram represent the similarities.

Random Forest

The Random Forest analysis of spider families to shrub species as mean decrease accuracy (Figure 4.6) indicates habitat association for Salticidae and Oxyopidae with juniper. There was also habitat association specifically for Philodromidae and Dictynidae with the shrub species greasewood, rabbitbrush and sandsage. Araneidae and Thomisidae were associated with greasewood and juniper to a lesser degree. Unlike the analyses used above, habitat association was not reflected for the spider families Agelenidae or Thomisidae to any specific shrub species. The Random Forest analysis also suggests habitat association for Eutichuridae with sandsage and for Mimetidae with juniper at CNG.

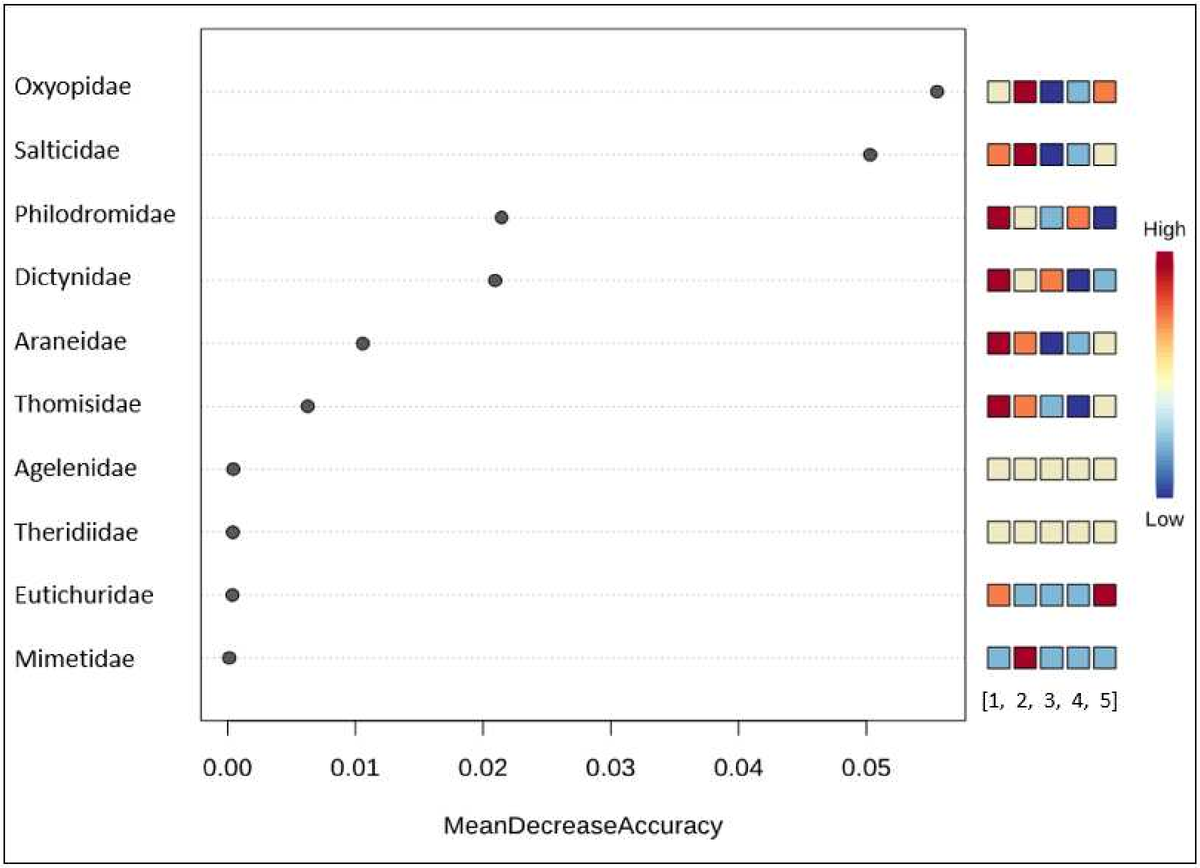

Figure 4.6**.** Variable importance according to Mean Decrease Accuracy of the Random Forest classifier for the top predictor spider families associated with shrub species for Comanche National Grassland, Colorado. The colored columns to the right of the figure display the variations in individual shrub peak intensities compared between groups 1. greasewood (*S. vermiculatus*), 2. juniper (*J. monosperma*)*,* 3. rabbitbrush (*E. nauseosa*), 4. sandsage (*A. filifolia*), 5. skunkbush (*R. trilobata*). The Mean Decrease Accuracy plot expresses how much accuracy the model loses by excluding each variable in this case, with higher values indicating importance of shrub species in predicating occurrence of a given spider family.

Discriminant Analysis of Principal Components

Discriminant Analysis of Principal Components (DAPC) of CNG spider family data (Figure 4.7) suggested that spider communities on sandsage, greasewood, and rabbitbrush, which were at canyon bottoms, differ from juniper and skunkbush, which are not limited to the canyon bottoms. Of these, rabbitbrush was most distinct, with almost no overlap with juniper and skunkbush.

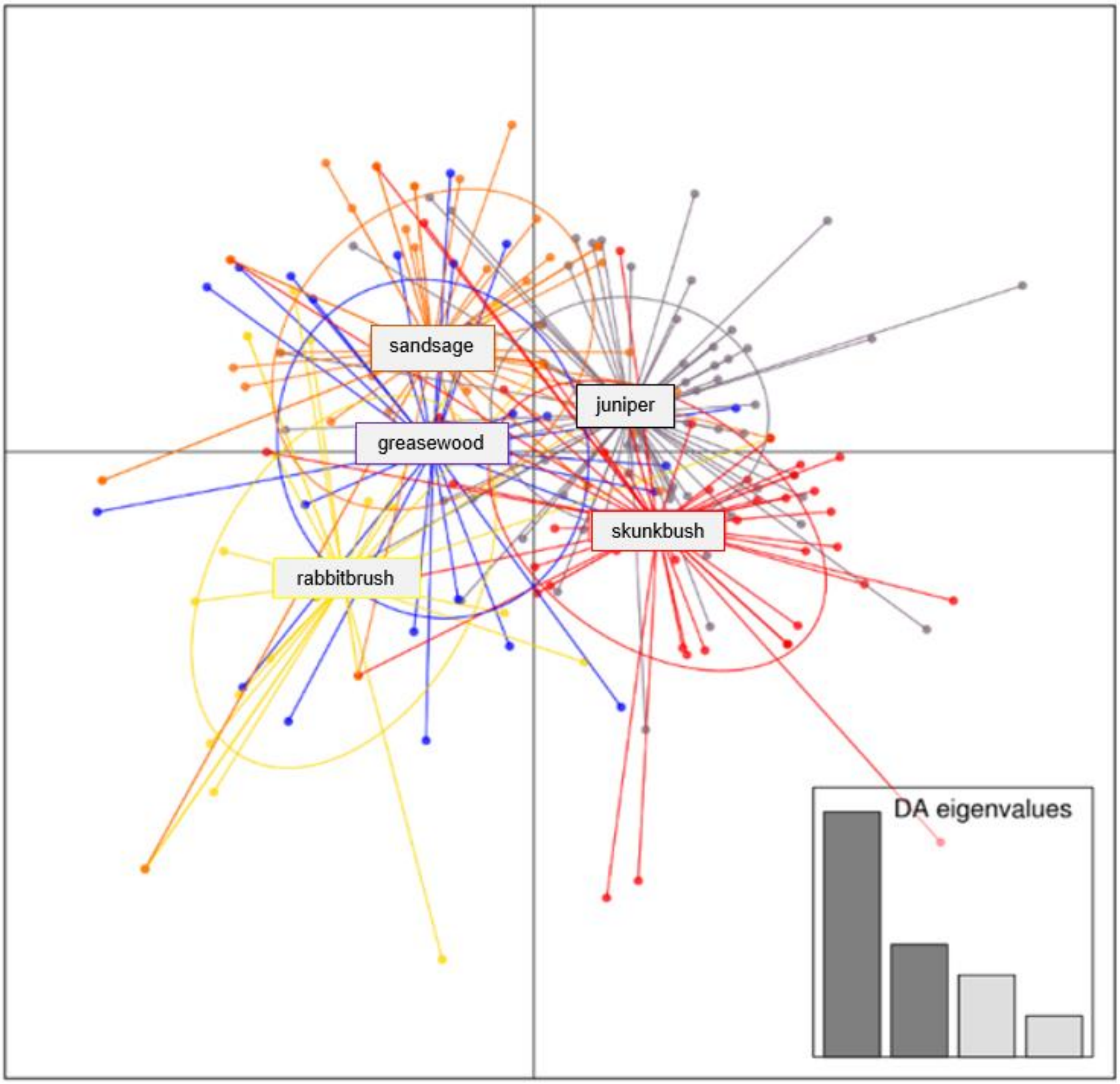

Figure 4.7. Discriminant Analysis of Principal Components (DAPC) scatter plot for spider family count data grouped by shrub by canyon-sample date at Comanche National Grassland. Variance in samples is partitioned into between-group and within-group components. Individuals are represented as dots and the groups as inertia ellipses. The axes represent the first two discriminant functions. Shrubs: juniper (*J. monosperma*) (grey), skunkbush (*R. trilobata*) (red), greasewood (*S. vermiculatus*) (blue), rabbitbrush (*E. nauseosa*) (yellow), and sandsage (*A. filifolia*) (orange).

Spider Genera-Shrub Species Combination

Of the 87 observed spider genera-shrub combinations, only six were observed in all six sampled canyons (Table S3). Of these, there were 20 spider genera found on juniper and five genera (*Neoscona,* *Dictyna, Oxyopes, Phidippus, Mecaphesa*) were conserved across all six canyons and another four combinations were observed across five of the six canyons, meaning that about half of the shrub-genera combinations observed were present in all or nearly all of the canyons sampled. These spider-juniper combinations included genera from seven different spider families. Similarly, five spider genera (*Cheiracanthium, Dictyna, Oxyopes, Phidippus, Mecaphesa*) observed, were found with skunkbush in at least five of the six canyons sampled. Together, these observations suggest that niches for these diverse genera are consistently present and colonized by spiders in juniper and skunkbush in these canyons.

There was more variability of spider genera in two of the shrub species found primarily on the canyon bottoms. Sandsage was the only shrub found at the bottom of all six canyons and of the 17 genera of spiders found on this shrub, none were found in all six canyons and only three genera (*Dictyna, Philodromus, Phidippus*) were found in five of the six canyons. Rabbitbrush was found in five of the six canyons and of the 14 spider genera captured from rabbitbrush, only one genus (*Phidippu*s) was found in all five canyons. There were 19 spider genera found on greasewood in these two canyons, and nine were found in both canyons. Seven genera from four different families were only captured from Minnie canyon and of these, six were on canyon-bottom shrubs, with five of the genera (*Ebo, Titanebo, Dendryphantine, Salticus, Xysticus*) only captured from greasewood, suggesting that greasewood provides a unique habitat not replicated by other shrubs. It appears that canyons with more variation in elevation provided increased available shrub habitat and resulted in greater complexity of arboreal spider communities.

DISCUSSION

High biodiversity is often associated with high environmental complexity (MacArthur & Wilson, 1967) or heterogeneity (Pickett & Cadenasso, 1995). To preserve biodiversity in an area, understanding how diversity is affected by different management strategies is required. However, sampling all species in a region when assessing management strategies is not feasible, so establishment of indicator species is important for development of ecosystem management. I found that shrub occupancy can indicate patterns in spider composition. Spiders are highly abundant locally and diverse with specialization for foraging behavior and hunting strategy, and spiders, in turn, are indicators of arthropod communities and habitat use in grasslands (Wise, 1993). Spiders on shrubs can also efficiently be captured with a single method since they do not fly. All of these characteristics, along with their deep evolutionary divergence, make spiders excellent models for ecological testing.

Indicator species can be used to identify community types, habitat conditions, or environmental changes (Carignan & Villard, 2002). Indicator species are usually determined using an analysis of the relationship between the observed presence–absence or abundance values in a set of sampled sites (Dufrene & Legendre, 1997). Often groups of sites in the classification may represent distinct characteristics of the ecosystem, such as habitat or community types or environmental states (De Cáceres et al., 2012). Thus, indicator species analysis allows characterization of environmental preferences of target species. In some instances, the presence of specific taxa can be predicted by the presence of other taxa, however, variation in study sites, and spatial scales can limit predictions (Rodrigues & Brooks, 2007; Yanahan & Taylor, 2014). Other characteristics can include climate, topography, or plant communities (Cleland et al., 1997). Plant communities in these grassland systems provide unique local shrub communities that can act as indicators for arboreal spider diversity and community structure. Here, I examined the relationship between the local plant community and the arboreal spider community and found that spider families segregate between shrub species, across habitat zones in canyons. The different shrub species provide potential niche differentiation, which has influence on diversity, density, and distribution of spider taxa (Greenstone, 1984; Gunnarson, 1990; Uetz, 1991). These shrub associations could be due to shrub structure, prey availability, and/or microclimate differences and were apparent at the spider family level (Cutler et al., 1977; Robinson, 1981; Greenstone, 1984; Vasconcellos-Neto et al., 2007).

Spiders respond to habitat differences at multiple spatial scales (Rypstra et al., 1999). However, the degree to which spatial heterogeneity affects diversity may be highly dependent on spatial scale (Pickett & Cadenasso, 1995) and may vary between species depending on whether structural attributes are viewed as fragmented (Tews et al., 2004). Both the Hierarchical Cluster Analysis and the Discriminant Analysis of Principal Components (DAPC) indicated that distinct spider communities were associated with local plant communities found at different elevations. In addition, the different community analyses techniques used, which vary in sensitivity to taxa rarity, also all showed habitat association of spiders with specific shrub species. Collectively, these analyses showed that different spider taxa were associated with shrubs predominantly located on canyon bottoms compared to those associated with juniper and skunkbush, which are found at higher elevation regions of canyons. These trends suggest that the spider communities are defined by the shrub species within these canyons. Larger shrubs may provide more habitat complexity than smaller shrubs. Spiders were most diverse in juniper which is taller than other shrub species at CNG. While juniper and sandsage had higher density than greasewood. The greater surface area of the shrubs could increase available microhabitats, providing greater ecological flexibility for co-existence of multiple spider species and increase habitat complexity, allowing habitat partitioning.

The complexity in habitat conditions provided by shrubs in grasslands offer unique niche conditions that allow spiders to segregate. Niche segregation of species to local habitat, can suggest broader community structure in an ecological system. Thus, habitat complexity of shrub species in CNG allow spiders to segregate in the grassland habitats. Differences in environmental factors such as differences in diversity from spatial environmental heterogeneity (Tilman, 2004) drive the distribution of species and therefore alter the composition of communities (Hutchinson, 1958; Gravel et al., 2006). Habitat partitioning of species to local habitats can suggest broader community structure in an ecological system. The variation in resources, habitats, or environments used by a species can alter community complexity across environmental gradients. Identifying these patterns can allow us to predict habitat suitability for conservation use (Liu et al., 2005; Chefaoui et al., 2005). In this case, the canyons created environmental gradients that affected shrub position, and in turn, affected which spider taxa were likely to be present. The habitat heterogeneity of the plant communities influenced the distribution of arboreal spiders. However, other factors such as the shrubs' structure can affect spider occupancy. Certainly, differing local temperature and moisture gradients would also affect the position of the shrubs in a landscape as well each, offering different available niche conditions. During each field season in the canyons at Comanche National Grassland, I observed that skunkbush grew in regions near the cliff slope (above and below) that promoted moisture runoff and accumulation. seems to benefit from partial shadow and areas where moisture can settle, either at cliff boundaries or near large junipers. Interestingly, juniper appears large enough in volume to create its own microclimate. I often observed dense leaf litter under juniper, which presumably allows further saturation during summer rainfall events but also enough spatial area to collect morning dew and retain cooler temperatures. This appears to indicate a level of spatially relevant microclimate impacting the spider habitat.

Since different local species utilize different kinds of habitat and how plant assemblages are expected to shift in response to climate change (Williams & Jackson, 2007), conservation efforts require identification of taxa vulnerable to habitat loss (Fahrig, 2001). For grasslands this includes increased seasonal and annual temperatures and altering local precipitation trends (Finch, 2012). For instance, drought is likely to lead to loss of habitat in grassland ecosystems which could alter the distribution and composition of shrubs, which could then be used to predict effects in arthropod distribution in these arid lands. Such trends emphasize the importance of data collection and categorizing interactions between arthropods and plants to predict potential outcomes of climate change (Brantley & Ford, 2012). Documenting these interactions will improve habitat suitability predictions and development of management protocols.

Although I could not analyze my data at the genus level, trends were still evident. Although results varied among the analyses, there was considerable conservation in which genera were found in the six different canyons (Table S2). For example, three of the five shrubs were found in all canyons sampled and of the 53 spider-shrub combinations observed, 17 were found in at least five of the six canyons, suggesting that similar niches are consistently filled by the same genera, even in canyons separated by considerable distance. In contrast, greasewood was sampled in only two of the canyons and six spider genera were found on greasewood in only one of the canyons. This suggests that canyons that lack greasewood also lack important spider habitat and have reduced spider diversity and hints at the magnitude of diversity loss if even one shrub species is missing from an environment.

This research provides one of the first detailed habitat specific community analyses for arboreal spiders of native shrubs in grasslands of the shortgrass steppe and this work may support identification of habitat necessary for maintaining community structure for multiple predator-prey species in this system. Since spider habitat is restricted, habitat associations can be used to indicate specific spider community assembly and suggest transitions between habitat zones. By measuring habitat heterogeneity effects (shrub composition), patterns of arboreal spider community assembly may be used to identify specific habitat that suggest ecological niche overlap (Broennimann et al., 2011). Given the expected change in global climate, understanding the impact these changes have on target species begins with knowledge of their current position and habitat use in an ecological system. Due to this, ecological monitoring of indicator taxa, such spiders of shrub species in grassland systems, can assist with future grassland conservation efforts and promote effective management planning.

Through this research, I have shown that arboreal spiders in grassland shrubs can be used as a model for predicting niche partitioning and habitat specialization through frequencies in abundance and community composition patterns. Ecologically marginal species may tend to be less tolerant to changes in ecological conditions leading to restricted distributions (Brotons et al., 2004). Species-habitat relationships are also sensitive to the spatial scales at which they are evaluated (McGarigal et al., 2016; Chase et al., 2019). Native shrub occupancy in grasslands is finite, and thus is the available habitat for shrub dwelling spiders. In a restricted local space, shrub species in grassland landscapes may be abundant and dense in an area and then become more fragmented, intermixing with other plant species that will possess their own habitat restrictions. Abundance and distribution of shrubs is limited, and thus, arboreal spider distribution in these grasslands restricted Arboreal spider habitat use in grasslands makes a data-rich ecological system to study niche partitioning and community structure interactions. This model ecological system could also suggest past vegetation gradients along riparian habitat now since transformed. Globally, community patterns of spider-habitat associations may be found in similar grassland-shrub environments.

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CHAPTER 5: HABITAT COMPLEXITY AND COMMUNITY STRUCTURE OF ARBOREAL SPIDERS IN GRASSLAND-SHRUB SYSTEMS

SUMMARY

My first research question addressed how different grassland shrub species affect arboreal spider diversity. To study how habitat complexity can affect species diversity for arboreal spiders in grasslands, I hypothesized that plant type (shrub species) will affect habitat availability of arboreal spiders. I predicted that significant differences in diversity of arboreal spiders will be observed between shrub species. To evaluate this, I first tested explanatory strength of different variables on spider composition profiles using Analysis of Variance (ANOVA). At Comanche National Grassland, spider diversity within *Sarcobatus vermiculatus* and *Juniperus monosperma* was significantly higher as compared to other shrubs sampled. For PNG, the highest diversity was observed in big sagebrush compared to *Atriplex canescens*, *Ericameria nauseosa*, and *Artemisia filifolia,* although no significant differences were determined among shrub species. Tests for explanatory variables between National Grassland sites for spider diversity between shrubs showed that at Comanche National Grassland, shrub species and month were significant explanatory factors.

High biodiversity is often associated with high environmental complexity (MacArthur & Wilson, 1967) or heterogeneity (Pickett & Cadenasso, 1995). But one aspect of the environment may be important to one group of organisms but may not be important to another group (Tews et al., 2004). Due to this, data analysis is necessary concerning the ecological requirements of species (niche) to predict how the environment influences their diversity. Often, diversity indices (mathematical measures of species diversity in a community) are used to study ecological communities (species number, composition). The Shannon-Wiener index (H') considers species richness and proportion of each species within the local community. In this way, diversity indices provide information about rare and common species in a community. To preserve biodiversity in an area, understanding how diversity is impacted by different management strategies is required. The ability to quantify diversity in this way is a key step to understanding spider community structure. Different components of shrub habitat can have different effects on spider diversity. First, explanatory variables affecting spider diversity were compared and concluded that shrub species was significant to diversity. The seasonal factor suite was not found to be highly relevant to spider diversity. However, if spider samples are identified to genus, or the species level, it is likely that seasonal factors would be more impactful to spider diversity.

My second research question addressed insect biodiversity at tow natianl grasslands in Colorao . At Pawnee National Grassland, the insect families Chrysomelidae, Cicadellidae, Cleridae, Formicidae, Meloidae, and Miridae were abundant primarily from four-winged saltbush. At Comanche National Grassland insect families Acrididae, Aphididae, Chrysomelidae, Cleridae, Coccinellidae, Formicidae, Lygaeidae, Miridae, and Reduviidae were abundant from local shrub communities.

My third research question addressed how spider community structure varies depending on local plant community structure. For this, I predicted that local plant vegetation composition would affect spider community assemblages. Multilevel pattern analysis and hierarchal clustering analysis suggested that depending on the shrubs available, different trends in spider community structure can be observed. Different families of spiders occurred in different shrub species. However, depending on the shrub species present, different patterns emerge for spider habitat use at the family level. This included Dictynidae associated with rabbitbrush; Philodromidae associated with greasewood, rabbitbrush and sandsage; Oxyopidae associated with skunkbush; and Salticidae primarily associated with juniper but also with skunkbush, rabbitbrush and sandsage.

Of the spiders collected, many that were abundant at both CNG and PNG, do not depend on specific web building. Given that many of these spiders that exhibited distinct habitat association also have unique foraging requirements corresponding to specific structural arrangements, it is possible that many of the arboreal spiders that are successful in these native shrub communities out-perform spiders restricted to specific web attachment requirements. Given the expected change in global climate, understanding the impact these changes have on target species and the habitat they occupy begins with knowledge of their current position and habitat use in a system. This research provides community analysis for arboreal spiders of native shrubs in grasslands of the shortgrass steppe which may allow detection of critical habitat necessary for maintaining community structure for multiple predator species in this system.

I was also interested in how spatial heterogeneity of a landscape could affect habitat availability and alter spider diversity. I predicted that if landscape attributes (elevation) can determine the location of vegetational habitat zones, then spider diversity will differ depending on elevation-based shrub habitat zones [steppe, cliff region of canyon slope, lower canyon region]. Because different plant communities adhere to unique ecological parameters, shrubs in these systems can be quantified and may allude to taxa-specific spider habitat and suggest transitions between habitat zones that may support species from neighboring communities. For this, I used GIS and image analysis applications to classify the vegetation classifications and identify spider habitat zones. I found that elevation above canyon floor could predict shrub species habitat to some extent, however additional attributes such as slope and aspect would enhance predictions of local shrub species occupancy. Here, the habitat heterogeneity of the plant communities in this study influenced the distribution of arboreal spiders. As shown above, these spiders appear to vary depending on the shrubs available and/or the foraging strategy they used.

The major theory for this research includes ecological niche and applications of habitat/spatial heterogeneity/complexity theory. It also invites metacommunity topics with the shrubs interpreted as patches. However, this research does not adhere to the full requirements of metacommunity (Gilpin & Hanski, 1991; Hubbell, 2011; Holyoak et al., 2005). Primary, this research lacks dispersal estimates. Metacommunity combines local and regional factors to explain patterns of species distributions that occur at different spatial scales. There are four theoretical frameworks that utilize different processes of importance for metacommunity that are used for predicting community patterns. One of these, the patch dynamics model, examines species composition among multiple patches, such as islands. Species can persist on patches through colonization ability so that some species can disperse to unoccupied patches faster than local extinction rate. Another, source-sink models explore how dispersal and environmental heterogeneity interact to determine local and regional abundance and composition. A third, neutral theory (Hubbell, 2001) which assumes all species are similar in movement and interaction is random. Finally, species sorting models account for variation in abundance and composition within the metacommunity due to species response to environmental heterogeneity. Under this perspective, species can persist in patches with suitable environmental conditions resulting in a strong correlation between local species composition and the environment. Species sorting emphasizes how resource gradients or types of islands cause differences in local species density and species interactions along with dispersal patterns to express community effects (Leibold et al., 2004). Of these metacommunity processes, species sorting appears to have the most connection to this research for interpreting interactions with habitat, tolerance, and persistence for spiders on shrubs even without a direct connection to patch. If this research is viewed with varied composition rates across gradients (elevation for shrub occupancy), then the shrubs in these systems would not facilitate classic patch dynamics theory. Rather, a species sorting framework may assist with interpreting any patterns of spider communities (with shrub as the co-variate) would excite interpretation of local dispersal.

Since landscape complexity can be evaluated at multiple scales, landscape characteristics can be significant predictors of species occupancy and abundance. By measuring habitat heterogeneity effects (shrub composition), patterns of arboreal spider community assembly may be used to identify core habitat for these spiders. Shrub positioning appears to suggest transitions between habitat suitability requirements and restraints for arboreal spiders at CNG with a recognized habitat region in bottom of the canyons with abundant greasewood, sandsage, and rabbitbrush, while differences in spider community assembly can be recognized in another habitat region along the mid elevation of the canyons with juniper and skunkbush. The spatial scale of the study system could accommodate further measurements of shrubs by area in more detail and could be expanded outward to larger geographic regions, with diversity /community measures changing with increased spatial scale. Diversity changes depending on spatial scale. Multiple species groups, on multiple arboreal habitat (restricted spatially) will have different patterns for diversity, which will vary depending on spatial scale. One can also observe differences in these patterns with changes in shrubs being present (sampled) for individual CNG canyons, community patterns change. Shrub occupancy can be altered by elevation change (along soil, moisture gradients). If the shrubs could be mapped, then any predictions to different spatial scales or across different areas of habitat density/fragmentation could be validated with future field surveys, thereby expanding the depth of knowledge of how community patterns shift with available habitat and spatial scale relevant to suggest local colonization success. Appendix I attempts to provide proof of concept for testing this with remote sensing techniques to classify and quantify habitat from a small (meters) to larger spatial scales (kilometers). This methodology allows for measuring patterns in local populations at multiple spatial scales of habitat and could be applied to conservation management strategies, precision agriculture and urban ecology landscapes.

Since these spiders are restricted to specific shrubs, habitat associations can be used to indicate specific spider community assembly and suggest transitions between habitat zones. The spatial scale used for this study may also be applied to similar natural systems, in agrosystems, or in urban ecological context., requiring habitat specificity. Since spider surveys in grasslands often focus on ground dwelling habitat (as the most common) this arboreal habitat has been largely overlooked. This research addresses, in part, this deficiency for spiders of the shortgrass steppe region. Shrubs provide potential habitat for spiders that otherwise may not successfully inhabit grasslands. Past studies have shown that spider communities are strongly influenced by habitat type and land-use patterns. For instance, spider fauna most captured in pitfall traps may be considered primarily ground-dwelling (Uetz & Unzicker, 1976) but ground-dwelling spiders can further segregate into recognizable habitats (Robinson, 1981; Cady, 1984). Arboreal spider assembly also appears to segregate at fine spatial scales, restricted to different habitat zones with assorted shrub species. This means that shrub species and the landscape that they inhabit should be utilized in future habitat models for spider communities that can indicate a larger arthropod community structure. It is also possible with knowledge of genera and spider species data; short-term rainfall and pollination events may be observed with staggered and shifting habitat-use at recognized temporal measurements.

Due to limitations in potential predator-prey analysis, the insects that were collected as part of this study were composed into a separate publication. A critical concern was that many of the fast-flying insects (Hymenoptera, Diptera) were observed to leave the shrubs before sampling occurred. Also, many of the insects may have only been exhibiting temporary resting behavior and not indicate any habitat association to specific shrub species. Furthermore, there were hundreds of insect species collected for CNG and PNG. Isolating specific insect groups with specific collecting methods is recommended. Additional research at the spider genus level would likely indicate further habitat generalists and specialists which would presumably tie to insect habitat. Barcoding spider specimens to genus and species would likely allow for further specific temporal and spatially restricted habitat associations. Given that climate change has led to phenological shifts in flowering plants and insect pollinators and altering pollinator networks, documenting habitat associations for predators of insects can allude to deeper multi-species, community interactions. By separating the habitat that arboreal spiders inhabit by landscape features that dictate the distribution of the shrubs, we can further isolate spider habitat at the spatial scale relevant to observe these changes.

Destruction and degradation of natural ecosystems are the primary causes of declines in global biodiversity (Rands et al., 2010). Habitat destruction typically leads to fragmentation, the division of habitat into smaller and more isolated fragments separated and is often detrimental to the maintenance of biodiversity (Didham et al., 2012). Without including shrub habitat and its occupants into modern grassland models, we cannot determine what biotic and abiotic features of a landscape are crucial to their persistence. However, most spiders that have been sampled in grassland ecosystems have focused on ground dwelling taxa or those associated with agricultural production systems. Despite many studies on spider-habitat interactions, only limited data exists for shrub-dwelling species, and few studies have compared arboreal spider distribution across different grassland shrub species. The data collected here is complementary to the previous work on spiders within grassland systems which has historically focused on ground dwelling taxa and provides insight to arboreal spider distribution across different grassland shrub species in the Great Plains. It appears that slight alterations of availability of habitat impacts local spider communities. Since these spiders are restricted to specific combinations of shrubs, shrub dwelling, spider community patterns in this grassland system may suggest how some shrub species are better indicators of habitat use and niche partitioning than others. Patterns of community structure with specific native shrubs may reflect niche partitioning in these canyons system that may be indicative to habitat across a network of canyons in the shortgrass steppe region. Given the expected change in global climate, understanding the impact these changes have on target species and the habitat they occupy begins with knowledge of their current position and habitat use in a system. This research provides one of the first detailed habitat specific, community analysis for arboreal spiders of native shrubs in grasslands of the shortgrass steppe which may allow detection of critical habitat necessary for maintaining community structure for arboreal spiders in this system.

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APPENDIX I: APPLICATION OF AGENT-BASED MODELING TECHNIQUES TO STUDY DISTRIBUTION PATTERNS OF ARBOREAL SPIDERS IN GRASSLAND-SHRUB SYSTEMS

Introduction

Recent advances in species distribution models (SDMs) may allow us to assess habitat heterogeneity and community organization in new, spatially explicit ways. This may allow us to study how ecological variation and geography function as major factors generating biodiversity (Chefaoui et al., 2005) and how assist in understanding community structure and its relationship to spatial dynamics (Leibold et al., 2004; Holyoak et al., 2005) or predicting species distributions affects conservation efforts (Canran et al., 2005). The structure of multi-species groups along environmental gradients can then be analyzed for community assembly factors and to model ecological complexity. For instance, population sizes are expected to increase with the patch size which reduces the local extinction risk (Hanski, 1997).

The objective was to leverage image analysis and remote sensing tools to model native shrub species for habitat quantification in relation to vegetation composition, spatial heterogeneity, and habitat fragmentation for arboreal spider habitat. The data source for this model was from arboreal spider count data collected on different shrub species along canyons of the shortgrass steppe in Comanche National Grassland, Colorado. Spiders are a diverse taxonomic group and fill many microhabitats of grassland ecosystems. However, relatively little is known about arboreal species in grassland systems. Arboreal spiders, as generalist predators, with uncommon dispersal methods, make a unique ecological system to study habitat use and community interactions. In terms of community ecology, plant species composition is considered one of the major factors of arthropod species communities (Schaffers et al., 2008). Because different plant communities adhere to unique ecological parameters, shrubs in these systems can be quantified and may relate to taxa-specific spider habitat and suggest habitat generalists and specialists across landscape features. This may also indicate factors associated with habitat fragmentation (Mazerolle & Villard, 1999; Fahrig, 2003; Ewers et al., 2006) which can also alter species presence and abundance in a multiple spatial construct for patch dynamics.

The model presented here uses knowledge of arboreal spiders to address questions such as how their populations are affected by (H1) type of habitat (shrub spp.) and (H2) how the habitat is more, or less abundant. I predicted that the increased density of shrubs in a canyon would increase the diversity of spiders. I also predicted that habitat connectivity and spider diversity will decrease with habitat fragmentation. I expected that regions of high shrub complexity would allow higher spider diversity and community structure; and regions of dense shrub habitat, would facilitate higher spider density per area. The model can run raster layers of shrub agents to spider agents at multiple scales.

The Model

An Agent Based Model (ABM) was constructed to examine community patterns and habitat use of arboreal spiders inhabiting shrub communities in grasslands systems. The model attempts to simulate population dynamics of arboreal spiders in shrublands with a focus on spatial dynamics to obtain realistic estimates of habitat use. The variables and entities in the model are the patches for the landscape features and agents representing spiders. Each patch in the landscape is characterized by the following state variables: (1) location (x- and y-coordinate); (2) shrub species: Juniper, Greasewood, Cholla and Rabbitbrush. The four habitat types differ in quality of vegetation cover-habitat quality. Spiders use the most preferred habitat based on field collections and observations. (3) Host: the spider which owns the patch as part of its home range; more than one spider can own a patch. In the model, spiders are distinguished into three life stages: juveniles, sub-adults, and adults. Each individual spider is characterized by: (1) identity number; (2) age; (3) previous nest sites (4) current site position, (5) fecundity: egg batch size at end of season based on food consumption.

The model was run on a portion of field site within Comanche National Grassland (36.997242, -102.700475) in southeastern Colorado. The plant communities consist of sand sagebrush (*Artemisia filifolia*) Torr., four-winged saltbush (*Atriplex canescens*) (Pursh) Nutt., rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh)), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), and one-seed juniper (*Juniperus monosperma*).

Results

Design concepts: General assumptions include how links between local variation of community structure and broader spatial patterns may predict local variation. Species in a local community are isolated populations, with unequal contributions to the community. The key processes in the model are those that determine spider occupancy based on plant cover. Population dynamics, age structure and spatial distribution emerge from the individuals' behavior and interactions. Image preparation: To access a realistic setting of patches for the background, I used a satellite image from Earth Explorer. The justification for this was that the smaller shrub species that are located within the lower regions of the Purgatoire River Canyon not clearly defined, so using the image below (Figure 1A), I was able to manually select the location of individual shrubs. The image was then adjusted, setting the color variation to a color band, and then setting a specific color number sequence to the band. (Figure 1B). The image was then projected through the import-colors method into NetLogo.

The resulting model constructed can display many outcomes based on how the parameters are set (Figure 2). For instance, depending on the movement attempts set in the model, some spider species will not have a high success rate where it is non optimal habitat. The model has sliders of spider 'species' initial abundance. A monitor is also provided to track the tick-day shown in Julian date until it is repeated. The spiders start on the initial plant species set and begin, based on Julian date aerial disperse downwind until reaching optimal habitat or death. If the agents reach this optimal patch (plant species), they consume a set amount of energy in their surrounding area to reach maturity.

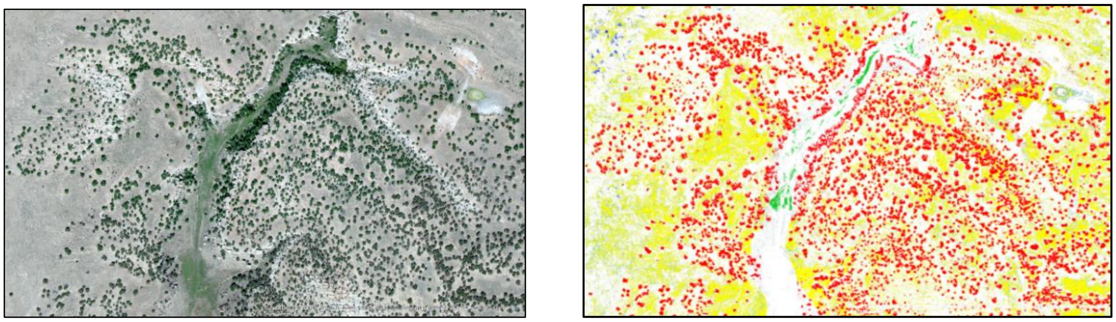

Figure 1. (A-left) Image of test site Comanche NG. (B-right). Image adjusted through paint program to represent vegetation (shrub species-juniper in red).

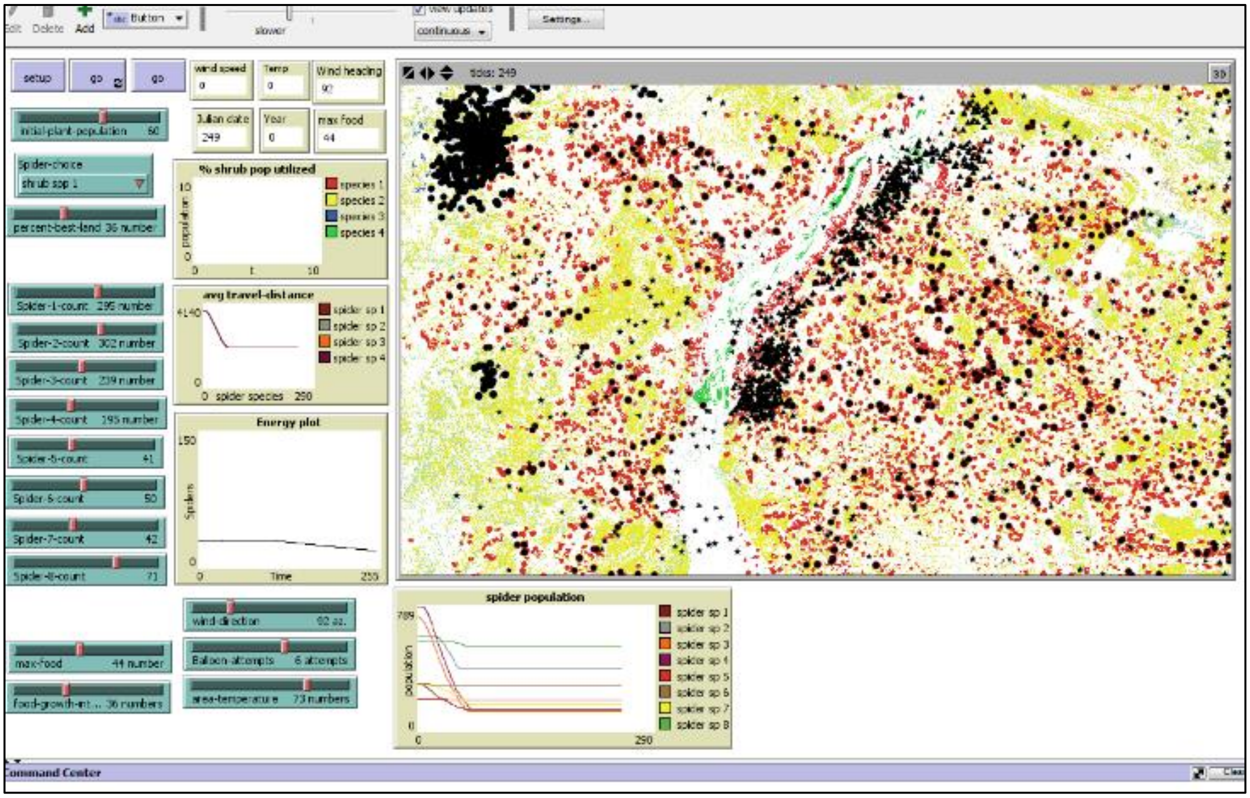

Figure 2**.** Image from active Agent Based Model for examining arboreal spider occupancy and local distribution between shrub species (red shrubs representing juniper) for region in Comanche National Grassland (image used from subset of Vogel Canyon) including sliders for richness and abundance for spider families and genera. The model allows adjustments to spiders as individual agents occupancy based on success of reaching and establishing range of ideal habitat.

Remote sensing image analysis is often used for classifying vegetation for ecological studies. In grassland systems, many of the shrubs have not been categorized down to individual shrub level or quantified by area. Classification of vegetation of the study area is required to delineate habitat zones for spiders that inhabit the shrubs of interest. Since ABMs can run raster layers of shrub agents to spider agents for richness-abundance the resulting data can then be used to determine how different spider taxa respond to the surrounding landscape over a range of multiple spatial scales.

Image analysis of shrub habitat

Satellite images with a spatial resolution of 2.0 meters of the study area were obtained from DigitalGlobe (www.digitalglobe.com) 2015 Image Grant [WV2, WV3, GE1 2013-2016 sources]. Image preparation included individual tiles of image products were inspected for coverage of study sites (canyons) so that separate image files were combined as a mosaic. ENVI image processing software was used to perform unsupervised pixel-based classification of the images to identify shrub species in the study area. Ground truth data was collected and used to evaluate the accuracy of an elevation classification scheme. The accuracy of classification was also evaluated by visual inspection of the product in the panchromatic view.

Categorization of Juniper

ENVI software with unsupervised pixel-based methods was used to classify imagery for area estimates of juniper coverage within the study area in CNG Timpas Unit canyons. Steps to convert ENVI derived shapefiles to usable points for juniper are provided below (Figures 3-7).

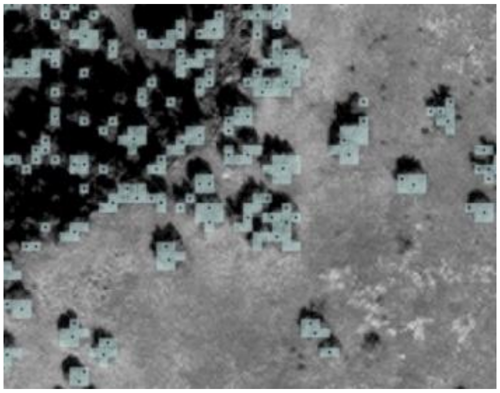

Figure 3. Converted multipart feature (classes 17 and 19) to combined singlepart feature ("Multipart to Singlepart").

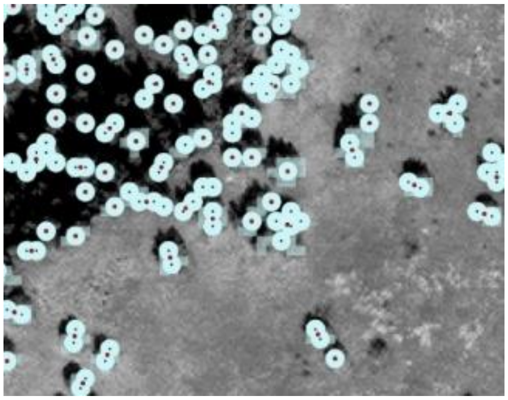

Figure 4. 2-m. radius buffer for multipart feature class from centroids.

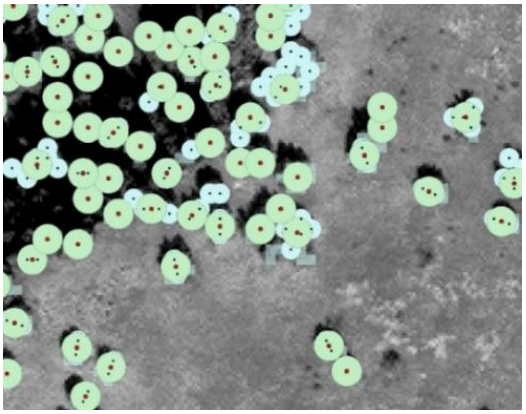

Figure 5. Converted buffer-1 multipart feature to buffer-1 singlepart feature.

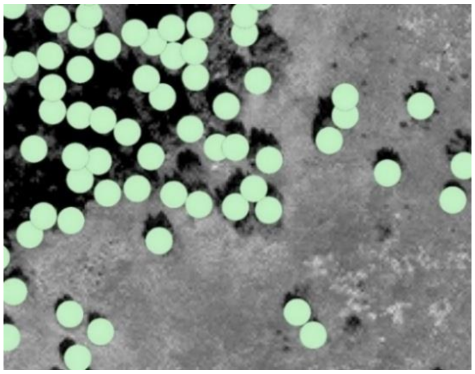

Figure 6. Created centroids-2 for singlepart buffer-1 feature ("Feature to Point") and 3-meter radius buffer-2 feature class from centroids-2. ("Buffer")

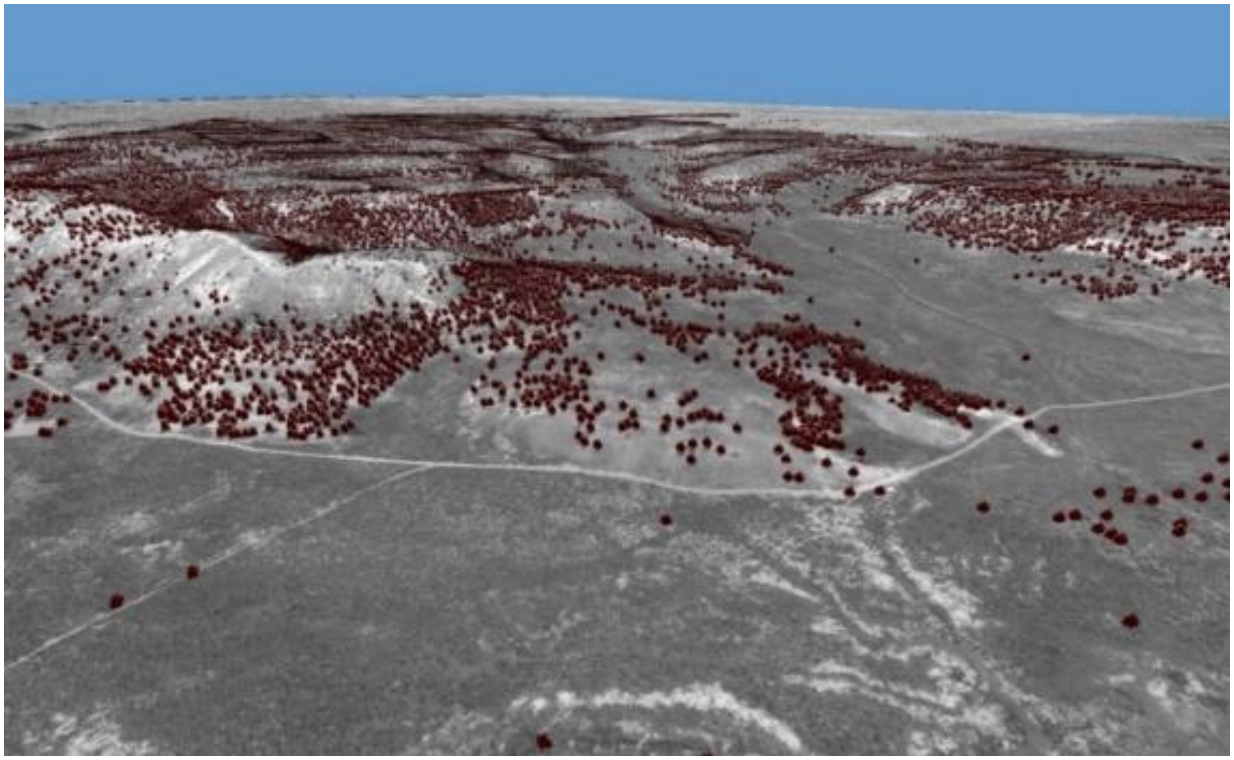

Figure 7. 3D version in ArcGlobe. Juniper is represented with 3D Symbology tools in red with size and height adjustments applied. Background with Panchromatic (2 meter) for higher resolution. Constructed in 2018 for juniper point data for Comanche National Grassland, Colorado: Minnie Canyon.

The objective was to construct an ABM to evaluate how arboreal spider communities associated with different dominant native shrubs can be linked to landscape features (vegetation composition, spatial heterogeneity). Image analysis and remote sensing tools were used to identify native shrub species for habitat quantification in relation to habitat fragmentation over the landscape. I was able to map the largest shrub used for study, juniper was able to map with ENVI methods in ENVI (Figure 3-7). Unfortunately, I was unable to complete this for all shrubs in ENVI. Object Based Imaging Analysis (OBIA) is an image processing software platform that uses a hierarchical processing tree when classifying or manipulating any image data, was used to delineate the shrubs of the study area. It uses an object-based processing and classification scheme rather than traditional pixel-based methods. The segments (image objects) are then classified, based on object metrics and statistics such as pixel values, texture, shape, and size and allows image information represented at different scales by different object layers. OBIA techniques may function for the satellite resolution available to classify shrub species in these systems, thereby allowing analysis of spider community patterns in more detail.

Advances in remote sensing and geospatial data processing allow us to understand the relationship between landscape metrics and ecological patterns in the context of spatial. Landscape ecology studies the relationship between ecological systems at multiple spatial scales with landscapes as spatially heterogeneous areas that can be characterized according metapopulation (Levins, 1969) model with patches that differ in configuration. Remote sensing techniques were used to classify shrub habitat, an underrepresented component of grassland ecosystems, in canyons of Comanche National Grasslands. This research utilizes remote sensing driven, spatially explicit approaches to estimate shrub occupancy in select canyons of CNG in southeastern Colorado. Because different plant communities adhere to unique ecological parameters, shrubs in these systems can be quantified and may relate to taxa-specific spider habitat. This research characterized habitat zones which may assist in addressing habitat use and niche space of arboreal spiders in grasslands with a focus on diversity patterns along environmental gradients.

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APPENDIX II: EXPLOITING LITERATURE-BASED METADATA FOR VISUALIZATION OF PAST RESEARCH WITH AGENT BASED MODELLING APPROACHES

Introduction

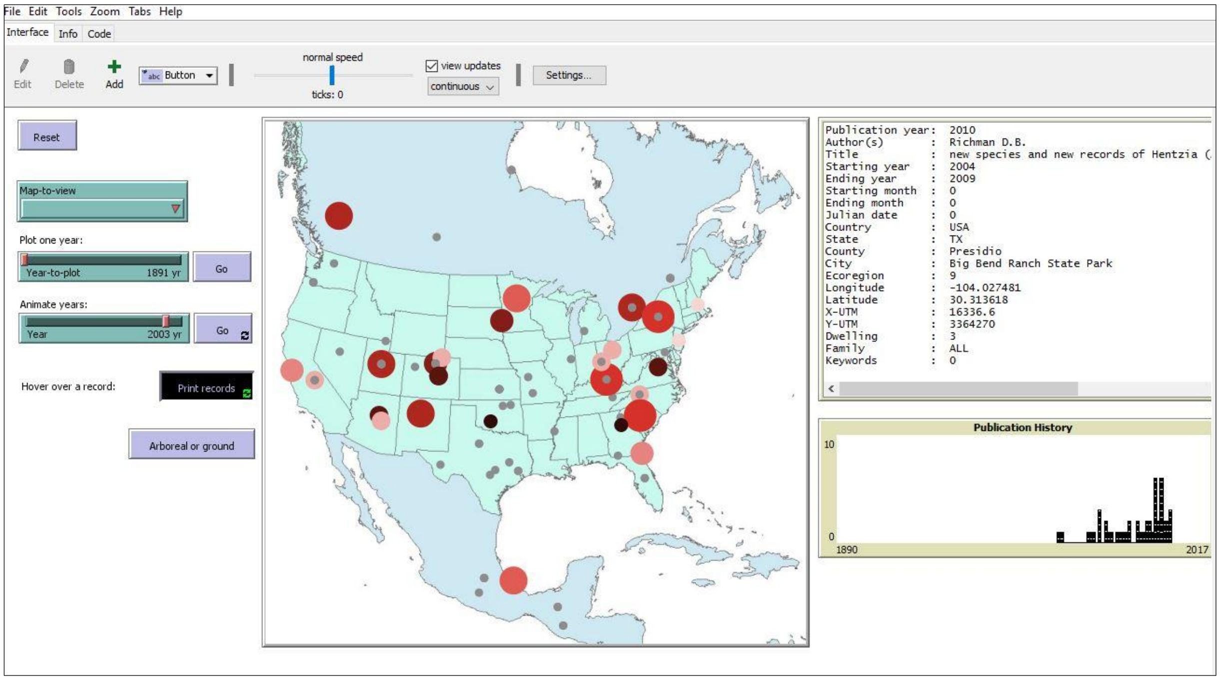
Many ecologists are interested in animated maps for data visualization such as those involved in public policy and landscape planning. However, previous approaches describing past literature are often with stationary data on a map. These methods limit how an audience can perceive the complexity of geographical changes in research emphasis. Although R and ArcGIS tools are available for geo-referencing data points of interest, they do not provide an interface and filter tools found in NetLogo, a multi-agent programmable modeling environment (Wilensky, 1999). Agent based modeling (ABM) is a computational technique used to simulate spatiotemporal interactions and has increased over the last decades (Chen, 2012). Initially NetLogo could only import image files, however it is possible to import both raster (ASCII files) and vector data (shapefiles). This allows a range of possibilities for the creation of spatially explicit models. Here, we present a novel approach to visualize and analyze patterns of past research studies with ABM techniques. The objective was to create an animated interactive map with filter tools, to illustrate the temporal and spatial distribution of literature review-based occurrence data.

Methods

In this case, ABM tools were leveraged to highlight many of the occurrences of ecological studies (papers, reports) of spiders in North America with a focus on separating arboreal and ground-dwelling studies by geographic region and time-period. Data within the model stems from a literature source that can be linked to geographically explicit locations. The application was constructed to map the temporal and spatial distribution and the growth and decline of studies in an area of any topic, as an animated interactive map. This is not an ABM. Rather, it uses NetLogo to display and organize by filter and slider tools, any subject matter of literature geographically. Literature searches were not exhaustive but after screening articles for data of interest (date range of study, taxa specific foci, habitat type, etc.) a data set was constructed to examine the spread of ecological studies in the area. Journal articles reflecting ecological studies were then examined manually to compile GPS coordinates, and others features of interest. Many sources did not specify habitat for spider research. While many were focused on ground associated taxa, few studies focused on arboreal habitat. Variables of interest included: publication year, years of the study or survey, months of the study or survey, Julian year transformation of year/month data, ecoregion of the study based on Omernik (1987) decimal latitude and longitude of the study, the focal spider family (if listed) and a descriptor of the habitat use (if available).

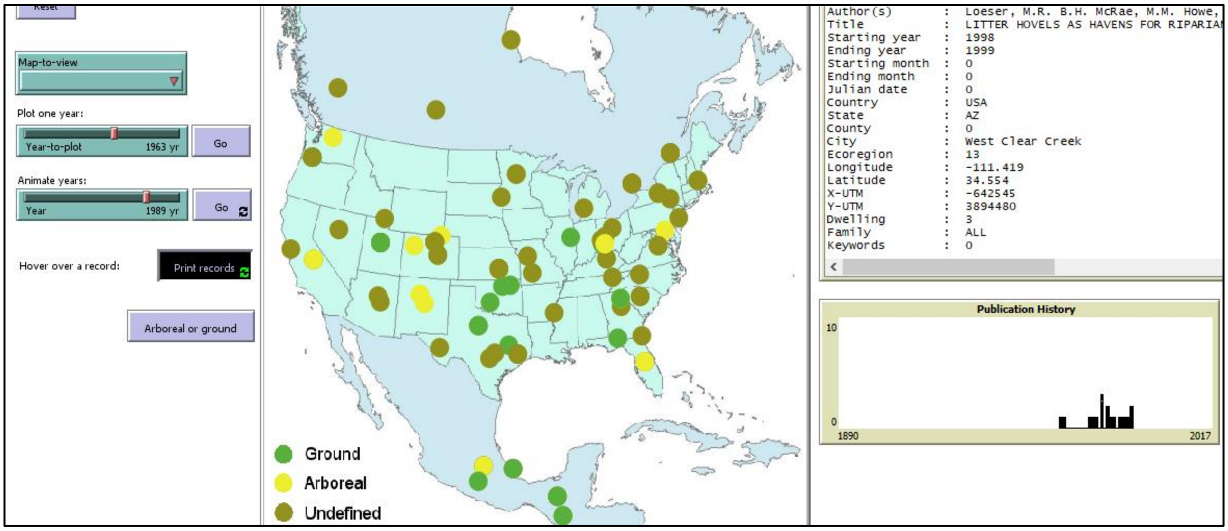
Results

Output of model can be seen below for spider-habitat directed studies (Figure 1) and data for ground versus arboreal spider focused studies seen below (Figure 2).



```
Publication year:  2010
Author(s)       :  Richman D.B.
Title           :  new species and new records of Hentzia (
Starting year   :  2004
Ending year     :  2009
Starting month  :  0
Ending month    :  0
Julian date     :  0
Country         :  USA
State           :  TX
County          :  Presidio
City            :  Big Bend Ranch State Park
Ecoregion       :  9
Longitude       :  -104.027481
Latitude        :  30.313618
X-UTM           :  16336.6
Y-UTM           :  3364270
Dwelling        :  3
Family          :  ALL
Keywords        :  0
```

Figure 1. Screenshot of interactive literature mapping tool. Red circles represent the occurrence of specific ecological studies. Variables of interest included: publication year, years of study or survey, Julian year, decimal latitude, and longitude of the study transformation of year/month data, the focal spider family (if listed) and a descriptor of the habitat use (if available). The time step of the model is one year; start at the year 1900 and run through 2017. The right-hand screen displays specific literature sources if the cursor is placed in a location, a decay radius was constructed to display the extent of each study. To run, GO will simulate the records until the time limit expires. Each year is represented as red circles for occurrence of ecological studies.



Year-to-plot 1963 yr

Year 1989 yr

```
Author(s)        :  Loeser, M.R. B.H. McRae, M.M. Howe,
Title            :  LITTER HOVELS AS HAVENS FOR RIPARIA
Starting year    :  1998
Ending year      :  1999
Starting month   :  0
Ending month     :  0
Julian date      :  0
Country          :  USA
State            :  AZ
County           :  0
City             :  West Clear Creek
Ecoregion        :  13
Longitude        :  -111.419
Latitude         :  34.554
X-UTM            :  -642545
Y-UTM            :  3894480
Dwelling         :  3
Family           :  ALL
Keywords         :  0
```

Figure 2. Screenshot of interactive literature map displaying ground, arboreal and undefined spider related studies in literature source results.

Discussion

As the importance of species occupancy and habitat use data continues to grow, the demand for effectively visualizing the information expands. Using animation tools, one can plot comparable data over time for specific sets of parameters. Currently, this study explores history of research of spiders of North America with additional tests for arboreal vs. ground however, additional data sets (of any subject) would allow the mapping tool to display additional studies of interest spatially and temporally.

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Wilensky, U. (1999). NetLogo. http://ccl.northwestern.edu/netlogo/. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

APPENDIX III: SUPPLEMENTRY TABLES AND FIGURES

Table S1. Insects collected on shrubs at Pawnee (PNG) and Comanche National Grasslands (CNG), Colorado.

Locality	Order	Family	Genus	species
CNG	Coleoptera	Anthicidae	*Anthicus*	
CNG	Coleoptera	Anthicidae	*Ischyropalpus*	
CNG	Coleoptera	Anthicidae	*Notoxus*	
CNG	Coleoptera	Brentidae	*Apion*	
CNG	Coleoptera	Buprestidae	*Anthaxia*	*flavimania*
CNG	Coleoptera	Buprestidae	*Chrysobothris*	
CNG	Coleoptera	Cantharidae	*Chauliognathus*	*marginatus*
CNG	Coleoptera	Cantharidae	*Chauliognathus*	*scutellaris*
CNG	Coleoptera	Cantharidae	*Chauliognathus*	
CNG	Coleoptera	Cantharidae	*Trypherus*	*latipennis*
CNG	Coleoptera	Carabidae	*Cicindelidia*	*obsoleta*
CNG	Coleoptera	Cerambycidae	*Tetraopes*	*femoratus*
CNG	Coleoptera	Chrysomelidae	*Acanthoscelides*	
CNG	Coleoptera	Chrysomelidae	*Altica*	
CNG	Coleoptera	Chrysomelidae	*Aphthona*	
CNG	Coleoptera	Chrysomelidae	*Blepharida*	*rhois*
CNG	Coleoptera	Chrysomelidae	*Brachypnoea*	*tristis*
CNG	Coleoptera	Chrysomelidae	*Chaetocnema*	
CNG	Coleoptera	Chrysomelidae	*Chelymorpha*	*cassidea*
CNG	Coleoptera	Chrysomelidae	*Diabrotica*	*undecimpunctata*
CNG	Coleoptera	Chrysomelidae	*Diabrotica*	
CNG	Coleoptera	Chrysomelidae	*Disonycha*	*triangularis*
CNG	Coleoptera	Chrysomelidae	*Disonycha*	
CNG	Coleoptera	Chrysomelidae	*Epitrix*	
CNG	Coleoptera	Chrysomelidae	*Glyptina*	*atriventris*
CNG	Coleoptera	Chrysomelidae	*Monoxia*	
CNG	Coleoptera	Chrysomelidae	*Pachybrachis*	*bivittatus*
CNG	Coleoptera	Chrysomelidae	*Pachybrachis*	
CNG	Coleoptera	Chrysomelidae	*Paranapiacaba*	*tricincta*
CNG	Coleoptera	Chrysomelidae	*Paria*	
CNG	Coleoptera	Chrysomelidae	*Phyllotreta*	
CNG	Coleoptera	Chrysomelidae	*Saxinis*	*saucia*
CNG	Coleoptera	Chrysomelidae	*Systena*	
CNG	Coleoptera	Chrysomelidae	*Tricholochmaea*	
CNG	Coleoptera	Chrysomelidae	*Trirhabda*	*nitidicollis*
CNG	Coleoptera	Chrysomelidae	*Trirhabda*	
CNG	Coleoptera	Chrysomelidae	*Zygogramma*	*disrupta*
CNG	Coleoptera	Chrysomelidae		
CNG	Coleoptera	Chrysomelidae	*Cryptocephalus*	
CNG	Coleoptera	Cleridae	*Enoclerus*	*coccineus*
CNG	Coleoptera	Cleridae	*Phyllobaenus*	
CNG	Coleoptera	Cleridae		
CNG	Coleoptera	Coccinellidae	*Coccinella*	*novemnotata*

CNG	Coleoptera	Coccinellidae	*Coccinella*	*septempunctata*
CNG	Coleoptera	Coccinellidae	*Hippodamia*	*convergens*
CNG	Coleoptera	Coccinellidae	*Hippodamia*	*parenthesis*
CNG	Coleoptera	Coccinellidae	*Hippodamia*	
CNG	Coleoptera	Coccinellidae	*Hyperaspis*	*lateralis*
CNG	Coleoptera	Coccinellidae	*Hyperaspis*	
CNG	Coleoptera	Coccinellidae	*Scymnus*	
CNG	Coleoptera	Coccinellidae		
CNG	Coleoptera	Curculionidae	*Anthonomus*	
CNG	Coleoptera	Brentidae	*Apion*	
CNG	Coleoptera	Curculionidae	*Baris*	
CNG	Coleoptera	Curculionidae	*Ophryastes*	
CNG	Coleoptera	Curculionidae	*Tychius*	
CNG	Coleoptera	Curculionidae		
CNG	Coleoptera	Dermestidae		
CNG	Coleoptera	Lathridiidae		
CNG	Coleoptera	Lycidae	*Calopteron*	*reticulatus*
CNG	Coleoptera	Meloidae	*Epicauta*	*ferruginea*
CNG	Coleoptera	Meloidae	*Epicauta*	*normalis*
CNG	Coleoptera	Meloidae	*Epicauta*	*sericans*
CNG	Coleoptera	Meloidae	*Epicauta*	
CNG	Coleoptera	Meloidae	*Zonitis*	*atripennis*
CNG	Coleoptera	Melyridae	*Amecocerus*	
CNG	Coleoptera	Melyridae	*Attalus*	
CNG	Coleoptera	Melyridae	*Collops*	
CNG	Coleoptera	Melyridae		
CNG	Coleoptera	Mordellidae	*Mordellistena*	
CNG	Coleoptera	Nitidulidae	*Carpophilus*	
CNG	Coleoptera	Phalacridae	*Olibrius*	
CNG	Coleoptera	Phalacridae	*Stilbus*	
CNG	Coleoptera	Phalacridae		
CNG	Coleoptera	Scarabaeidae	*Diplotaxis*	
CNG	Coleoptera	Scarabaeidae	*Euphoria*	*kernii*
CNG	Coleoptera	Scarabaeidae	*Euphoria*	
CNG	Coleoptera	Scarabaeidae	*Phyllophaga*	*lanceolata*
CNG	Coleoptera	Scraptiidae	*Anaspis*	
CNG	Coleoptera	Staphylinidae		
CNG	Coleoptera	Tenebrionidaae	*Bothrotes*	*plumbeas*
CNG	Coleoptera	Tenebrionidaae	*Bothrotes*	
CNG	Coleoptera	Tenebrionidaae	*Lobopoda*	
CNG	Diptera	Anthomyiidae	*Delia*	
CNG	Diptera	Anthomyiidae		
CNG	Diptera	Asilidae	*Efferia*	
CNG	Diptera	Asilidae	*Lampria*	*bicolor*
CNG	Diptera	Cecidomyiidae		
CNG	Diptera	Ceratopogonidae		
CNG	Diptera	Chironomidae		
CNG	Diptera	Chloropridae		
CNG	Diptera	Conopidae	*Thecophora*	
CNG	Diptera	Culicidae	*Aedes*	
CNG	Diptera	Muscidae		

CNG	Diptera	Mycetophilidae	*Sciophila*	
CNG	Diptera	Mycetophilidae		
CNG	Diptera	Scenopinidae	*Scenopinus*	
CNG	Diptera	Sciaridae		
CNG	Diptera	Syrphidae		
CNG	Diptera	Tachinidae		
CNG	Diptera	Tephritidae	*Aciurina*	*bigeloviae*
CNG	Diptera	Tephritidae	*Aciurina*	
CNG	Diptera	Tephritidae	*Eutreta*	*diana*
CNG	Diptera	Tephritidae	*Trupanea*	*bisetosa*
CNG	Diptera	Terphritidae	*Urophora*	*cardui*
CNG	Diptera	Ulidiidae	*Chrysomyza*	
CNG	Ephemeroptera	Baetidae		
CNG	Hemiptera	Anthocoridae	*Orius*	
CNG	Hemiptera	Anthocoridae		
CNG	Hemiptera	Aphididae		
CNG	Hemiptera	Berytidae	*Pronotacantha*	*annulata*
CNG	Hemiptera	Cercopidae		
CNG	Hemiptera	Cicadellidae	*Cuerna*	
CNG	Hemiptera	Cicadellidae		
CNG	Hemiptera	Cicadidae	*Okanagana*	*hesperia*
CNG	Hemiptera	Cixiidae	*Cixius*	
CNG	Hemiptera	Cixiidae	*Oliarus*	
CNG	Hemiptera	Cixiidae		
CNG	Hemiptera	Coreidae	*Chelinidea*	*vittiger*
CNG	Hemiptera	Coreidae	*Leptoglossus*	*clypealis*
CNG	Hemiptera	Coreidae	*Leptoglossus*	*phyllopus*
CNG	Hemiptera	Coreidae	*Leptoglossus*	
CNG	Hemiptera	Coreidae	*Mozena*	
CNG	Hemiptera	Coreidae	*Narnia*	*snowi*
CNG	Hemiptera	Issidae	*Aphelonema*	
CNG	Hemiptera	Caliscelidae	*Bruchomorpha*	
CNG	Hemiptera	Clastopteridae	*Clastoptera*	
CNG	Hemiptera	Tropiduchidae	*Dictyssa*	
CNG	Hemiptera	Caliscelidae	*Fitchiella*	
CNG	Hemiptera	Caliscelidae		
CNG	Hemiptera	Lygaeidae	*Crophius*	
CNG	Hemiptera	Lygaeidae	*Emblethis*	*vicarius*
CNG	Hemiptera	Lygaeidae	*Geocoris*	
CNG	Hemiptera	Lygaeidae	*Lygaeus*	*kalmii*
CNG	Hemiptera	Lygaeidae	*Lygaeus*	
CNG	Hemiptera	Lygaeidae	*Melacoryphus*	*lateralis*
CNG	Hemiptera	Lygaeidae	*Melanopleurus*	*beifragei*
CNG	Hemiptera	Lygaeidae	*Neacoryphus*	*bicrucis*
CNG	Hemiptera	Lygaeidae	*Nysius*	
CNG	Hemiptera	Lygaeidae	*Sphragisticus*	*nebulosus*
CNG	Hemiptera	Lygaeidae	*Xyonysius*	
CNG	Hemiptera	Lygaeidae		
CNG	Hemiptera	Membracidae		
CNG	Hemiptera	Miridae	*Lygus*	
CNG	Hemiptera	Miridae	*Phytocoris*	

CNG	Hemiptera	Miridae	*Taedia*	*deleticus*
CNG	Hemiptera	Miridae	*Taedia*	
CNG	Hemiptera	Nabidae	*Nabis*	*alternatus*
CNG	Hemiptera	Nabidae	*Nabis*	
CNG	Hemiptera	Nabidae		
CNG	Hemiptera	Pentatomidae	*Banasa*	
CNG	Hemiptera	Pentatomidae	*Brochymena*	
CNG	Hemiptera	Pentatomidae	*Chlorochroa*	*ligata*
CNG	Hemiptera	Pentatomidae	*Chlorochroa*	*sayi*
CNG	Hemiptera	Pentatomidae	*Chlorochroa*	*viridicata*
CNG	Hemiptera	Pentatomidae	*Chlorochroa*	
CNG	Hemiptera	Pentatomidae	*Tepa*	
CNG	Hemiptera	Pentatomidae	*Thyanta*	*custator*
CNG	Hemiptera	Pentatomidae	*Thyanta*	
CNG	Hemiptera	Piesmatidae	*Piesma*	
CNG	Hemiptera	Psyllidae		
CNG	Hemiptera	Reduviidae	*Apiomerus*	
CNG	Hemiptera	Reduviidae	*Phymata*	*americana*
CNG	Hemiptera	Reduviidae	*Phymata*	
CNG	Hemiptera	Reduviidae	*Sinea*	
CNG	Hemiptera	Reduviidae	*Zelus*	
CNG	Hemiptera	Rhopalidae	*Arhyssus*	
CNG	Hemiptera	Rhopalidae	*Aufeius*	*impressicollis*
CNG	Hemiptera	Rhopalidae		
CNG	Hemiptera	Rhyparochromidae	*Cryphula*	
CNG	Hemiptera	Scutelleridae	*Euptychodera*	*corrugata*
CNG	Hemiptera	Scutelleridae	*Phimodera*	*binotata*
CNG	Hemiptera	Scutelleridae		
CNG	Hemiptera	Thyreocoridae	*Corimelaena*	
CNG	Hemiptera	Thyreocoridae		
CNG	Hymenoptera	Andrenidae	*Perdita*	
CNG	Hymenoptera	Argidae	*Schizocerella*	*pilicornis*
CNG	Hymenoptera	Bethylidae		
CNG	Hymenoptera	Braconidae	*Chelonus*	*sericeus*
CNG	Hymenoptera	Braconidae	*Chelonus*	
CNG	Hymenoptera	Braconidae		
CNG	Hymenoptera	Chalcididae		
CNG	Hymenoptera	Chalicidoidea		
CNG	Hymenoptera	Chrysididae		
CNG	Hymenoptera	Figitidae		
CNG	Hymenoptera	Formicidae	*Crematogaster*	
CNG	Hymenoptera	Formicidae	*Dorymyrmex*	
CNG	Hymenoptera	Formicidae	*Formica*	
CNG	Hymenoptera	Formicidae	*Lasius*	
CNG	Hymenoptera	Formicidae	*Monomorium*	*minimum*
CNG	Hymenoptera	Formicidae	*Myrmecocystus*	
CNG	Hymenoptera	Formicidae	*Myrmica*	
CNG	Hymenoptera	Formicidae	*Solenopsis*	*molesta*
CNG	Hymenoptera	Formicidae	*Solenopsis*	
CNG	Hymenoptera	Formicidae	*Tapinoma*	*sessile*
CNG	Hymenoptera	Formicidae		

CNG	Hymenoptera	Halictidae	*Halictus*	
CNG	Hymenoptera	Haliticidae	*Agapostemon*	
CNG	Hymenoptera	Haliticidae	*Lasioglossum*	
CNG	Hymenoptera	Haliticidae		
CNG	Hymenoptera	Ichneumonidae	*Ophion*	
CNG	Hymenoptera	Ichneumonidae		
CNG	Hymenoptera	Megachilidae	*Coelioxys*	
CNG	Hymenoptera	Mutillidae	*Dasymutilla*	
CNG	Hymenoptera	Scelionidae		
CNG	Hymenoptera	Tenthredinidae		
CNG	Hymenoptera	Vespidae	*Polistes*	*apachus*
CNG	Lepidoptera	Erebidae		
CNG	Lepidoptera	Gelechiidae		
CNG	Lepidoptera	Geometridae		
CNG	Lepidoptera	Noctuidae		
CNG	Lepidoptera	Noctuidae		
CNG	Lepidoptera	Pieridae	*Colias*	
CNG	Lepidoptera	Pyralidae		
CNG	Lepidoptera	Sphingidae		
CNG	Lepidoptera	Tortricidae		
CNG	Mantodea	Mantidae	*Stagmomantis*	*carolina*
CNG	Mantodea	Mantidae		
CNG	Neuroptera	Chrysopidae	*Chrysopa*	
CNG	Neuroptera	Chrysopidae	*Chrysoperla*	
CNG	Neuroptera	Chrysopidae	*Eremochrysa*	
CNG	Neuroptera	Chrysopidae		
CNG	Orthoptera	Acrididae	*Aeoloplides*	*turnbulli*
CNG	Orthoptera	Acrididae	*Dactylotum*	*bicolor*
CNG	Orthoptera	Acrididae	*Eritettex*	*simplex*
CNG	Orthoptera	Acrididae	*Hesperotettix*	*urdis*
CNG	Orthoptera	Acrididae	*Hesperotettix*	
CNG	Orthoptera	Acrididae	*Melanoplus*	*sanguinipes*
CNG	Orthoptera	Acrididae	*Melanoplus*	*splendidus*
CNG	Orthoptera	Acrididae	*Melanoplus*	*bowditchi*
CNG	Orthoptera	Acrididae	*Melanoplus*	*differentialis*
CNG	Orthoptera	Acrididae	*Melanoplus*	*packardii*
CNG	Orthoptera	Acrididae	*Melanoplus*	*sanguinipes*
CNG	Orthoptera	Acrididae	*Melanoplus*	
CNG	Orthoptera	Acrididae	*Parapomala*	*wyomingensis*
CNG	Orthoptera	Acrididae	*Parapomala*	
CNG	Orthoptera	Acrididae	*Tropidolophus*	*formosus*
CNG	Orthoptera	Acrididae		
CNG	Orthoptera	Gryllidae	*Neonemobius*	
CNG	Orthoptera	Gryllidae	*Oecanthus*	
CNG	Orthoptera	Gryllidae		
CNG	Orthoptera	Gryllidae		
CNG	Orthoptera	Tettigoniidae	*Pediodectes*	
CNG	Orthoptera	Tettigoniidae	*Scudderia*	*texensis*
CNG	Orthoptera	Tettigoniidae		
CNG	Psocoptera			
CNG	Thysanoptera	Aeolothripidae	*Aeolothrips*	

CNG	Thysanoptera	Aeolothripidae		
CNG	Thysanoptera	Thripidae	*Franklinella*	
CNG	Thysanoptera	Thripidae		
CNG	Thysanoptera	Thripidae		
PNG	Coleoptera	Anthicidae	*Notoxus*	
PNG	Coleoptera	Carabidae	*Lebia*	*viridis*
PNG	Coleoptera	Carabidae	*Microlestes*	
PNG	Coleoptera	Chrysomelidae	*Altica*	
PNG	Coleoptera	Chrysomelidae	*Brachypnoea*	
PNG	Coleoptera	Chrysomelidae	*Chaetocnema*	
PNG	Coleoptera	Chrysomelidae	*Diabrotica*	*virgifera*
PNG	Coleoptera	Chrysomelidae	*Epitrix*	
PNG	Coleoptera	Chrysomelidae	*Gastrophysa*	
PNG	Coleoptera	Chrysomelidae	*Glyptina*	*atriventris*
PNG	Coleoptera	Chrysomelidae	*Graphops*	
PNG	Coleoptera	Chrysomelidae	*Monoxia*	
PNG	Coleoptera	Chrysomelidae	*Pachybrachis*	*bivittatus*
PNG	Coleoptera	Chrysomelidae	*Pachybrachis*	
PNG	Coleoptera	Chrysomelidae	*Scelolyperus*	
PNG	Coleoptera	Chrysomelidae	*Spintherophyta*	*globosa*
PNG	Coleoptera	Chrysomelidae	*Systena*	*blanda*
PNG	Coleoptera	Chrysomelidae	*Trirhabda*	
PNG	Coleoptera	Chrysomelidae		
PNG	Coleoptera	Cleridae	*Enoclerus*	*cordifer*
PNG	Coleoptera	Cleridae	*Phyllobaenus*	
PNG	Coleoptera	Cleridae		
PNG	Coleoptera	Coccinellidae	*Coccinella*	*novemnotata*
PNG	Coleoptera	Coccinellidae	*Coccinella*	*septempunctata*
PNG	Coleoptera	Coccinellidae	*Hippodamia*	*convergens*
PNG	Coleoptera	Coccinellidae	*Hippodamia*	*parenthesis*
PNG	Coleoptera	Coccinellidae	*Hippodamia*	
PNG	Coleoptera	Coccinellidae	*Hyperaspis*	
PNG	Coleoptera	Coccinellidae		
PNG	Coleoptera	Curculionidae	*Anthonomus*	
PNG	Coleoptera	Curculionidae	*Sitonia*	
PNG	Coleoptera	Curculionidae	*Tychius*	
PNG	Coleoptera	Curculionidae		
PNG	Coleoptera	Hydrophilidae	*Cercyon*	
PNG	Coleoptera	Lathridiidae	*Melanophthalma*	
PNG	Coleoptera	Meloidae	*Epicauta*	*normalis*
PNG	Coleoptera	Meloidae	*Epicauta*	
PNG	Coleoptera	Melyridae	*Amecocerus*	
PNG	Coleoptera	Melyridae	*Attalus*	
PNG	Coleoptera	Melyridae	*Collops*	
PNG	Coleoptera	Melyridae	*Trichochrous*	
PNG	Coleoptera	Melyridae		
PNG	Coleoptera	Mordellidae	*Mordellistena*	
PNG	Coleoptera	Nitidulidae	*Carpophilus*	
PNG	Coleoptera	Phalacridae	*Olibrus*	
PNG	Coleoptera	Phalacridae	*Stilbus*	
PNG	Coleoptera	Phalacridae		

PNG	Coleoptera	Tenebrionidaae	*Bothrotes*	
PNG	Diptera	Anthomyiidae		
PNG	Diptera	Ceratopogonidae		
PNG	Diptera	Chironomidae		
PNG	Diptera	Culicidae	*Aedes*	*vexans*
PNG	Diptera	Dolichopodidae	*Medetera*	
PNG	Diptera	Empididae		
PNG	Diptera	Muscidae		
PNG	Diptera	Pipunculidae	*Tomosvaryella*	
PNG	Diptera	Scenopinidae	*Scenopinus*	
PNG	Diptera	Sciaridae		
PNG	Diptera	Tephritidae	*Eutreta*	*diana*
PNG	Diptera	Tephritidae	*Trupanea*	
PNG	Diptera	Therevidae	*Ozodiceromya*	
PNG	Hemiptera	Anthocoridae	*Orius*	
PNG	Hemiptera	Aphididae		
PNG	Hemiptera	Cercopidae	*Clastoptera*	
PNG	Hemiptera	Cicadellidae	*Cuerna*	
PNG	Hemiptera	Cicadellidae		
PNG	Hemiptera	Cixiidae	*Cixius*	
PNG	Hemiptera	Cixiidae	*Pentastiridius*	
PNG	Hemiptera	Caliscelidae	*Bruchomorpha*	
PNG	Hemiptera	Clastopteridae	*Clastoptera*	
PNG	Hemiptera	Caliscelidae		
PNG	Hemiptera	Lygaeidae	*Crophius*	
PNG	Hemiptera	Lygaeidae	*Cymus*	*angustatus*
PNG	Hemiptera	Lygaeidae	*Geocoris*	
PNG	Hemiptera	Lygaeidae	*Lygaeus*	*kalmii*
PNG	Hemiptera	Lygaeidae	*Lygaeus*	*reclivatus*
PNG	Hemiptera	Lygaeidae	*Melanopleurus*	*lateralis*
PNG	Hemiptera	Lygaeidae		
PNG	Hemiptera	Miridae	*Lygus*	*elisus*
PNG	Hemiptera	Miridae		
PNG	Hemiptera	Nabidae	*Nabis*	*alternatus*
PNG	Hemiptera	Nabidae	*Nabis*	
PNG	Hemiptera	Pentatomidae	*Brochymena*	
PNG	Hemiptera	Pentatomidae	*Chlorochroa*	*ligata*
PNG	Hemiptera	Pentatomidae	*Chlorochroa*	*sayi*
PNG	Hemiptera	Pentatomidae	*Chlorochroa*	
PNG	Hemiptera	Pentatomidae	*Tepa*	
PNG	Hemiptera	Pentatomidae	*Thyanta*	*custator*
PNG	Hemiptera	Pentatomidae	*Thyanta*	
PNG	Hemiptera	Pentatomidae		
PNG	Hemiptera	Piesmatidae	*Piesma*	
PNG	Hemiptera	Reduviidae	*Zelus*	
PNG	Hemiptera	Rhopalidae	*Stictopleurus*	
PNG	Hemiptera	Scutelleridae	*Euptychodera*	*corrugata*
PNG	Hemiptera	Scutelleridae	*Homaemus*	*parvulus*
PNG	Hemiptera	Scutelleridae	*Vanduzeeina*	*balli*
PNG	Hemiptera	Tingidae		
PNG	Hymenoptera	Bethylidae		

PNG	Hymenoptera	Braconidae		
PNG	Hymenoptera	Chalcididae		
PNG	Hymenoptera	Chalicidoidea		
PNG	Hymenoptera	Chrysididae		
PNG	Hymenoptera	Figitidae		
PNG	Hymenoptera	Formicidae	*Crematogaster*	
PNG	Hymenoptera	Formicidae	*Formica*	
PNG	Hymenoptera	Formicidae	*Lasius*	
PNG	Hymenoptera	Formicidae	*Solenopsis*	
PNG	Hymenoptera	Formicidae	*Tapinoma*	*sessile*
PNG	Hymenoptera	Formicidae		
PNG	Hymenoptera	Ichneumonidae	*Pterocormus*	
PNG	Hymenoptera	Ichneumonidae		
PNG	Hymenoptera	Mutillidae		
PNG	Lepidoptera	Erebidae		
PNG	Lepidoptera	Gelechiidae		
PNG	Lepidoptera	Geometridae		
PNG	Lepidoptera	Noctuidae		
PNG	Lepidoptera	Tortricidae		
PNG	Mantodea	Mantidae	*Stagmomantis*	*carolina*
PNG	Neuroptera	Chrysopidae	*Chrysopa*	
PNG	Orthoptera	Acrididae	*Hesperotettix*	
PNG	Orthoptera	Acrididae	*Melanoplus*	
PNG	Orthoptera	Gryllidae	*Oecanthus*	*argentinus*
PNG	Orthoptera	Gryllidae		
PNG	Thysanoptera	Aeolothripidae	*Aeolothrips*	
PNG	Thysanoptera	Thripidae	*Frankliniella*	
PNG	Thysanoptera	Thripidae		

Table S2. Multilevel Pattern Analysis with *multipatt* function R package *indicspecies* for Comanche National Grassland Canyon at the family level. Spider families were assigned to the groups of shrubs juniper (*J. monosperma*), skunkbush (*R. trilobata*), sandsage (*A. filifolia*), rabbitbrush (*E. nauseosa*), and greasewood (*S. vermiculatus*). for which they achieved the Indicator Value (IndVal) as described in (Dufrêne and Legendre 1997; De Caceres et al., 2012; De Caceres, 2020). Significance of the relationship between species and habitat was based on permutation tests using 999 random permutations to estimate p-values. Significance: 0 '***' 0.001 '**' 0.01 '*' 0.05.).

Family	Canyon	juniper	skunkbush	sandsage	rabbitbrush	greasewood	IndVal	p value
Agelenidae	Picture	**X**					0.279	0.036 *
Araneidae	Vogel	X	X				0.439	0.248
Araneidae	Iron			X			0.546	0.108
Araneidae	Minnie	X	X	X		X	0.294	0.389
Araneidae	Withers	X	X	X	X		0.431	0.184
Dictynidae	Withers			X	X	X	0.512	0.088
Dictynidae	Minnie				**X**	**X**	0.466	0.002 **
Eutichuridae	Vogel		X				0.348	0.133
Eutichuridae	Minnie		X				0.239	0.193
Eutichuridae	Picture		X				0.22	0.173
Oxyopidae	Iron	X	X		X		0.588	0.405
Oxyopidae	Minnie	**X**	**X**				0.488	0.003 **
Oxyopidae	Withers	X	X				0.491	0.144
Philodromidae	Vogel			**X**			0.62	0.003 **
Philodromidae	Minnie	X	X	X		X	0.459	0.282
Philodromidae	Picture	**X**		**X**			0.46	0.046 *
Philodromidae	Withers			**X**			0.628	0.004 **
Salticidae	Iron		X	X	X		0.699	0.223
Salticidae	Withers	X	X	X	X		0.561	0.288
Thomisidae	No Name		X	X	X		0.597	0.169

Table S3. Count of spiders by family and genus by shrubs in canyons sampled at Comanche National Grassland, Colorado.

Family	***genus***	**shrub**	**Picture**	**Vogel**	**Withers**	**Minnie**	**No name**	**Iron**
Agelenidae	*Agelenopsis*	juniper	8	1	1			1
		skunkbush	1					
Araneidae	*Araneus*	skunkbush	1					
	Argiope	greasewood				1		
		sandsage	1					
	Lariniodes	greasewood				1		
	Mangora	skunkbush	1	1				
	Metepeira	greasewood				2		
	Neoscona	greasewood				7		
		juniper	7	9	5	4	2	2
		rabbitbrush					5	
		sandsage	4		1			1
		skunkbush	4	6	6	1		
Dictynidae	*Dictyna*	greasewood			35	104		
		juniper	11	9	3	8	7	3
		rabbitbrush		1	16	56	4	
		sandsage	15	3	10		3	1
		skunkbush	8	4	2	4	1	
Eutichuridae	*Cheiracanthium*	greasewood			2	1		
		juniper	1	1	1			1
		rabbitbrush			1	1		
		skunkbush	4	4	1	4	1	
Mimetidae	*Ero*	skunkbush			1			
	Mimetus	greasewood			17	5		
		juniper	1		6	2	3	3
		rabbitbrush			1			
		sandsage	4					
		skunkbush			6			
Oxyopidae	*Oxyopes*	greasewood			27	29		
		juniper	49	72	29	26	8	17
		rabbitbrush			1	2	1	1
		sandsage	28	5		3	1	
		skunkbush	118	21	19	30	8	4
	Scalaris	rabbitbrush		2				
Philodromidae	*Ebo*	greasewood				15		
		juniper	7	5		5		1
		rabbitbrush				16	2	
		sandsage	20	7	1	10		
		skunkbush	10	1	1	1		
	Philodromus	greasewood			17	55		
		juniper	5	1		2	6	1
		rabbitbrush				3	3	
		sandsage	27	4	12	2		1
		skunkbush	1			1		
	Thanatus	juniper				1		
		sandsage	1					
	Titanebo	greasewood				4		

Salticidae	Dendryphantine	greasewood				1		
		juniper	3	3				
	Habronattus	sandsage	1					
	Metaphidippus	juniper		10		2		2
	Pelegrina	juniper	16	12		1	1	1
		rabbitbrush		1				
		skunkbush	5					
	Phidippus	greasewood			12	38		
		juniper	15	21	8	14	5	8
		rabbitbrush		1	1	21	4	3
		sandsage	25		2	1	2	
		skunkbush	26	6	3	7	1	
	Salticus	greasewood				1		
		juniper				2		
		sandsage	1			1		
	Sassacus	greasewood			1	3		
		rabbitbrush				3	1	
		sandsage	7	3	2	2		
Tetragnathidae	*Tetragnatha*	sandsage				1		
		skunkbush	1					
Theridiidae	*Latrodectus*	juniper		1				
	Steatoda	juniper				3		
	Theridion	greasewood				1		
		skunkbush		1				
Thomisidae	*Mecaphesa*	greasewood			8	18		
		juniper	9	1	1	13		1
		rabbitbrush			3	15	8	
		sandsage	25	1	1	4	1	
		skunkbush	25	3		5	3	
	Mecaphesa	greasewood			6	10		
		juniper		1	1	4	3	3
		rabbitbrush			4	2	2	
		sandsage	12					
		skunkbush	6	6	4	1	1	
	Misumena	juniper			1			
		sandsage	2					
	Misumenoides	rabbitbrush				1		
	Xysticus	greasewood				5		
		juniper	2	5	5	5	2	5
		sandsage	1					

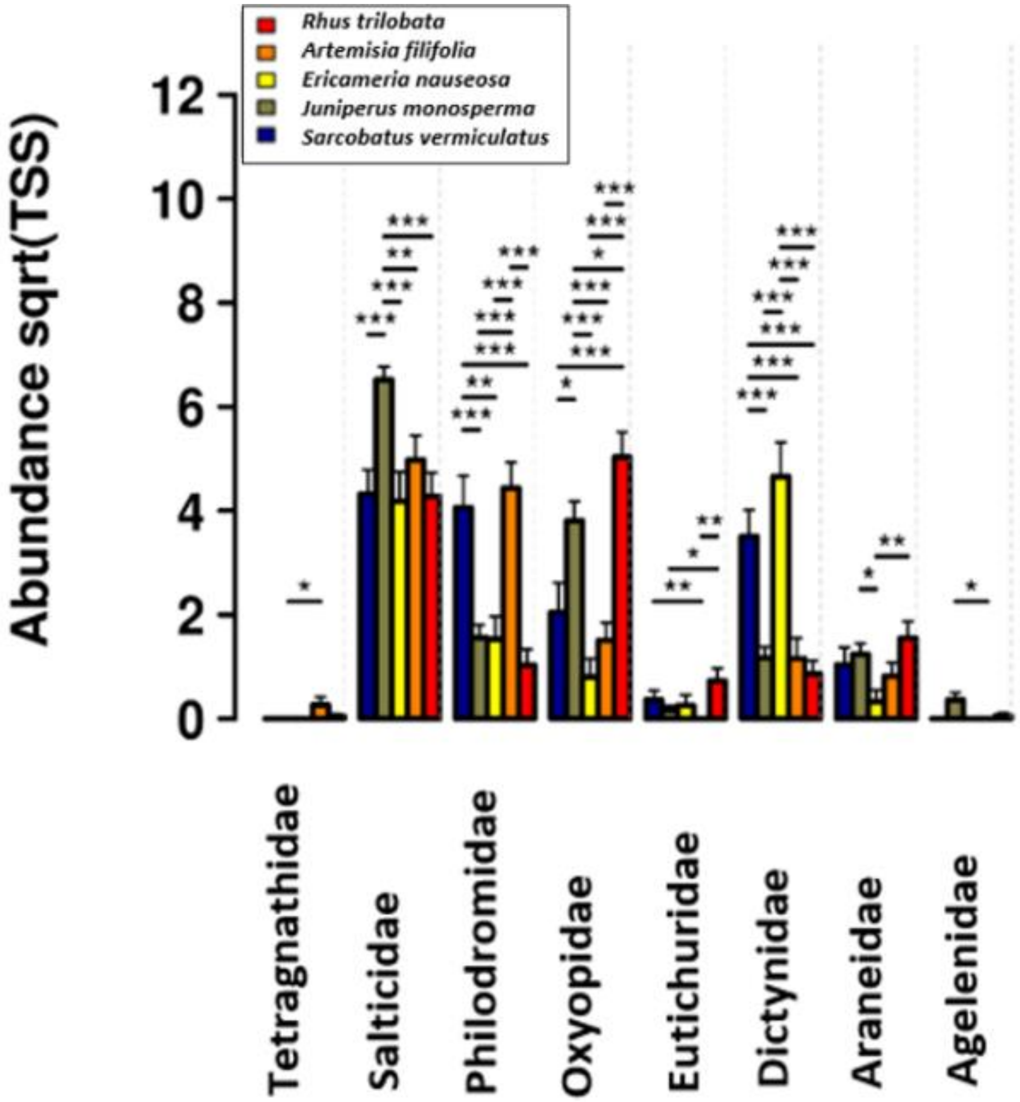


Figure S1. ANOVA bar plot (P <0.05). Spider family abundance data compared across sample groups to shrub species at Comanche National Grassland. Standard error is depicted by error bars. Pair-wise comparisons are done by t-test and annotated as *: P <0.05, **: P <0.01, ***: P <0.001. Shrub species in CNG canyons sampled: Greasewood (*Sarcobatus vermiculatus*) (blue), juniper (*Juniperus monosperma*) (green), rabbitbrush (*Ericameria nauseosa*) (yellow), sandsage (*Artemisia filifolia*) (orange), and skunkbush (*Rhus trilobata*) (red).

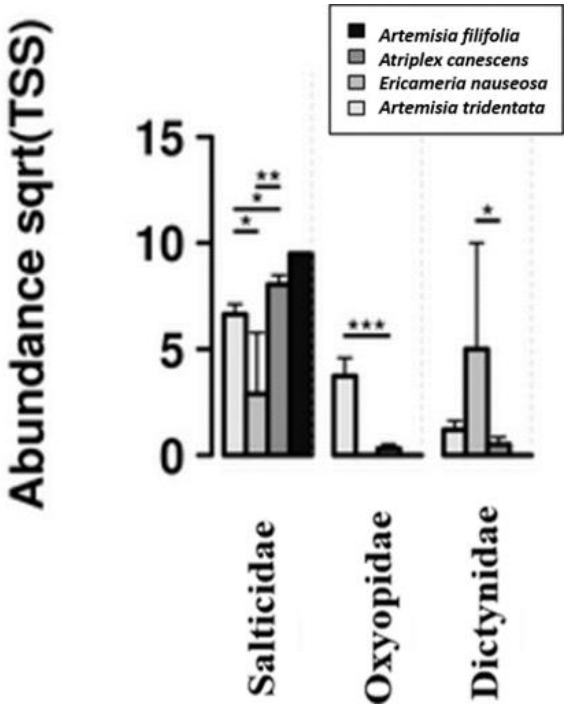


Figure S2. ANOVA bar plot (P <0.05). Spider family abundance data compared across sample groups to shrub species at Pawnee National Grassland spider family grouped by shrub. (P < 0.05). Standard error is depicted by error bars. Pair-wise comparisons are done by t-test and annotated as *: P<0.05, **: P<0.01, ***: P<0.001. Shrub sampled: sandsage (*Artemisia filifolia*), fourwing saltbush (*Atriplex canescens),* rabbitbrush (*Ericameria nauseosa*), and big sagebrush (*Artemisia tridentata*).

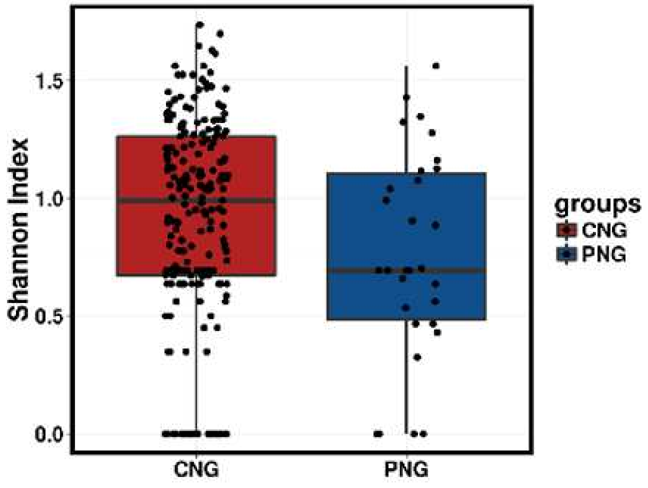


Figure S3. Shannon Index (P =0.091, F=2.9) for diversity of spiders (count data) between shrub species sampled at each national grassland. Box plot for groups: Comanche National Grassland (left), Pawnee National Grassland (right).

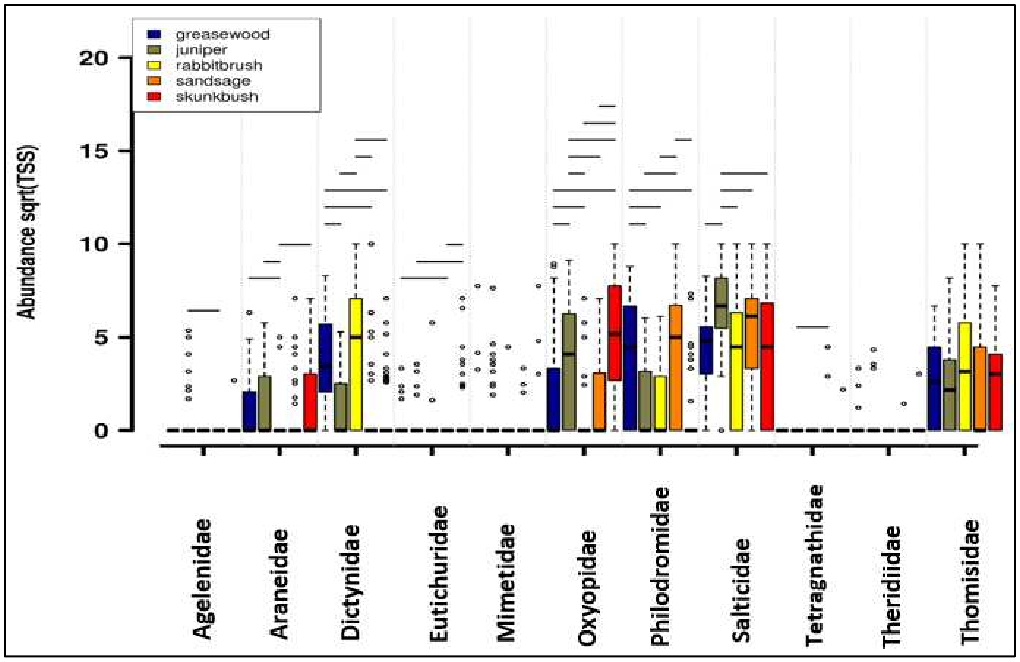


Figure S4. ANOVA plot (P < 0.5). Comanche National Grassland (CNG) spider family count data grouped by shrub. Pair-wise comparisons are done by t-test and annotated as *: p <0.05, **: p <0.01, ***: p <0.001. Standard error is depicted by error bars. Shrub species in CNG canyons sampled: Greasewood (*S. vermiculatus*) (blue), juniper (*J. monosperma*) (green), rabbitbrush (*E. nauseosa*) (yellow), sandsage (*A. filifolia*) (orange), and skunkbush (*R. trilobata*) (red).

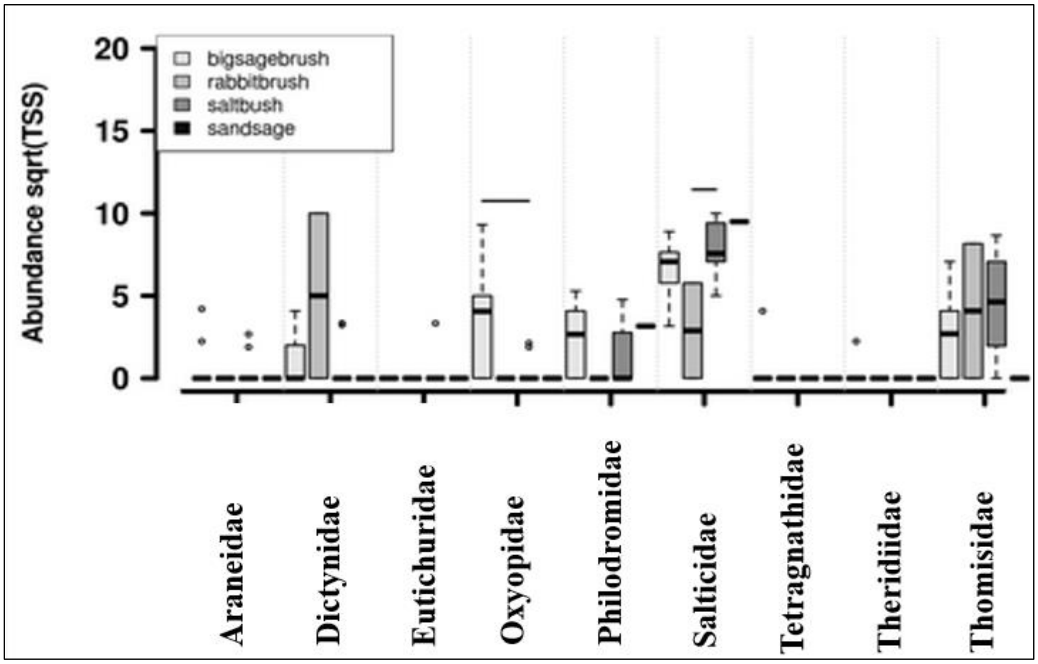


Figure S5. ANOVA plot (P < 0.5). Spider family data in different shrubs at Pawnee National Grassland. Standard error is depicted by error bars. Pair-wise comparisons are done by t-test. Pair-wise comparisons are done by t-test and annotated as *: p <0.05, **: p <0.01, ***: p <0.001.

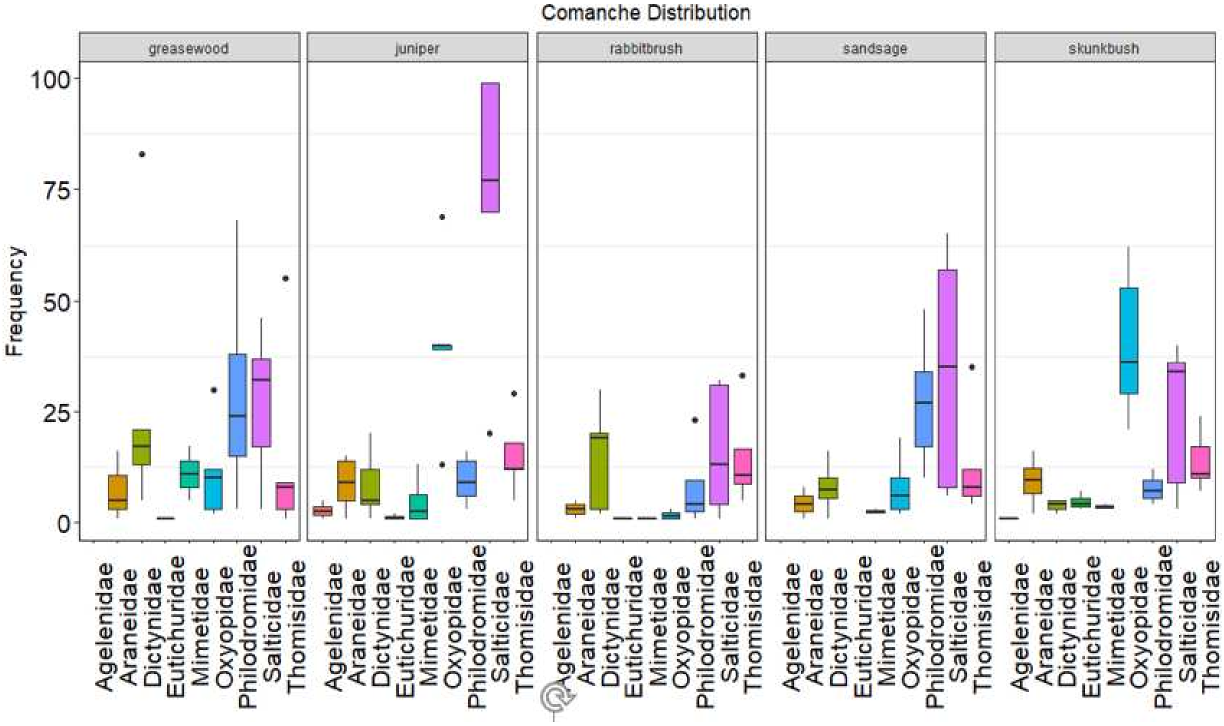


Figure. S6. Frequency spider families to native shrubs at Comanche National Grassland as box plots for average count of spider family per shrub sampled (mean shrub sample size: 33) for all years (2014-2017) combined for May-September. Shrub species sampled at Comanche National Grassland: greasewood (*S. vermiculatus),* juniper (*J. monosperma),* rabbitbrush (*E. nauseosa)*, sandsage (*A. filifolia)*. skunkbush (*R. trilobata*).

Landcover Classification for Arboreal Spider Habitat

To provide percent cover for juniper and area estimates for potential habitat for juniper, skunkbush, and lowland shrubs including greasewood and rabbitbrush I used the 'short frames' (seen below in Figure S7) to represent the sampling area within the overall canyon boundary boxes (not shown). I used a southeastern Colorado region-based DEM for the sampling area and applied the ArcGIS reclassify tool" to re-set individual canyon DEM's to 15 elevation classes to segregate the area of potential habitat for skunkbush and lowland shrubs. A suite of elevation, slope and aspect are attainable to predict shrub occupancy for a potential course habitat suitability model for spider taxa to shrub species by canyon.

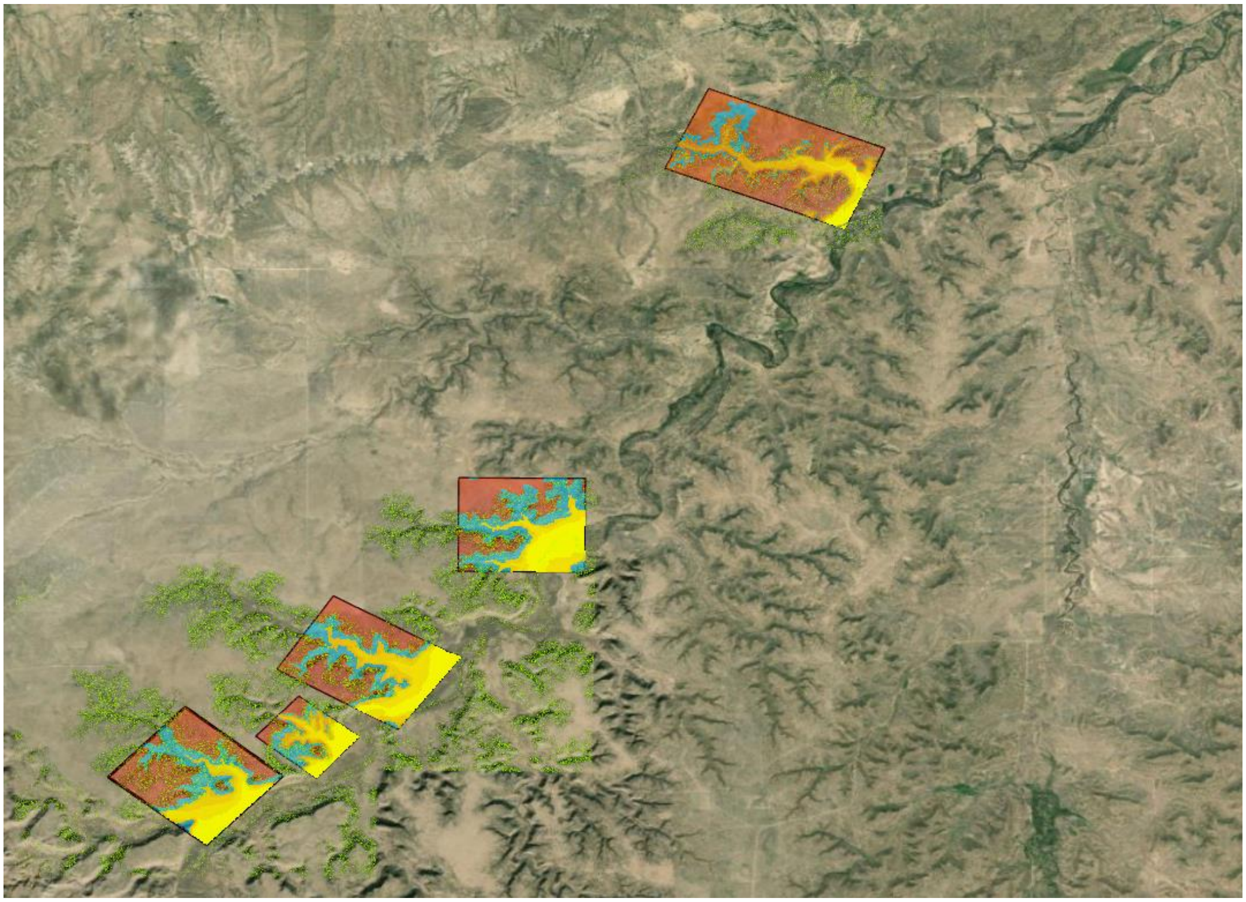
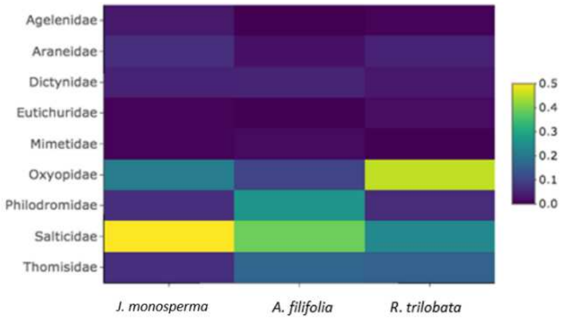
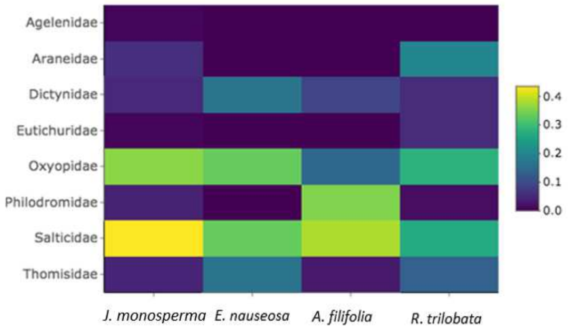


Figure S7. Blue bands representing area of skunkbush potential habitat using 're-classify' tools in GIS of individual canyon DEM with 15 elevation classes. Yellow region representing area containing lowland vegetation of canyon including greasewood and rabbitbrush. Local canyon range for juniper crosses over these areas with most juniper occurrence restricted to red region.

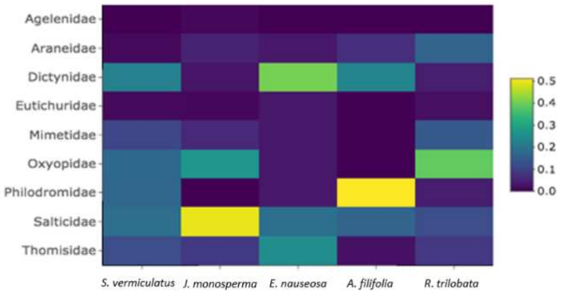
Figure S8. Correlation heatmap (Index: Spearman) generated from hierarchical clustering analysis for spider family-shrub association for canyons sampled of Comanche National Grassland, Colorado. Color bar indicates level of standardized value. Matrix of eigenvalues with brightest colors (yellow) indicating highest abundance between all combinations in local plant community. A. Picture. B. Vogel. C. Withers, D. Minnie, E. No Name. F. Iron. Shrub species sampled at Comanche National Grassland: greasewood (*S. vermiculatus),* juniper (*J. monosperma),* rabbitbrush (*E. nauseosa)*, sandsage (*A. filifolia)*. skunkbush (*R. trilobata*).



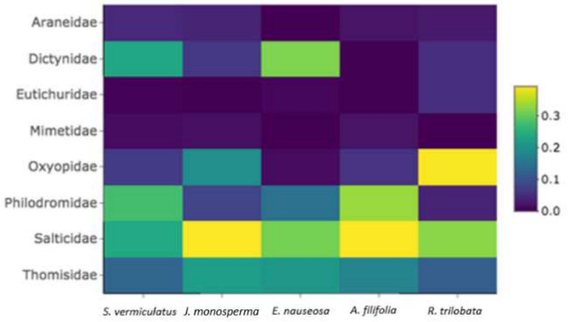
A. Picture canyon



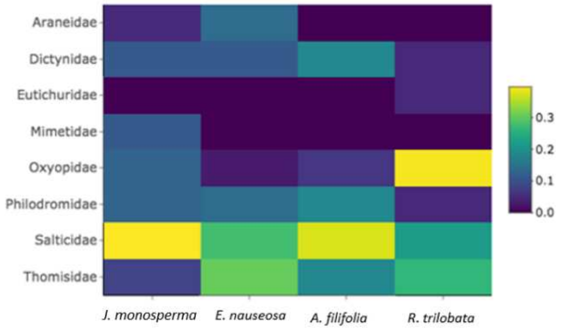
B. Vogel. Canyon



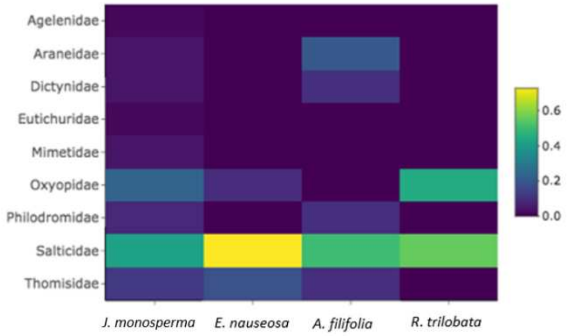
C. Withers canyon



D. Minnie canyon



E. No Name canyon



F. Iron canyon

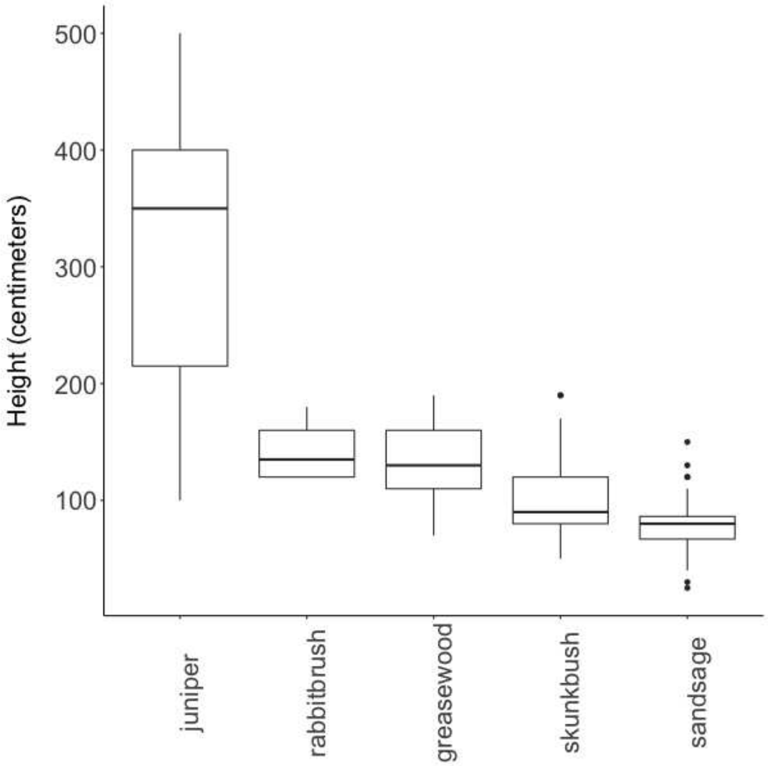


Figure S9. Results from shrub height, sampled of Comanche National Grassland, Colorado. Height in centimeters. Dots represent outliers. Bars represent maximum or minimum within range of 1.5 IQR rule.

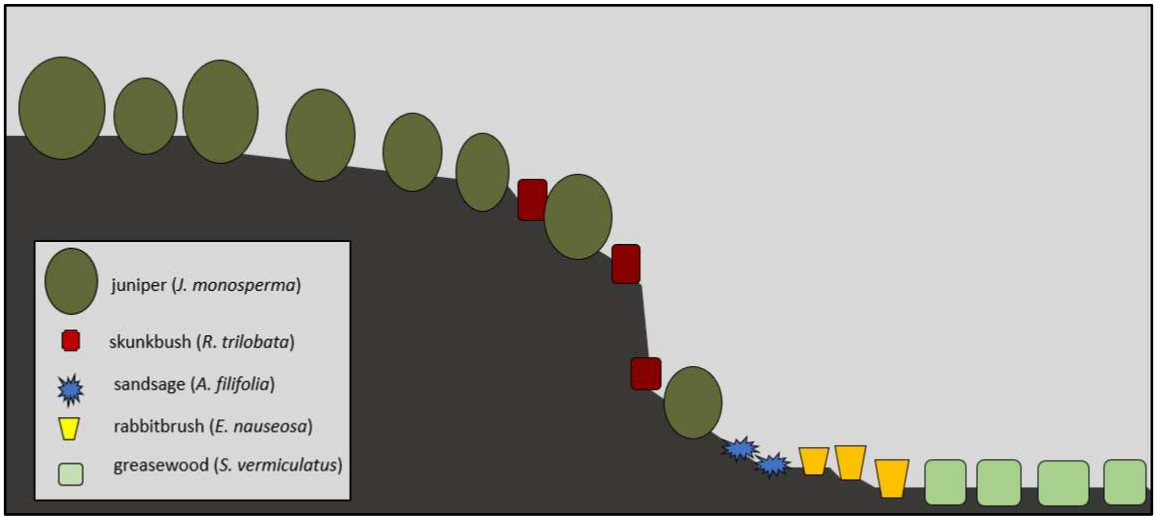


Figure S10. Cartoon of the elevation zone of shrubs sampled at Comanche National Grassland, Colorado.