EFFECTS OF INVASIVE PLANT SPECIES ON

NATIVE BEE COMMUNITIES IN THE SOUTHERN

GREAT PLAINS

By

KAITLIN M. O'BRIEN

Bachelor of Science in Rangeland Ecology &

Management

Texas A&M University

College Station, Texas

2015

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
May, 2017

EFFECTS OF INVASIVE PLANT SPECIES ON

NATIVE BEE COMMUNITIES IN THE SOUTHERN

GREAT PLAINS

Thesis Approved:

Dr. Kristen A. Baum

Thesis Adviser

Dr. Karen R. Hickman

Dr. Dwayne Elmore

ACKNOWLEDGEMENTS

I would like to begin by thanking my advisor, Dr. Kristen Baum, for all of her guidance and expertise throughout this research project. She is an exemplary person to work with, and I am so grateful to have shared my graduate school experience with her. I would also like to recognize my committee members, Dr. Karen Hickman and Dr. Dwayne Elmore, both of whom provided valuable insight to this project. A huge thank you goes out to the Southern Plains Network of the National Park Service, specifically Robert Bennetts and Tomye Folts-Zettner. Without them, this project would not exist, and I am forever grateful to have been involved with their network and parks, both as a research student and summer crew member. A special thank you for Jonathin Horsely, who helped with plot selection, summer sampling, and getting my gear around. I would also like to thank the Baum Lab members, always offering their support and guidance as we navigated through graduate school. And lastly, I would like to thank my family, especially my fiancé Garrett, for believing in me and supporting me as I pursued my goals.

Name: KAITLIN M. O'BRIEN

Date of Degree: MAY, 2017

Title of Study: EFFECTS OF INVASIVE PLANT SPECIES ON NATIVE BEE
COMMUNITIES IN THE SOUTHERN GREAT PLAINS

Major Field: INTEGRATIVE BIOLOGY

Abstract: The worldwide decline of native insect pollinators is of growing concern, as well as the decrease in populations of many flowering forbs. In the southern Great Plains region of the United States, grasslands are one of the most important vegetation types for providing resources to pollinators. Non-native and invasive plant species can alter grassland plant communities, although it is not clear how invasive plants affect native bee populations and communities. We evaluated the response of the native plant community and the native bee community across a gradient of invasion levels for two common invasive plants in the southern Great Plains: *Kochia scoparia* and *Salsola tragus*. Study sites were located within four National Parks, with approximately 10 plots representing the gradient of invasion levels sampled at each park, for a total of 40 plots. Pan traps were used to assess the native bee community and both native and non-native plant species and cover classes were recorded for each plot. Data were also recorded on bare ground availability due to its importance for solitary ground-nesting bees. Regression models were used to evaluate how the bee community (richness and abundance) responds to invasive plant species cover and bare ground cover, with an analysis performed for *K. scoparia* and *S. tragus* combined, since these two species commonly occur together and are expected to have similar impacts on the native bee community. Our findings suggest grasslands with no or low levels of invasive species support higher bee species richness, but did not affect abundance. Plots with higher levels of bare ground showed a significant correlation with bee richness. Possible factors contributing to the observed patterns could be the lack of floral resources from invasive plants (e.g. *K. scoparia* and *S. tragus*), which require limited insect pollination, and reduced abundance and diversity of native forbs. This study suggests that invasive plant species control is important for improving grasslands to support diverse native bee communities.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure   Page

CHAPTER I

INVASIVE PLANT SPECIES AND NATIVE BEE COMMUNITIES

Introduction

Native bees provide vital ecological and economical services to humans, and the decline of wild bee populations and communities will negatively affect global food sources (Klein et al. 2007, Potts et al. 2010, Vanbergen 2013, Cole et al. 2015). Insect pollinators provide increased crop yields for up to 70% of crop species, and account for 35% of agricultural production across the world (Klein et al. 2007, Vanbergen 2013, Cole et al. 2015). This amounts to pollination services valued at $215 billion globally (Gallai et al. 2008, Vanbergen 2013). While the major global food staples are dominated by wind pollinated or self-pollinated crops (e.g. corn, wheat), insect pollination accounts for the majority of fruit, nut, and vegetable crops, providing valuable micronutrients and diversity to human diets (Klein et al. 2007, Vanbergen 2013). In North America, farmers typically utilize commercial honeybees (*Apis mellifera*) to pollinate their crops. However, honeybees are not effective pollinators for some crops (like tomatoes) and do not provide all of the needed pollination services, increasing the importance of the native bee community (Kremen et al. 2002, Klein et al. 2007). Crop yields can be increased when nearby native plant communities promote and support native bee populations, and when crop diversity provides resources throughout the year (Kremen et al.

2002, Garibaldi et al. 2011, Vanbergen 2013). Thus, maintaining native bee populations and communities is critical for supporting agricultural production and a diverse food supply.

Grasslands, considered prime habitat for native bees, are one of the most endangered ecosystems in the world, with up to 99.9% of native tallgrass prairies lost. Most of the remaining areas have been developed for agricultural purposes like farming or managing introduced forage for grazing (Howe 1994, Samson & Knopf 1994, Mogren et al. 2016), and are prone to invasion by non-native plant species (Hejda et al. 2009, Twidwell et al. 2012). The remaining native grasslands often have multiple land uses and/or management practices, and varying levels of degradation. Pollination services are critical to maintaining native grassland plant diversity, which in turn provides habitat for pollinators (Ashman et al. 2004, Westphal et al. 2008). The decline of native insect pollinators is paralleled by a decrease in the populations of many flowering forbs (Westphal et al. 2008, Potts et al. 2010). While native grasslands are still prominent in the southern plains region, large tracts of land are managed for introduced forage for livestock grazing (Twidwell et al. 2012), and treated with herbicides to reduce unwanted species, which, limits the floral resources available to sustain native bee populations and communities.

The decline of native bees can be attributed to multiple factors, including habitat loss, fragmentation and degradation, intensification of agricultural practices, pesticide applications, and increased invasive species (Klein et al. 2007, Potts et al. 2010, Vanbergen 2013, Hung et al. 2015, Mogren et al. 2016). In the Great Plains of North America, fire suppression and the removal of grazing by large ungulates has also

contributed to grassland degradation, encroachment by woody species (Howe 1994, Fuhlendorf et al. 2008), and reduced species richness of native bee communities (Hung et al. 2015, Martin et al. 2015). Introduced forage species and improper grazing have further homogenized and degraded grasslands. Altogether, these practices have resulted in declines of native forb diversity (Fuhlendorf & Engle 2004). Furthermore, the most common crops in the region are in the Poaceae family, including corn (*Zea mays*), winter wheat (*Triticum aestivum*), and sorghum (*Sorghum bicolor*) (Friedman & Harder 2004). These staple crops are wind-pollinated and generally not visited by bees, resulting in additional fragmentation and isolation of bee habitats. While some flowering crops can provide floral resources in intensely managed areas, they typically do not provide enough resources during the full active period of native bees (Westphal et al. 2008, Vanbergen 2013, Mogren et al. 2016). Pesticide applications associated with crops and the use of herbicides to remove "weedy" species from rangelands and pastures have negatively affected bees by reducing floral resources (Potts et al. 2003, Potts et al. 2010). Thus, numerous agricultural practices, coupled with increasing urbanization, have contributed to the loss of pollinator habitat and driven the decline of native bees.

There is little documentation on the impacts of invasive plant species on grassland ecosystems in the context of how changes in the plant community could affect native bee populations and communities (Potts et al. 2010). Invasive species are a concern in the southern Great Plains, where habitat fragmentation and alteration of grasslands has contributed to an increased risk for invasion. Invasive species often outcompete native flora and decrease heterogeneity with opportunistic traits such as early emergence and rapid growth, creating monocultures that further fragment habitat (Vilà et al. 2009,

Wolkovich & Cleland 2014). Understanding how invasive plants affect native bees would provide important information for managing habitat for pollinators. There is speculation that some invasive plants, such as those that are entomophilous with showy flowers and floral resources (nectar and pollen), could support native generalist bees, but could be less useful for specialist pollinators (Lopezaraiza-Mikel et al. 2007, Stout & Morales 2009). It is also possible that monocultures of wind pollinated invasive plants could disrupt plant-pollinator interactions through displacement of native plant species and their associated floral resources (Ghazoul 2005, Potts et al. 2010). By altering the distribution and abundance of floral resources, as well as plant phenology and flowering times, invasive plants can have direct effects on plant-pollinator interactions. This project focuses on two invasive plants common within the southern Great Plains: *Kochia scoparia* and *Salsola tragus*.

Kochia scoparia is a weedy dicot native to Eurasia that was introduced into North America in the mid 1800's, and was planted as an ornamental shrub in gardens (Friesen et al. 2008). It belongs to the Chenopodiaceae (goosefoot) family, is an annual herb growing to over 2 m tall with a bushy shape, and is a prolific seed producer (Friesen et al. 2008). *Kochia scoparia* is an early colonizer and germinator with rapid growth rates adapted to arid and semi-arid regions, and survives well in the southern Great Plains (Friesen et al. 2008). It has a deep taproot system, and the plant will break off at the stem base, forming a "tumbleweed", which aids in seed dispersal by wind (Baker et al. 2008, Friesen et al. 2008). The goosefoot family contains a mixture of anemophilous and entomophilous plants (Blackwell & Powell 1981). Wind- and self-pollination are considered the primary forms of pollination for *K.scoparia*, but it is also thought to

4

benefit from bee pollination due to its extensive pollen production capabilities and flowering phenology (Blackwell & Powell 1981, Beckie et al. 2016).

Salsola tragus is also a member of the Chenopodiaceae family. Salsola is a genus of annual plants, often invading and dominating disturbed rangeland sites (Crompton & Bassett 1981). Salsola tragus was introduced from Europe in the late 1800's when flax seed was imported and planted, beginning the invasion process (Beatley 1973). It has naturalized in a variety of environmental conditions, being widely distributed across the U.S. (Crompton & Bassett 1981). Salsola is an herbaceous plant during its initial growth early in the season, hardening off and breaking at the stem to form a "tumbleweed", very similar to K. scoparia, and the prolific number of seeds is then dispersed as the plant is blown across the landscape (Baker et al. 2008). Salsola tragus is largely wind-pollinated, but similarly to K. scoparia, exhibits a flowering phenology that supports pollination by bees (Blackwell & Powell 1981, Beckie & Francis 2009). Both genera produce prolific amounts of pollen, with the emergence of stigmas on the plant lasting about a week as a receptacle for bee pollination (Crompton & Bassett 1981, Stallings et al. 1995, Beckie & Francis 2009). Large colonies and monocultures of both K. scoparia and S. tragus occur across the southern Great Plains, and could potentially influence native bee abundance and diversity by displacing native flora and modifying the availability of floral resources.

The first objective of this study was to determine the effect of invasive plant species on native bee communities in the southern Great Plains. I evaluated the native bee community along a gradient of invasion levels of the invasive species selected for this study, which were chosen based on their anticipated influence on the native bee community. This objective included an evaluation of bare ground availability as a factor

influencing the bee community, since bare ground is an important nesting substrate for ground nesting bees. While *K. scoparia* and *S. tragus* are predominantly wind-pollinated species, they also rely on insect pollination. Because of their emergence early in the spring, this could increase floral resources for generalist bees for a short period. However, once pollination has taken place, the presence of these invasive plants could have negative effects on the native bee community due to displacement of floral resources provided by the native plant community throughout the rest of the growing season. I discuss the results in the context of invasive species management practices for supporting pollinator habitat.

Methods

This study was conducted in coordination with the Southern Plains Network (SOPN), an Inventory and Monitoring Program branch of the U.S. Department of Interior- National Park Service. This network includes eleven parks across the states of Texas, Oklahoma, Kansas, Colorado, and New Mexico (Figure 1). We selected four parks for this study, based on the presence of native grasslands and the selected study species. *Kochia scoparia* and *S. tragus* were chosen because they are the most prominent invasive species across the study parks. While other invasive plant species are present, *Kochia* and *Salsola* occur at high densities and are two of the most problematic species. Mowing is the most common control method for *K. scoparia* and *S. tragus* across the study parks, with the goal of preventing seed set (T. Folts-Zettner, personal communication, Mar 14, 2016). Herbicide application was previously used, but both of these species show resistance to herbicides (T. Folts-Zettner, personal communication, Mar 14, 2016; Beckie et al. 2016). Prescribed fire is used as a general management tool

on all four parks, but not necessarily in association with invasive species control efforts, with fire locations occurring in different areas every few years. *Site Descriptions*

Washita Battlefield National Historic Site (WABA) is located 1.5 km northwest of Cheyenne, Oklahoma (Struthers et al. 2014). It is approximately 132 ha of primarily mixedgrass prairie. The park consists mostly of Tillman and Deandale series, Quintan, Vernon and Woodward soil series, with most of the original topsoil lost in the 1930's Dust Bowl (MLRA 78C 2016, Struthers et al. 2014). The average annual precipitation ranges from 560 to 760 mm, the average temperature ranges from 13 to 18°C and the growing season lasts approximately 230 days (MLRA 78C 2016). Management consists primarily of mowing, herbicide, and mechanical treatments. There are no livestock or grazing plans currently in place, but the land was historically used for livestock production similar to the surrounding area, starting in the early 1900's (Wilson 2009). Approximately one mile of the Washita River flows through the center of the park (Struthers et al. 2014), and flooded the park in 2015. Flooding occurred across most of the park, with the floodplain inundated for approximately four weeks starting late May of 2015, leading to high vegetation production late in the summer (R. Zahm, personal communication, Mar 21, 2016).

Lake Meredith National Recreation Area (LAMR) is located 65 km north of Amarillo, Texas. The park is approximately 18,202 ha surrounding the lake with upland and floodplain plant communities (Struthers et al. 2016). LAMR is mostly short- and mixedgrass prairie situated on the Texas High Plains and Rolling Plains. It is part of the Canadian River watershed, with the Sanford Dam creating the reservoir (Struthers et al. 2016). There are numerous soil series across the park, the most prominent being the

Alibates series, Manson series, Plemons series, and Ady series (MLRA 77E 2016). The average annual precipitation for LAMR is 405-635 mm, the average annual temperature ranges from 13 to 16°C and the growing season lasts approximately 215 days (MLRA 77E 2016). Various parts of the park receive herbicide application, mechanical treatments, mowing, and prescribed fire. There are no livestock or grazing plans in use, but the park has multiple trails, boat launches, off-roading trails, and camping and horseback riding areas. Lowland areas in the park were flooded in May of 2015.

Sand Creek Massacre National Historic Site (SAND) is located approximately 24 km northeast of Eads, Colorado. It is 966 ha and consists mostly of shortgrass prairie and sage shrubland, including the northwest and southeast corners as reclaimed cropland (Struthers et al. 2013). There are stands of cottonwood trees along the Big Sandy Creek that intermittently run through the park (Struthers et al. 2013). The soils on SAND are made up of Baca, Vona and Wiley series (MLRA 69 2016). The average annual precipitation on the park is 255 to 485 mm, the average temperature is 8 to 12°C and the growing season lasts approximately 170 days (MLRA 69 2016). There are presently no livestock, and management applications include herbicide, prescribed fire, and mowing. There are walking trails in the southwest corner of the park; however, most of the park is closed to visitors.

Bent's Old Fort National Historic Site (BEOL) is also located in southeastern Colorado, 13 km northeast of La Junta. The park is 324 ha, with a fort and multiple walking trails in addition to natural areas, and is surrounded by farms and ranches (Struthers et al. 2015). BEOL is classified as shortgrass prairie and includes wetland plant species along the Arkansas River, which flows through the park, supporting wetland and

riparian plant communities (Struthers et al. 2015). Much of the soils in the park are alluvial deposits from the river, and include Limon, Manvel and Rocky Ford series (MLRA 69 2016). The average annual precipitation for BEOL is approximately 255 to 485 mm, the average temperature is 8 to 12°C and the growing season lasts 170 days (MLRA 69 2016). Parts of the park are mowed for hay, and there is a small herd of oxen and two donkeys permanently living there. Other management methods include herbicide application, mowing, and mechanical removal. Prescribed fire is a rare occurrence.

Sampling Methods along an Invasive Species Gradient

Site Selection: Sites were chosen along a gradient of invasive species cover from 0% invasive species cover to approximately 75% invasive cover, so that plots represented different levels of cover along this gradient. Visual estimates and plant species density data previously collected through the SOPN were used for initial site selection. There were 10 plots sampled at each of the four parks, for 40 total plots. The data were combined across all sites to reflect the implications for the southern Great Plains region rather than individually evaluating each park. The GPS locations of the centers of each plot were recorded to ensure the same plots were sampled each visit. Plots were sampled during June and July (the sampling was combined as one sample for these two months due to logistical constraints associated with other ongoing surveys within the parks), August, and September for three total samples of each plot during 2016. Each sampling period included surveys for both the bee community and the plant community.

Bee Community: Pan traps, considered the most objective method for bee sampling (Gezon et al. 2015), were used to assess the species richness and abundance of the native bee community within each plot during 2016. Pan traps were placed in clusters

of three, with one white, one fluorescent blue, and one fluorescent yellow pan trap approximately 5 m apart arranged in a triangle. The pan trap colors represent different colors of flowers, with the selected colors being previously identified as collecting a diverse bee community (Stephen & Rao 2005, Vrdoliak & Samways 2011). There were three groups of three clusters of pan traps in each plot (or 9 total pan traps); clusters were located approximately 15 m apart, with the plot size (area sampled) around 55 x 55 m. In addition to the plot size, there was a buffer of 15 m around the pan trap array to reduce potential edge effects. Pan traps were placed in the field between 0700 to 0900 hours CDST and collected from 1400 to 1600 hours CDST. The insects collected in the pan traps were stored in vials (one per trap) with 70% ethanol until being prepared for identification.

Bees were identified to genus using Michener et al. (1994), and then further separated into morphospecies based on morphologically distinct characteristics. These morphospecies are intended to serve as a proxy for species and are referred to as species throughout the rest of this thesis. Based on identifications, species were also categorized based on nesting substrates and social behavior according to information available in the primary literature (Giles and Ascher 2006). All specimens will be deposited in the USDA ARS Bee Biology & Systematics Laboratory in Logan, Utah.

Plant Community: To estimate the density of the two invasive plant species chosen for this study, as well as native plant species, vegetation density was estimated using three, non-overlapping 10-m diameter quadrats placed within the same plots as the pan traps. Quadrat locations were randomized within the plot, and the plants, native and invasive, within each quadrat were identified to species to estimate species richness. Plant

species were categorized into functional groups (forb-blooming, forb-not in bloom, grass, woody), and classified as invasive or native, since there are other invasive plant species present besides the two chosen for this study. Bare ground cover was also estimated, since it is a vital habitat component for ground nesting bees. The Daubenmire Method was used to categorize the cover of each species and bare ground using the following categories: 1 (0-5%), 2 (>5-25%), 3 (>25-50%), 4 (>50-75%), 5 (>75-95%), 6 (>95-100%) (Towne et al. 2005). The data were used to classify each site according to varying levels of cover by the selected invasive species, as well as native and invasive plant floral resource availability for the native bee community.

Statistical Analysis

RStudio program was used for all analyses. Simple linear regression was used to analyze the relationship between bee species richness and abundance along the gradient of invasive species. Percent cover for *K. scoparia* and *S. tragus* was combined into one sum for each plot for the analyses due to the similarity of the species, which we anticipated would have similar effects on plant and pollinator communities. They also tended to co-occur in many locations. Analyses were performed on the effects of different levels of grass cover, forb cover and bare ground cover. Shapiro-Wilk normality tests were performed on the species richness and abundance before the analyses, and the data were normally distributed.

Results

Native Bee Richness and Abundance

A total of 6,959 Apiformes specimens were collected from June-September 2016, representing 35 different genera and 63 species. Twenty-five genera and 43 species were

collected at LAMR, 25 genera and 45 species at BEOL, 21 genera and 40 species at

SAND, and 19 genera and 34 species at WABA (Table 1). 2,219 bees were collected at

LAMR, while WABA and SAND both had just over 1,600 bees collected. BEOL had

1,456 bees collected. Five families were represented in the study: Andrenidae (12

species, 561 individuals), Apidae (29 species, 1,009 individuals), Colletidae (2 species, 6

individuals), Halictidae (10 species, 5,299 individuals) and Megachilidae (10 species, 84

individuals) (Table 1). Halictidae comprised approximately 76% of the bees collected,

and Apidae was the second most abundant family representing 14% of specimens. The

most abundant genus was *Halictus*, with 2,193 individuals or 32% of the specimens

collected. In terms of behavioral traits, 60.94% of individuals were eusocial, 26.68%

were solitary, and less than 1% (0.62) was parasitic. The remaining 11.76% did not have

clear behavioral traits documented in the literature. The majority of individuals (86.90%)

were soil nesters. Only 0.39% of specimens were cavity nesting, and 0.33% were hive

nesting (Table 1). Nesting substrates for parasitic bees rely on one or more host species,

and therefore are not included in the other categories, and account for less than 1% of

individuals. The remaining 11.73% were for individuals lacking well-documented nesting

substrate patterns.

There was a significant effect of invasive plant cover on the number of genera

collected (Figure 2; $F(1,32)=4.044$, $p=0.05$, $R^2=0.08445$). While the relationship was

significant, the correlation of the model was weak. The percentage of bare ground

showed a significant effect on genera richness, but also a weak correlation (Figure 3;

$F(1,32)=7.306$, $p=0.01$, $R^2=0.1604$). Finally, percent cover of native forbs was not

significantly correlated with the number of genera (Figure 4; $F(1,32)=0.8159$, $p=0.3731$,

R^2=-.005609). While invasive plant cover did not significantly affect bee species richness (Figure 5; $F_{(1,32)}$=2.884, p=0.099, R^2=0.05401), it was significantly impacted by bare ground cover (Figure 6; $F_{(1,32)}$=4.998, p=0.03, R^2=0.1081). Native forb cover also did not significantly influence the species richness of bees (Figure 7; $F_{(1,32)}$=0.2332, p=0.6325, R^2=-0.02379). No significant relationships were found between native bee abundance and the cover categories (Figures 8-10; invasive species: $F_{(1,32)}$=0.04287, p=0.8373, R^2=-0.02987; bare ground: $F_{(1,32)}$=0.589, p=0.4484, R^2=-0.01261; native forb: $F_{(1,32)}$=1.915, p=0.176, R^2=0.02697).

I documented 124 native and non-native plant species, representing 28 families across the four parks; this included 36 grasses, 73 forbs, 12 shrubs, and 3 trees (Table 2). Invasive plant cover significantly impacted the species richness of native grasses (Figure 11; $F_{(1,32)}$=17.42, p=0.00, R^2=0.3323). Invasive plant cover also significantly affected the species richness of native forbs (Figure 12; $F_{(1,32)}$=24.74, p=0.00, R^2=0.4185).

Discussion

The percent cover of *K. scoparia* and *S. tragus* influenced native bee richness, although this relationship was weak. There was no effect of percent cover of *K. scoparia* and *S. tragus* on native bee abundance. However, the number of bee genera seemed to increase again at very high levels of invasive plant cover (Figure 2). This pattern suggests the possibility of a threshold for invasive plant species cover affecting native bee communities. While lower levels of invasive plants have fewer impacts on the native plant community, high levels of invasive plant cover potentially displace floral resources for native bees (Lopezaraiza-Mikel et al. 2007). There are obvious differences between native plant communities and those dominated by invasive species. While the *Kochia* and

Salsola genera are predominantly wind-pollinated, both have been documented as benefitting from varying levels of insect pollination, mainly by bees in the Colletidae and Halictidae families (Beckie & Francis 2009). The broad pollination schemes of these plants could influence the bee community in different ways. *Kochia scoparia* and *S. tragus* could potentially provide floral resources for generalist bees in the spring, since both emerge early in the growing season. However, this could negatively affect specialist bees that are unable to utilize pollen from invasive plants, which displace the native floral resources required by these bees. These invasives bloom in the spring, and the floral resources they potentially provide would not be enough to support native bee communities throughout their entire activity period.

When invasive plant species requiring insect pollination establish in a novel environment, they typically depend on generalist pollinators (Palladini & Maron 2014), and can potentially facilitate pollination services for some native plants (Bartomeus et al. 2008, Goodell & Parker 2017) by attracting higher numbers of native bees into invaded areas. Species richness for native grasses and native forbs significantly decreased in *K. scoparia* and *S. tragus* invaded plots (Figures 11 & 12). While *K. scoparia* and *S. tragus* reduced the plant diversity within study sites, there was still an increased presence of native bees in highly invaded plots, which could suggest that the invasives are facilitating a higher number of generalist bees. Both *K. scoparia* and *S. tragus* have a limited time window for insect pollination to occur, and pollinator facilitation of native plants would be brief when considering the entire active period of native bees throughout the growing season. The facilitation of pollinators would also be limited by the level of floral specialization among different bee species. While generalists would benefit, there is still

a potential for decreases in plant species that require specialized pollinators, and thus fewer specialist bees (Albrecht & Ramis 2016). For example, Palladini & Maron (2014), documented an increase in bee visitation to native plants in invaded ecosystems, but also recorded fewer visits to specialized flowering species.

The level of floral specialization by the bees captured could also explain the higher numbers of genera found in highly invaded areas. Generalist bees may adapt more easily to novel, non-native plant species than specialist pollinators. Specialist bees that require floral resources from specific genera or species of native plants are expected to decline as native plant floral resources decline. Because no significant patterns were observed for bee abundance, there were potentially greater numbers of generalist bees in plots with high levels of invasive plant cover and more specialist bees in plots with very low invasive plant cover. This is especially true given that *K. scoparia* and *S. tragus* are both thought to be pollinated by sweat bees (Beckie & Francis 2009), which occurred at the highest abundance throughout the sampling period, including invaded plots.

Native bee communities not only depend on the availability of floral resources, but also the availability of nesting substrates within their foraging range. The majority of species documented in this study were solitary, ground nesting bees. The percentage of bare ground in each plot was estimated to evaluate habitat availability for these species. Genus and species richness were significantly correlated with the percentage of bare ground (Figures 3 & 6), suggesting that habitat quality is improved with the availability of both floral resources and nesting substrates. Nesting substrates are sometimes considered to be a limiting factor for native bee communities (Potts et al. 2005), and a lack of suitable nesting habitat even in the presence of adequate floral resources, could

negatively influence bee populations. It can also be difficult to quantify suitable nesting

substrates, since multiple factors influence site selection for solitary ground nesting bees,

including soil texture, moisture, slope, and compaction, with preferences varying among

bee species (Cane 1991).

Few management practices occurred on the plots during the study. Herbicide was

used on *K. scoparia* and *S. tragus* dominated plots after the June/July sample was taken

at LAMR and BEOL. Because these plots were already lacking in floral resources due to

the high cover of both of these invasive species, and since herbicide application occurred

after the blooming period, it most likely did not adversely affect the native bee

community. Effects of herbicide applications could become more evident over time, and

if resampling occurred in the next growing season pre- and post- herbicide application.

Changes may be difficult to detect when there are so few floral resources present prior to

herbicide use.

Limitations to the Study

Analyses were performed on the genus and species richness of native bees.

LeBuhn et al. (2013) suggest a high number of sites (100-300) should be sampled to

detect a 2% to 5% decline in species richness or abundance for a particular regional or

national monitoring program. In this case, we had 40 sites across the southern Great

Plains. The National Protocol Framework for Inventory and Monitoring of Bees notes

that sampling with pan traps should provide adequate data to detect changes in the native

bee community for a single site at the genus level (Droege et al. 2016). This provides one

explanation for why our data were significantly influenced by invasive plant cover for

bee genera and not bee species richness, as well as the multi-state region in which the sampling for the study occurred.

While pan traps are one of the most objective methods for sampling native bees (i.e., there is no observer bias), bee visitation and capture by pan traps can be influenced by floral resource availability (Cane et al. 2000, Baum & Wallen 2011). It is suggested that capture rates of pan traps may be negatively correlated with the availability of floral resources (Cane et al. 2000, Mayer 2005, Roulston et al. 2007, Wilson et al. 2008, Baum & Wallen 2011). In this study, plots with more than 75% invasive plant cover were lacking in floral resources from native plants throughout the season, making it likely that bees would be more readily attracted to the brightly colored pan traps. *Kochia scoparia* and *S. tragus* tend to bloom from May through early June, providing pollen for a short period early in the season, but leaving plots with minimal floral resources for the remainder of the growing season. Plots with abundant floral resources provide competition for the pan traps; therefore, the pan traps may not be as attractive to bees in plots with more floral resources. Future research should incorporate multiple approaches for assessing the native bee community to address these concerns.

Conclusion

As native grasslands continue to be lost and degraded, it is important to understand the impacts that invasive plants have on plant-pollinator interactions. While grassland plant communities provide floral resources and nesting habitat, they require critical pollination services provided by native bees that maintain the diversity of the flora. When this dynamic is interrupted by invasive plant species, changes to the plant and pollinator communities can occur. Understanding the effects that these invasive

plants have on the native bee community will provide the information needed to develop management strategies to improve pollinator habitat and control invasive species. Our findings suggest that native bee communities are affected by invasive species, but that the invasive plants are only one component in the ecosystem contributing to the observed patterns. Future studies should incorporate other factors, including landscape level interactions that could influence native bee communities. The composition of the bee community and level of floral specialization among species should also be considered. Management practices should focus on controlling invasive species while promoting native forb abundance and diversity, as well as the availability of nesting sites to support a variety of generalist and specialist native bees.

REFERENCES

Albrecht, M., M.R. Ramis. Pollinator-mediated Impacts of Alien Invasive Plants on the Pollination of Native Plants: the Role of Spatial Scale and Distinct Behavior Among Pollinator Guilds. *Biological Invasions* 2016, 18:101-1812.

Ashman, T.L., T.M. Knight, J.A. Steets, P. Amarasekare, M. Burd, D.R. Campbell, M.R. Dudash, M.O. Johnston, S.J. Mazer, R.J. Mitchell, M.T. Morgan, W.G. Wilson. Pollen Limitation of Plant Reproduction: Ecological and Evolutionary Causes and Consequences. Ecology 2004, 85(9):2408-2421.

Baum, K.A. & K.E. Wallen. Potential Bias in Pan Trapping as a Function of Floral Abundance. *Journal of the Kansas Entomological Society* 2011, 84(2):155-159.

Baker, D.V., K.G. Beck, B.J. Bienkiewicz, L.B. Bjostad. Forces Necessary to Initiate Dispersal for Three Tumbleweeds. *Weed Science* 2008, 1(1):59-65.

Bartomeus, I., M. Vilà, L. Santamaría. Contrasting Effects of Invasive Plants in Plant-Pollinator Networks. *International Association for Ecology* 2008, 155:761-770.

Beatley, J.C. Russian-Thistle (*Salsola*) Species in Western United States. *Journal of Range Management* 1973, 26(3):225-226.

Beckie, H.J., & A. Francis. The Biology of Canadian Weeds. 65. *Salsola tragus* L. (updated). *Canadian Journal of Plant Science* 2009, 89(4):775-789.

Beckie, H.J., R.E. Blackshaw, L.M. Hall, E.N. Johnson. Pollen- and Seed-Mediated Gene Flow in Kochia (*Kochia scoparia*). *Weed Science* 2016, 64:624-633.

Blackwell, W.H. & M.J. Powell. A Preliminary Note on Pollination in the

    Chenopodiaceae. *Annals of the Missouri Botanical Garden* 1981, 68: 524-526.

Cane, J.H. Soils of Ground-Nesting Bees (Hymenoptera: Apoidea): Texture, Moisture,

    Cell Depth and Climate. *Journal of the Kansas Entomological Society* 1991,

    64:406-413.

Cane, J.H., R.L. Minckley, & L.J. Kervin. Sampling Bees (Hymenoptera: Apiformes) for

    Pollinator Community Studies: Pitfalls of Pan-trapping. *Journal of the Kansas*

    Entomological Society 2000, 73(4):225-231.

Cole, L.J., S. Brocklehurst, D. Robertson, W. Harrison, D.I. McCracken. Riparian Buffer

    Strips: Their Role in the Conservation of Insect Pollinators in Intensive Grassland

    Systems. *Agriculture, Ecosystems and Environment* 2015, 211:207-220.

Crompton, C.W. & I.J. Bassett. The Biology of Canadian Weeds, *Salsola pestifer* A.

    Nels. *Canadian Journal of Plant Science* 1981, 65: 379-388

Droege, S., J. Engler, E. Sellers, L. O'Brien. 2016. National Protocol Framework for the

    Inventory and Monitoring of Bees. Inventory and Monitoring, National Wildlife

    Refuge System, U.S. Fish and Wildlife Service, Fort Collins, Colorado.

Friedman, J. & L.D. Harder. Inflorescence Architecture and Wind Pollination in Six

    Grass Species. *Functional Ecology* 2004, 18:851-860.

Friesen, L.F.,H.J. Beckie, S.I. Warwick, R.C. Van Acker. The Biology of Canadian

    Weeds. *Kochia scoparia* (L.) Schrad. *Canadian Journal of Plant Science.* 2008,

    89:141-167.

Fuhlendorf, S.D., D.M. Engle. Application of the Fire: Grazing Interaction to Restore a

> Shifting Mosaic on Tallgrass Prairie. *Journal of Applied Ecology* 2004, 41:604-
> 614.

Fuhlendorf, S.D., D.M. Engle, J. Kerby, R. Hamilton. Pyric Herbivory: Rewilding

> Landscapes through the Recoupling of Fire and Grazing. *Conservation Biology*
> 2008, 23:588-598.

Gallai, N., J.M. Salles, J. Settele, B.E. Vaissiere. Economic Valuation of the

> Vulnerability of World Agriculture Confronted with Pollinator Decline.
> *Ecological Economics* 2008, 68:810-821.

Garibaldi, L.A., I. Steffan-Dewenter, C. Kremen, J.M. Morales, R. Bommarco, S.A.

> Cunningham, L.G. Carvalheiro, N.P. Chacoff, J.H. Dudenhöffer, S.S. Greenleaf,
> A. Holzschuh, R. Isaacs, K. Krewenka, Y. Mandelik, M.M. Mayfield, L.A.
> Morandin, S.G. Potts, T.H. Ricketts, H. Szentgyörgyi, B.F. Viana, C. Westphal,
> R. Winfree, A.M. Klein. Stability of Pollination Services Decreases with Isolation
> from Natural Areas despite Honey Bee Visits. *Ecology Letters* 2011, 14:1062-
> 1072.

Gezon, Z.J., E.S. Wyman, J.S. Ascher, D.W. Inouye, R.E. Irwin. The Effect of Repeated,

> Lethal Sampling on Wild Bee Abundance and Diversity. *Methods in Ecology and*
> *Evolution* 2015, 6(9):1044-1054.

Ghazoul, J. Buzziness as Usual? Questioning the Global Pollination Crisis. *Trends in*

> *Ecology and Evolution* 2005, 20:367-373.

Giles, V. & J.S. Ascher. A Survey of the Bees of the Black Rock Forest Preserve, New

York (Hymenoptera: Apoidea). *Journal of Hymenoptera Research* 2006,

15(2):208-231.

Goodell, K., I.M. Parker. Invasion of a Dominant Floral Resource: Effects on the Floral

Community and Pollination of Native Plants. *Ecology* 2017, 98(1):57-69.

Hejda, M., P. Pysek, V. Jarosik. Impact of Invasive Species on the Species Richness,

Diversity and Composition of Invaded Communities. *Journal of Ecology* 2009,

97:393-403.

Hung, K.L.J., J.S. Ascher, J. Gibbs, R.E. Irwin, D.T. Bolger. Effects of Fragmentation on

a Distinctive Coastal Sage Scrub Bee Fauna Revealed Through Incidental

Captures by Pitfall Traps. *Journal of Insect Conservation* 2015, 19:175-179.

Howe, H.F. Managing Species Diversity in Tallgrass Prairie: Assumptions and

Implications. *Conservation Biology* 1994, 8:691-704.

Klein, A.M., B.E. Vaissiere, J.H. Cane, I. SteffanDewenter, S.A. Cunningham, C.

Kremen, T. Tscharntke. Importance of Pollinators in Changing Landscapes for

World Crops. *Proceedings of the Royal Society* 2007, 274:303-313.

Kremen, C., N.M. Williams, R.W. Thorp. Crop Pollination from Native Bees at Risk

from Agricultural Intensification. *Proceedings of the National Academy of

Sciences of the United States* 2002, 99:16812-16816.

LeBuhn, G., S. Droege, E.F. Connor, B. Gemmill-Herren, S.G. Potts, R.L. Minckley, T.

Griswold, R. Jean, E. Kula, D.W. Roubik, J. Cane, K.W. Wright, G. Frankie, F.

Parker. Detecting Insect Pollinator Declines on Regional and Global Scales.

Conservation Biology 2013, 27(1):113-120.

Lopezaraiza-Mikel, M.E., R.B. Hayes, M.R. Whalley, J. Memmott. The Impact of an
Alien Plant on a Native Plant-Pollinator Network: an Experimental Approach.
Ecology Letters 2007, 10:539-550.

Martin, L.M., M.A. Harris, B.J. Wilsey. Phenology and Temporal Niche Overlap Differ
Between Novel, Exotic- and Native-Dominated Grasslands for Plants, but not for
Pollinators. *Biological Invasions* 2015, 17:2633-2644.

Mayer, C. Does Grazing Influence Bee Diversity? *In* B.A. Huber, B.JJ. Sinclair, and K.H.
Lampe (eds.). *African Biodiversity: Molecules, Organisms, Ecosystems* 2005, pp.
173-179, Springer, New York. 443 pp.

Michener, C.D., R.J. McGinley, B.N. Danforth. The Bee Genera of North and Central
America. Smithsonian Institute Press 1994.

MLRA 69- Upper Arkansas Valley Rolling Plains. Land Resource Regions and Major
Land Resources Areas of the United States, the Caribbean, and the Pacific Basin.
USDA Agriculture Handbook 296, 2006.

MLRA 77E- Southern High Plains, Breaks. Land Resource Regions and Major Land
Resources Areas of the United States, the Caribbean, and the Pacific Basin.
USDA Agriculture Handbook 296, 2006.

MLRA 78C- Central Rolling Red Plains, Eastern Part. Land Resource Regions and Major
Land Resources Areas of the United States, the Caribbean, and the Pacific Basin.
USDA Agriculture Handbook 296, 2006.

Mogren, C.L., T.A. Rand, S.W. Fausti, J.G. Lundgren. The Effects of Crop
Intensification on the Diversity of Native Pollinator Communities. *Environmental
Entomology* 2016, 45:865-872.

Palladini, J.D., J.L. Maron. Reproduction and Survival of a Solitary Bee Along Native

    and Exotic Floral Resource Gradients. *Oecologia* 2014, 176:789-798.

Plants Database. United States Department of Agriculture- Natural Resources

    Conservation Service 2017. < https://plants.usda.gov/java/>

Potts, S.G., B. Vulliamy, A. Dafni, G. Ne'eman, P. Willmer. Linking Bees and Flowers:

    How do Floral Communities Structure Pollinator Communities? *Ecology* 2003,

    84(10):2628-2642.

Potts, S.G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'Eman, P. Willmer.

    Role of Nesting Resources in Organizing Diverse Bee Communities in a

    Mediterranean Landscape. *Ecological Entomology* 2005, 30:78-85.

Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, W.E. Kunin. Global

    Pollinator Declines: Trends, Impacts and Drivers. *Trends in Ecology and*

    Evolution 2010, 25:345-353.

Roulston, T.H., S.A. Smith, A.L. Brewster. A Comparison of Pan Trap and Intensive Net

    Sampling Techniques for Documenting Bee (Hymenoptera: Apiformes) Fauna.

    Journal of the Kansas Entomological Society 2007, 80:179-181.

Samson, F. & F. Knopf. Prairie Conservation in North America. *BioScience* 1994,

    44:418-421.

Stallings, G.P., D.C. Thill, C.A. Mallory-Smith, B. Shaf'ii. Pollen-Mediated Gene Flow

    of Sulfonylurea-Resistant Kochia (*Kochia scoparia*). *Weed Science* 1995,

    43(1):95-102.

Stephen, W.P. & S. Rao. Unscented Color Traps for Non-Apis Bees (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society* 2005, 78:373-380.

Stout, J.C. & C.L. Morales. Ecological Impacts of Invasive Alien Species on Bees. *Apidologie* 2009, 40:388-409.

Struthers, K., R.E. Bennetts, N. Chambers, T. Folts-Zettner, H. Sosinski, P. Valentine-Darby. (2013). Sand Creek Massacre National Historic Site Natural Resource Condition Assessment. Natural Resource Report NPS/SOPN/NRR- 2013/734.

Struthers, K., R.E. Bennetts, N. Chambers, T. Folts-Zettner, H. Sosinski, P. Valentine-Darby. (2014). Washita Battlefield National Historic Site Natural Resource Condition Assessment. Natural Resource Report NPS/SOPN/NRR- 2014/748.

Struthers, K., R.E. Bennetts, P. Valentine-Darby, N. Chambers, T. Folts-Zettner, H. Sosinski. (2015). Bent's Old Fort National Historic Site Natural Resource Condition Assessment. Natural Resource Report NPS/SOPN/NRR- 2015/998.

Struthers, K., P. Valentine-Darby, N. Chambers, A. Mathis, D. Shorrock, R.E. Bennetts, T. Folts-Zettner, H. Sosinski. (2016). Lake Meredith National Recreation Area/Alibates Flint Quarries National Monument Natural Resource Condition Assessment. Natural Resource Report NPS/SOPN/NRR- 2016/1124.

Towne, G.E., D.C. Hartnett, R.C. Cochran. Vegetation Trends in Tallgrass Prairie From Bison and Cattle Grazing. *Ecological Applications* 2005, 15(5):1550-1559.

Twidwell, D., W.E. Rogers, E.A. McMahon, B.R. Thomas, U.P. Kreuter, T.R. Blankenship. Prescribed Extreme Fire Effects on Richness and Invasion in Coastal Prairie. *Invasive Plant Science and Management* 2012, 5:330-340.

Vanbergen, A.J., Insect Pollinators Initiative. Threats to an Ecosystem Service: Pressures on Pollinators. *The Ecological Society of America* 2013, 11:251-259.

Vilà, M., I. Bartomeus, A.C. Dietzsch, T. Petanidou, I. Steffan-Dewenter, J.C. Stout, T. Tscheulin. Invasive Plant Integration into Native Plant-Pollinator Networks Across Europe. *Proc. R. Soc. B* 2009, 276:3887-3893.

Vrdoljak, S.M., & M.J. Samways. Optimizing Coloured Pan Traps to Survey Flower Visiting Insects. *Journal of Insect Conservation* 2011, 16:345-354.

Westphal, C., R. Bommarco, G. Carre, E. Lamborn, N. Morison, T. Petanidou, S. Potts, S.P.M. Roberts, H. Szentgyorgyi, T. Tscheulin, B.E. Vaissiere, M. Woyciechowski, J.C. Biesmeijer, W.E. Kunin, J. Settele, I. Steffan-Dewenter. Measuring Bee Diversity in Different European Habitats and Biogeographical Regions. *Ecological Monographs* 2008, 78:653-671.

Wilson, J.S., T. Griswold, & O.J. Messinger. Sampling Bee Communities (Hymenoptera: Apiformes) in a Desert Landscape: are Pan Traps Sufficient? Journal of the Kansas Entomological Society 2008, 81(3):288-300.

Wilson, L.D. 2009. "Roger Mills County," Encyclopedia of Oklahoma History and Culture. www.okhistory.org.

Wolkovich, E.M. & E.E. Cleland. Phenological Niches and the Future of Invaded Ecosystems with Climate Change. *AoB Plants* 2014, 6: plu013.

APPENDICES

Table 1. Native bee species collected at Washita Battlefield NHS, Lake Meredith NRA, Sand Creek Massacre NHS, and Bent's Old Fort NHS, 2016. Nomenclature followed Michener (1994) and life history traits were derived from classifications by Giles and Ascher (2006). Occurrence denotes the parks in which a species was collected.

Species	Family	Occurrence[a]				Abundance	% Individuals	Behavior[b,d]	Nest Substrate[c,e]
Agapostemon	Halictidae	W	L	S	B	269	3.87%	S	S
Andrena	Andrenidae		L	S	B	6	0.09%	S	S
Anthidium	Megachilidae		L		B	6	0.09%	S	C
Anthophora 1	Apidae	W	L	S	B	9	0.13%	S	S
Anthophora 2	Apidae				B	2	0.03%	S	S
Apis	Apidae		L		B	7	0.10%	E	H
Augochlorella	Halictidae	W	L		B	33	0.47%	E	S
Augochloropsis	Halictidae	W	L		B	812	11.67%	S	S
Bombus	Apidae	W	L		B	16	0.23%	E	H
Calliopsis	Andrenidae	W				2	0.03%	S	S
Centris 1	Apidae	W				1	0.01%	S	S
Centris 2	Apidae		L			1	0.01%	S	S
Coelioxys	Megachilidae			S		2	0.03%	P	-
Colletes	Colletidae		L		B	5	0.07%	S	S
Diadasia	Apidae		L	S	B	51	0.73%	S	S
Dianthidium 1	Megachilidae	W		S	B	3	0.04%	S	C
Dianthidium 2	Megachilidae		L	S	B	5	0.07%	S	C
Dianthidium 3	Megachilidae			S	B	10	0.14%	S	C
Exomalopsis 1	Apidae	W		S	B	4	0.06%	N/A	N/A
Exomalopsis 2	Apidae	W	L		B	31	0.45%	N/A	N/A
Exomalopsis 3	Apidae		L	S	B	32	0.46%	N/A	N/A
Exomalopsis 4	Apidae		L	S	B	14	0.20%	N/A	N/A
Exomalopsis 5	Apidae		L	S	B	51	0.73%	N/A	N/A
Florilegus	Apidae	W	L	S	B	145	2.08%	N/A	N/A
Halictus 1	Halictidae	W	L	S	B	2148	30.87%	E	S
Halictus 2	Halictidae	W	L		B	14	0.20%	E	S
Halictus 3	Halictidae	W	L	S	B	31	0.45%	E	S
Heterosarus	Andrenidae			S		1	0.01%	N/A	N/A
Holcopasites	Apidae				B	1	0.01%	N/A	N/A
Hylaeus	Colletidae		L			1	0.01%	S	C
Lasioglossum 1	Halictidae	W	L	S	B	872	12.53%	E	S

28

Lasioglossum 2	Halictidae	W	L		B	216	3.10%	E	S
Lasioglossum 3	Halictidae	W	L	S	B	904	12.99%	E	S
Lithurge 1	Megachilidae	W	L	S	B	44	0.63%	N/A	N/A
Lithurge 2	Megachilidae	W		S	B	10	0.14%	N/A	N/A
Lithurgus	Megachilidae			S		1	0.01%	N/A	N/A
Megachile	Megachilidae				B	1	0.01%	S	C
Melissodes	Apidae		L		B	3	0.04%	S	S
Melitoma	Apidae			S	B	4	0.06%	N/A	N/A
Nomada	Apidae	W		S		7	0.10%	P	-
Osmia	Megachilidae		L			2	0.03%	S	C
Panurginus	Andrenidae			S		2	0.03%	N/A	N/A
Peponapis 1	Apidae	W	L	S	B	15	0.22%	S	S
Peponapis 2	Apidae	W	L		B	10	0.14%	S	S
Peponapis 3	Apidae	W	L	S	B	59	0.85%	S	S
Peponapis 4	Apidae	W	L	S	B	34	0.49%	S	S
Perdita 1	Andrenidae	W	L	S	B	25	0.36%	S	S
Perdita 2	Andrenidae	W		S		20	0.29%	S	S
Perdita 3	Andrenidae	W				3	0.04%	S	S
Perdita 4	Andrenidae	W	L	S		79	1.14%	S	S
Perdita 5	Andrenidae	W				4	0.06%	S	S
Perdita 6	Andrenidae			S	B	318	4.57%	S	S
Perdita 7	Andrenidae		L	S		19	0.27%	S	S
Perdita 8	Andrenidae		L			9	0.13%	S	S
Perdita 9	Andrenidae		L			73	1.05%	S	S
Svastra	Apidae	W	L	S	B	53	0.76%	N/A	N/A
Tetraloniella 1	Apidae	W	L	S	B	415	5.96%	N/A	N/A
Tetraloniella 2	Apidae	W	L	S		9	0.13%	N/A	N/A
Tetraloniella 3	Apidae				B	1	0.01%	N/A	N/A
Triepeolus 1	Apidae	W		S	B	5	0.07%	P	-
Triepeolus 2	Apidae		L	S	B	13	0.19%	P	-
Triepeolus 3	Apidae		L	S		4	0.06%	P	-
Triepeolus 4	Apidae		L			1	0.01%	P	-
Triepeolus 5	Apidae			S	B	11	0.16%	P	-

[a]Occurrence- Washita Battlefield National Historic Site (W), Lake Meredith National Recreation Area (L), Sand Creek

National Historic Site (S), and Bent's Old Fort National Historic Site (B)

[b]Species were characterized as solitary (S) or communal (eusocial (E) or parasitic (P))

[c]Known nesting substrate of non-parasitic bees was categorized as soil (S), cavity (C), or hive (H)

[d]Not applicable due to insufficient data

[e]Nesting substrate for parasitic bees is unavailable due to parasitic species relying on one or multiple host species

Table 2. Comprehensive list of all native and non-native plant species found on Washita Battlefield National Historic Site, Lake Meredith National Recreation Area, Sand Creek Massacre National Historic Site, and Bent's Old Fort National Historic Site, 2016. Occurrence was classified by park, and plant names followed the most recent and accepted nomenclature by USDA-NRCS Plants Database (2017).

Species	Family	Occurrence[1]			
Abronia fragrans	Nyctaginaceae				SAND
Amaranthus	Amaranthaceae	WABA			
Ambrosia artemisifolia	Asteraceae			BEOL	
Ambrosia psilostachya	Asteraceae	WABA	LAMR		SAND
Amorpha canescens	Fabaceae		LAMR		SAND
Amphiachyris dracunculoides	Asteraceae	WABA	LAMR		
Andropogon gerardii	Poaceae	WABA	LAMR		
Aristida oligantha	Poaceae		LAMR		
Aristida purpurea	Poaceae	WABA	LAMR	BEOL	SAND
Artemisia filifolia	Asteraceae	WABA	LAMR	BEOL	SAND
Artemisia ludoviciana	Asteraceae	WABA	LAMR		SAND
Artemisia sp.	Asteraceae		LAMR		
Asclepias engelmanniana	Asclepiadaceae			BEOL	SAND
Asclepias latifolia	Asclepiadaceae			BEOL	
Asclepias verticillata	Asclepiadaceae			BEOL	SAND
Aster sp.	Asteraceae				SAND
Bothriochloa ishaemum	Poaceae	WABA	LAMR		
Bothriochloa laguroides	Poaceae	WABA	LAMR		
Bouteloua curtipendula	Poaceae	WABA	LAMR	BEOL	SAND
Bouteloua dactyloides	Poaceae		LAMR		SAND
Bouteloua eriopoda	Poaceae		LAMR		
Bouteloua gracilis	Poaceae	WABA	LAMR	BEOL	SAND
Bouteloua hirsuta	Poaceae		LAMR		
Bromus japonicus	Poaceae	WABA			
Bromus tectorum	Poaceae			BEOL	
Callirhoe involucrata	Malvaceae				SAND
Castilleja occidentalis	Scrophulariaceae	WABA			
Centaurea americana	Asteraceae		LAMR		
Chamaecrista nictitans	Fabaceae	WABA			
Chenopodium album	Chenopodiaceae		LAMR		SAND
Cirsuim ochrocentrum	Asteraceae	WABA	LAMR		SAND
Convolvulus (native)	Convolvulaceae		LAMR		
Convolvulus arvensis	Convolvulaceae	WABA	LAMR	BEOL	
Conyza canadensis	Asteraceae	WABA	LAMR		SAND
Croton sp.	Euphorbiaceae		LAMR		SAND
Cucurbita foetidissima	Cucurbitaceae	WABA		BEOL	
Cylindropuntia imbricata	Cactaceae		LAMR		
Dalea purpurea	Fabaceae	WABA	LAMR		
Descurainia pinnata	Brassicaceae			BEOL	
Desmanthus illinoensis	Fabaceae	WABA	LAMR		
Digitaria cognata	Poaceae		LAMR		SAND

Species	Family	WABA	LAMR	BEOL	SAND
Dimorphocarpa wislizeni	Brassicaceae		LAMR		
Distichlis spicata	Poaceae			BEOL	SAND
Echinacea pallida	Cactaceae	WABA			
Elymus canadensis	Poaceae	WABA			
Elymus elymoides	Poaceae		LAMR		SAND
Engelmannia pinnatifida	Asteraceae	WABA	LAMR		
Equisetum sp.	Equisetaceae				SAND
Eragrostis trichodes	Poaceae	WABA			
Ericameria nauseosa	Asteraceae				SAND
Erigeron sp.	Asteraceae		LAMR	BEOL	SAND
Eupatorium serotinum	Asteraceae	WABA			
Euphorbia davidii	Euphorbiaceae		LAMR		SAND
Euphorbia marginata	Euphorbiaceae				SAND
Gaillardia pulchella	Asteraceae	WABA	LAMR		
Gaura mollis	Onagraceae	WABA	LAMR	BEOL	
Grindelia squarrosa	Asteraceae	WABA	LAMR	BEOL	SAND
Gutierrezia sarothrae	Asteraceae				SAND
Helianthus maximilianii	Asteraceae	WABA			
Helianthus petiolaris	Asteraceae	WABA	LAMR	BEOL	SAND
Heterotheca villosa	Asteraceae			BEOL	
Hilaria mutica	Poaceae			BEOL	
Hoffmanseggia glauca	Fabaceae		LAMR		
Hordeum pusillum	Poaceae			BEOL	
Hymeopappus	Asteraceae				SAND
Ipomoea leptophylla	Convolvulaceae		LAMR	BEOL	
Kochia scoparia	Chenopodiaceae	WABA	LAMR	BEOL	SAND
Krameria lanceolata	Krameriaceae		LAMR		
Lactuca serriola	Asteraceae				SAND
Lespedeza sp.	Fabaceae	WABA	LAMR		SAND
Liatris punctata	Asteraceae	WABA	LAMR		
Lygodesmia juncea	Asteraceae			BEOL	SAND
Meliotus alba	Fabaceae	WABA			
Meliotus officinalis	Fabaceae	WABA			
Mentzelia nuda	Loasaceae	WABA	LAMR		SAND
Mimosa borealis	Fabaceae	WABA			
Mimosa nuttallii	Fabaceae	WABA			
Mimosa quadrivalvis	Fabaceae		LAMR		
Monarda citriodora	Lamiaceae	WABA	LAMR		
Muhlenbergia	Poaceae		LAMR		
Oenothera biennis	Onagraceae		LAMR		
Opuntia sp.	Cactaceae		LAMR	BEOL	SAND
Panicum hallii	Poaceae		LAMR		
Panicum obtusum	Poaceae		LAMR	BEOL	
Panicum virgatum	Poaceae	WABA			

Species	Family				
Pascopyrum smithii	Poaceae	WABA	LAMR	BEOL	SAND
Phyla sp.	Verbenaceae			BEOL	
Plantago sp.	Plantaginaceae	WABA	LAMR		SAND
Prosopis glandulosa	Fabaceae		LAMR		
Prunus angustifolia	Rosaceae	WABA	LAMR		
Psoralidium tenuiflorum	Fabaceae	WABA			
Ratibida columnifera	Asteraceae		LAMR		SAND
Ratibida tagetes	Asteraceae		LAMR	BEOL	SAND
Rhus aromatica	Anacardiaceae	WABA			
Rumex patienta	Polygonaceae	WABA			
Saccharum gigantea	Poaceae	WABA			
Salsola tragus	Chenopodiaceae		LAMR	BEOL	SAND
Schedonnardus paniculatus	Poaceae				SAND
Schizachruim scoparium	Poaceae	WABA	LAMR		
Scutellaria resinosa	Lamiaceae	WABA			
Setaria leucopila	Poaceae		LAMR		
Setaria sp.	Poaceae		LAMR		
Solanum rostratum	Solanaceae	WABA	LAMR		
Solidago sp.	Asteraceae	WABA			
Sorghastrum nutans	Poaceae	WABA	LAMR		
Sorghum halepense	Poaceae	WABA			
Sphaeralcea sp.	Malvaceae			BEOL	
Sphaeralcea ambigua	Malvaceae			BEOL	
Sphaeralcea angustifolia	Malvaceae		LAMR		
Sphaeralcea coccinea	Malvaceae		LAMR	BEOL	SAND
Sphaeralcea fendleri	Malvaceae		LAMR		
Sporobolus airoides	Poaceae			BEOL	SAND
Sporobolus compositus	Poaceae		LAMR		
Sporobolus cryptandrus	Poaceae	WABA	LAMR	BEOL	SAND
Stallingia sylvatica	Euphorbiaceae		LAMR		
Stanleya pinnata	Brassicaceae				SAND
Sumac sp.	Anacardiaceae	WABA			
Symphotrichum ericoides	Asteraceae	WABA	LAMR	BEOL	SAND
Tradescantia ohiensis	Commelinaceae		LAMR		
Tragopogon dubius	Asteraceae	WABA			SAND
Tridens albescens	Poaceae		LAMR		
Tridens muticus	Poaceae		LAMR		
Ulmus pumila	Ulmaceae	WABA			
Yucca sp.	Agavaceae	WABA	LAMR		SAND

[1]Occurrence: WABA- Washita Battlefield National Historic Site, LAMR- Lake Meredith National Recreation Area, BEOL- Bent's Old Fort National Historic Site, SAND- Sand Creek Massacre National Historic Site

Figure 1. Southern Plains Network Parks. The green outline denotes the network boundary with yellow dots indicating network parks and red stars identifying the study parks.
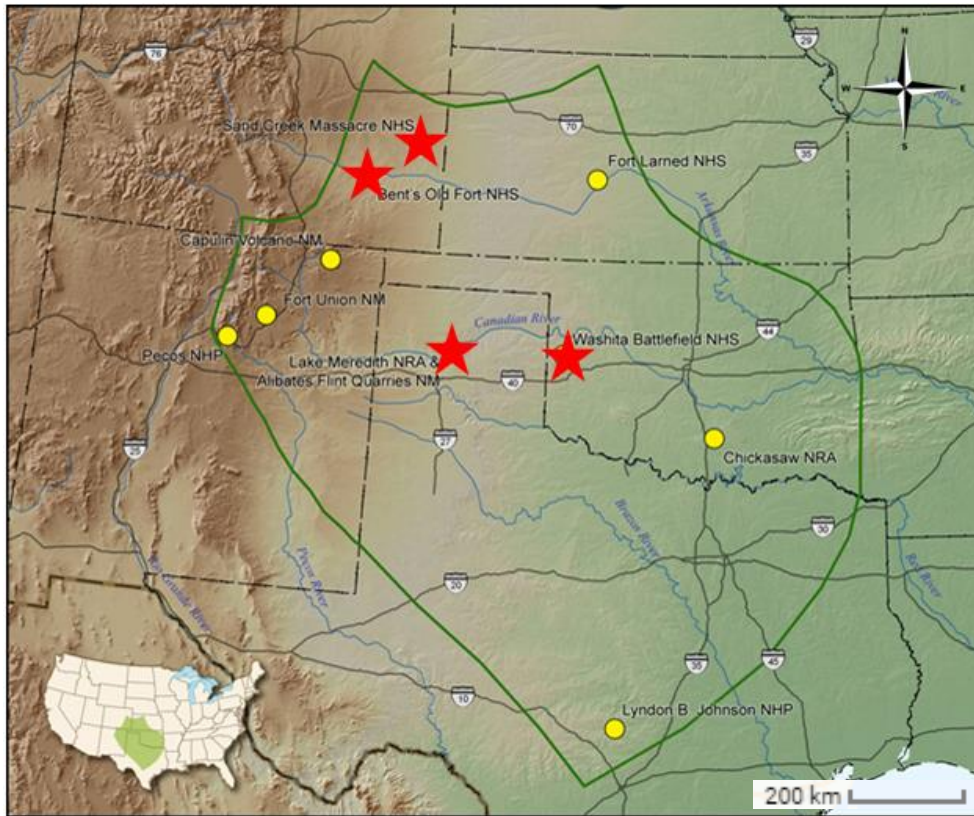
Figure 2. Native bee genus richness along the invasive species gradient of combined *Kochia scoparia* and *Salsola tragus* percent cover in the four study parks in the Southern Plains Network for 2016 ($F(1,32)=4.044$, p=0.05, $R^2=0.08445$).
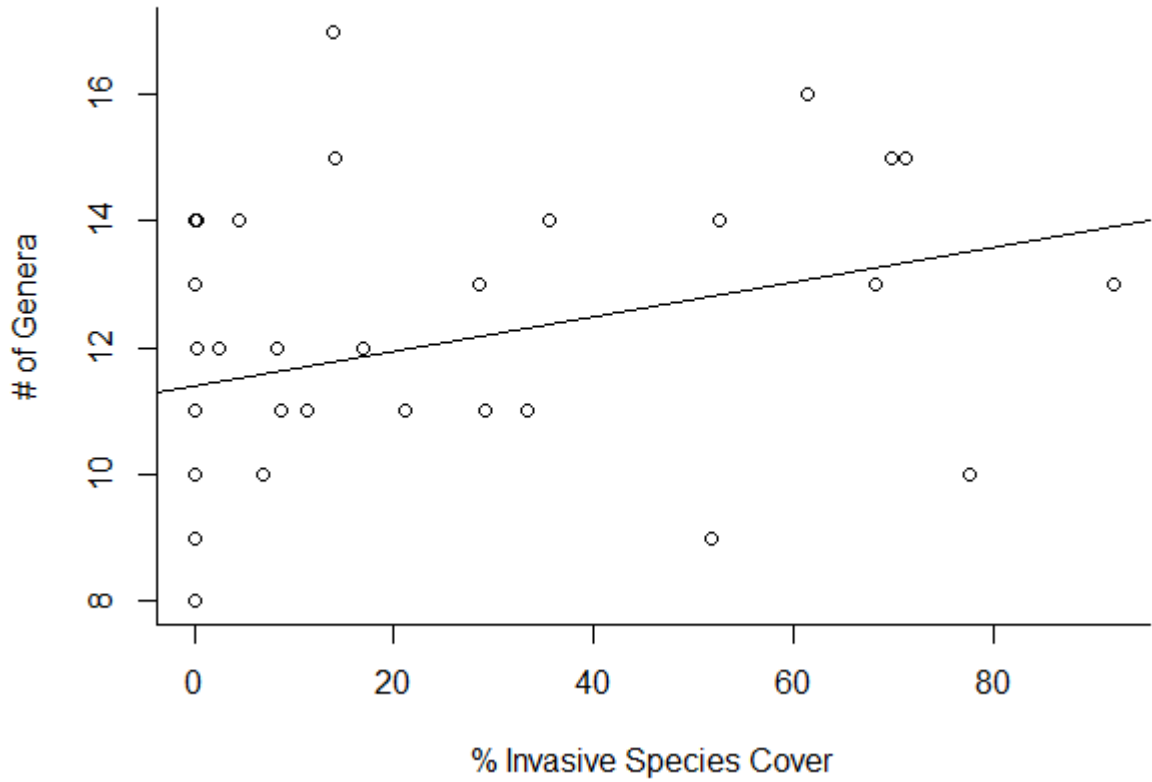
Figure 3. Native bee genus richness as a function of bare ground percent cover in the four study parks in the Southern Plains Network for 2016 ($F_{(1,32)}$=7.306, p=0.01, R^2=0.1604).
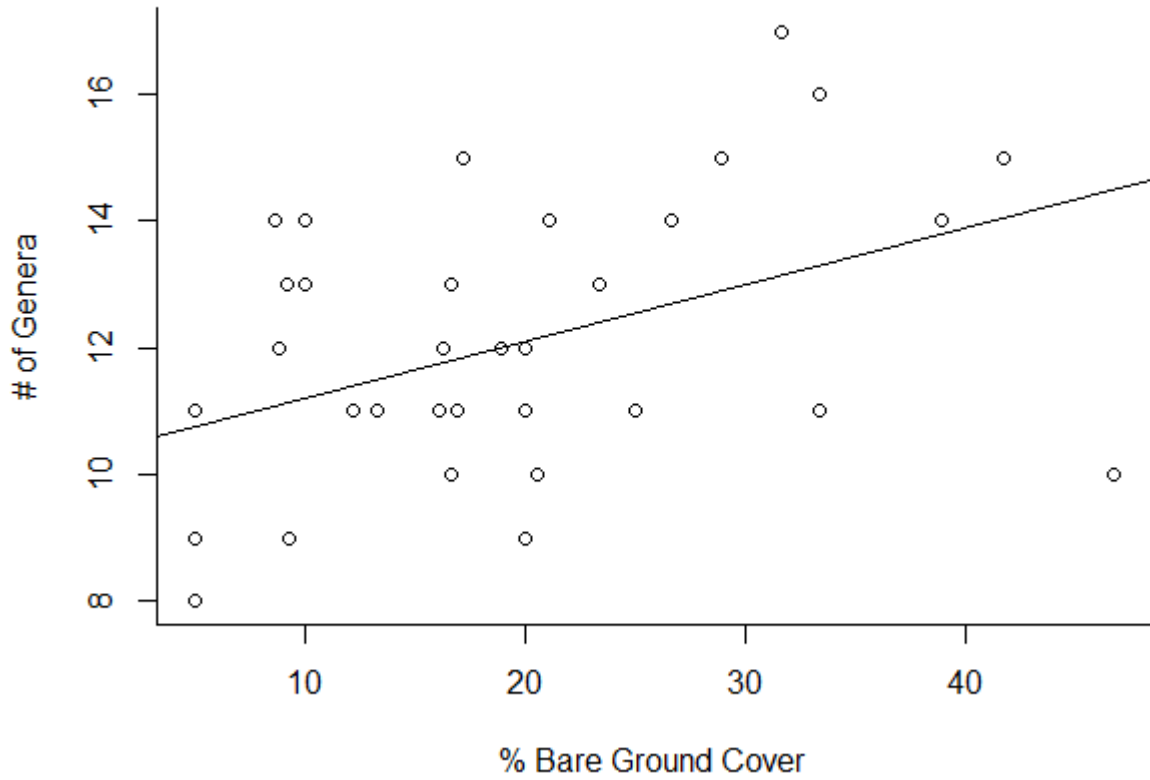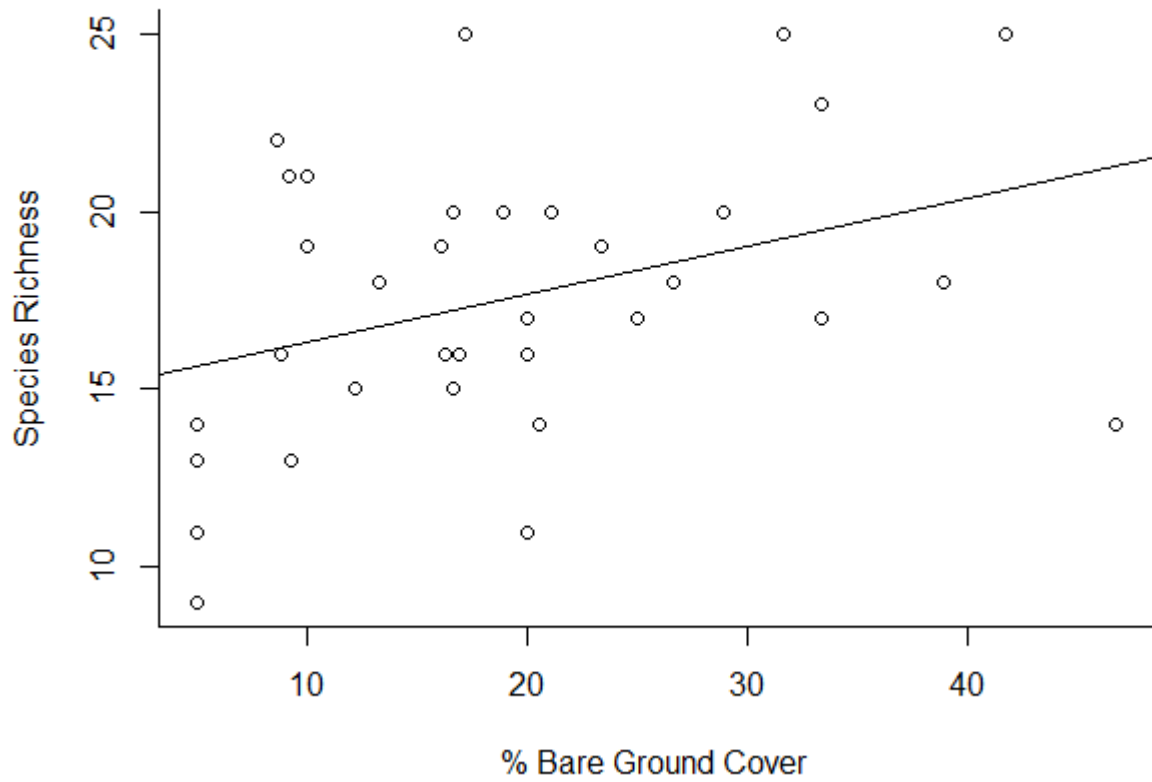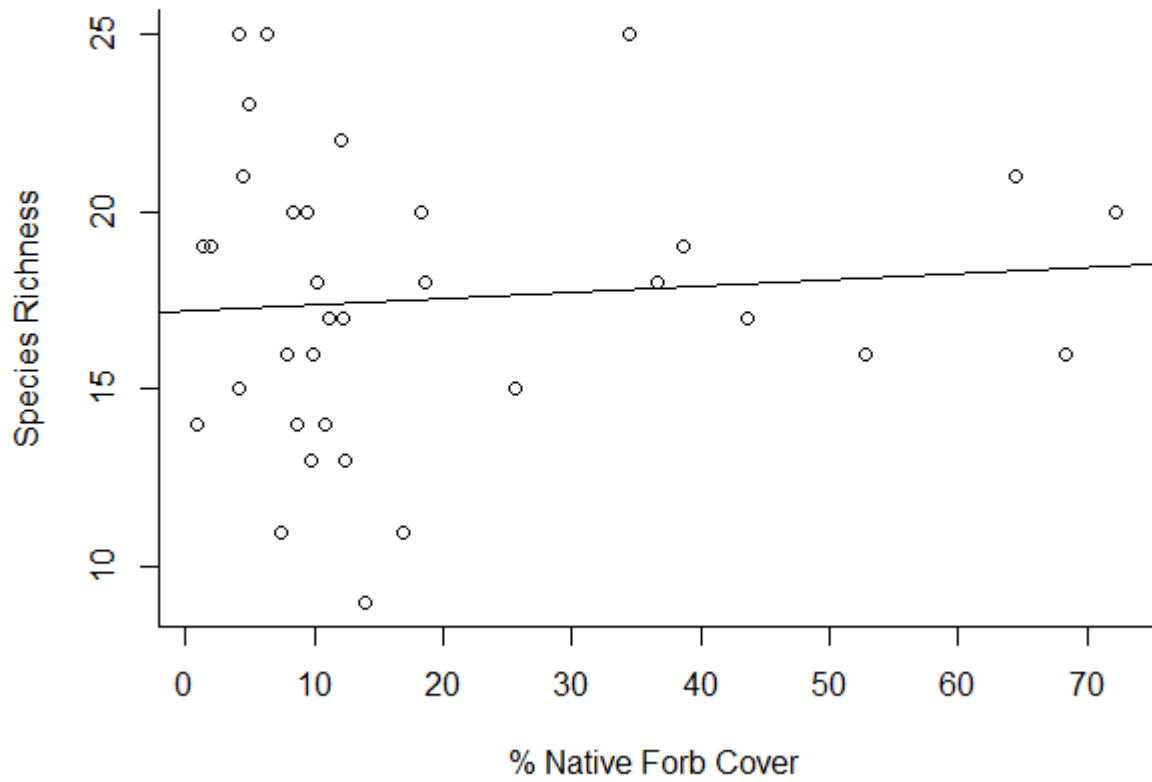
Figure 4. Native bee genus richness as a function of native forb percent cover in the four study parks in the Southern Plains Network for 2016 (F(1,32)=0.8159, p=0.3731, R^2=-.005609).
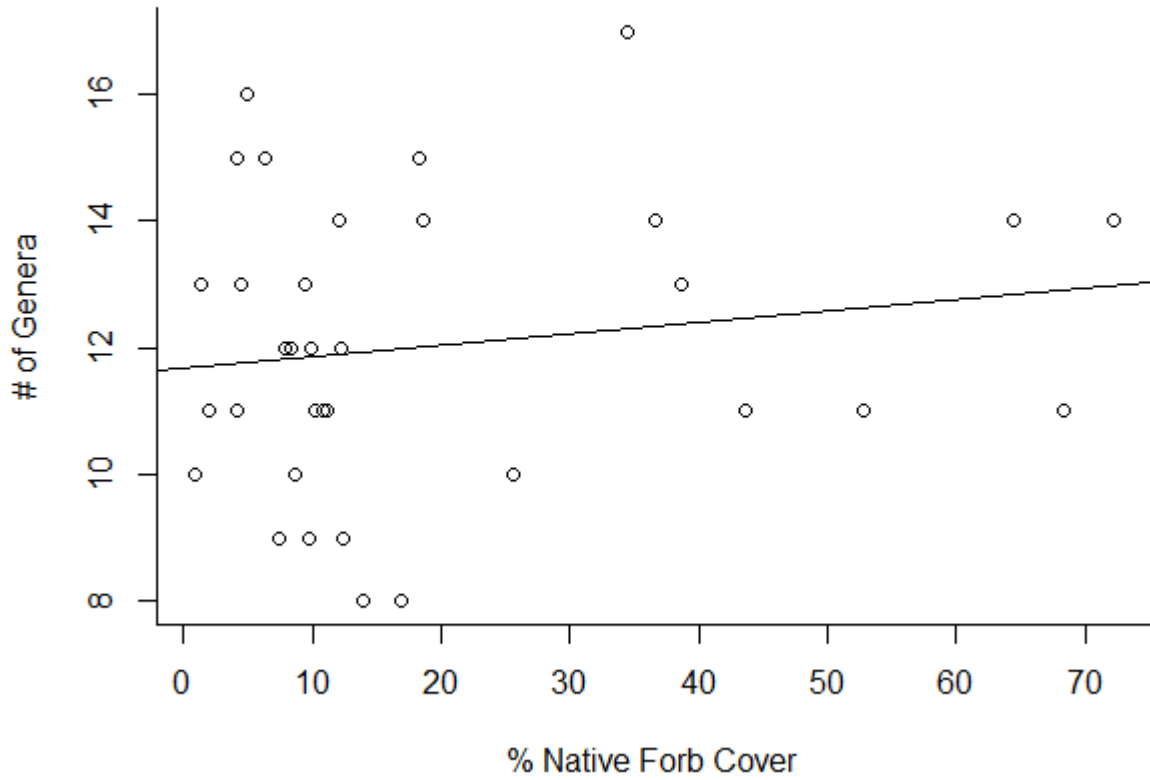
Figure 5. Native bee species richness along the invasive species gradient of combined *Kochia scoparia* and *Salsola tragus* percent cover in the four study parks in the Southern Plains Network for 2016 ($F(1,32)=2.884$, $p=0.099$, $R^2=0.05401$).
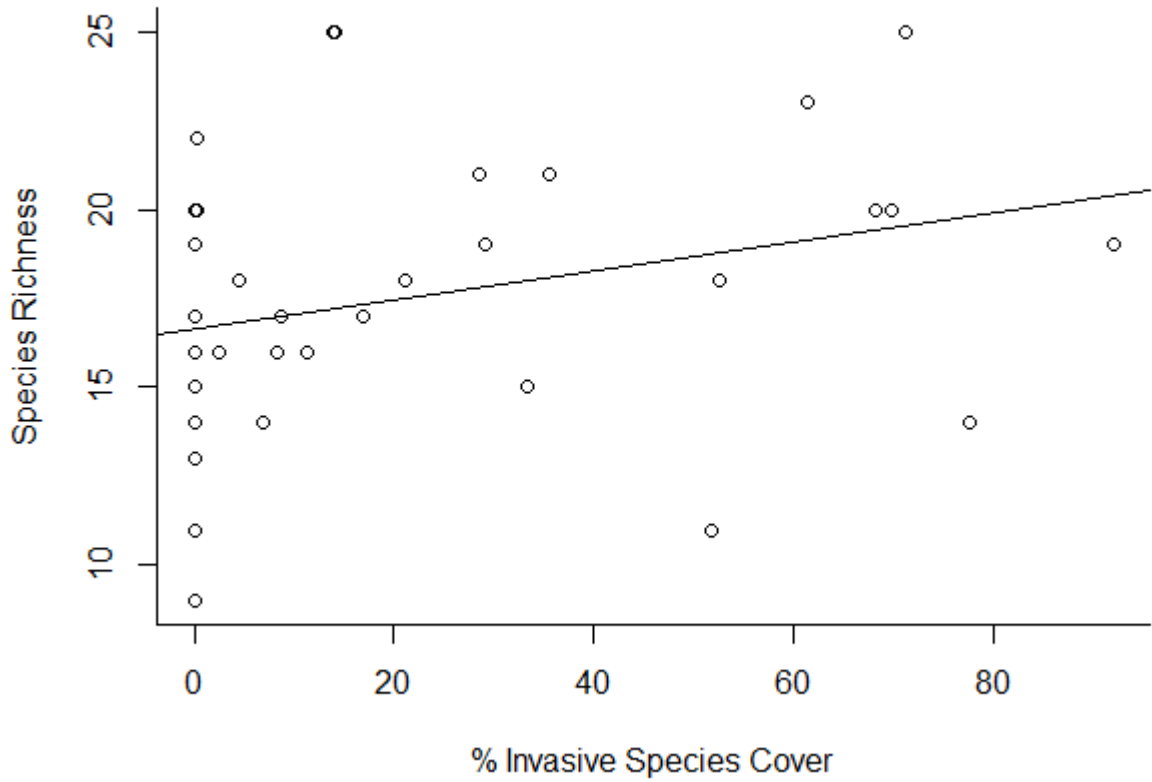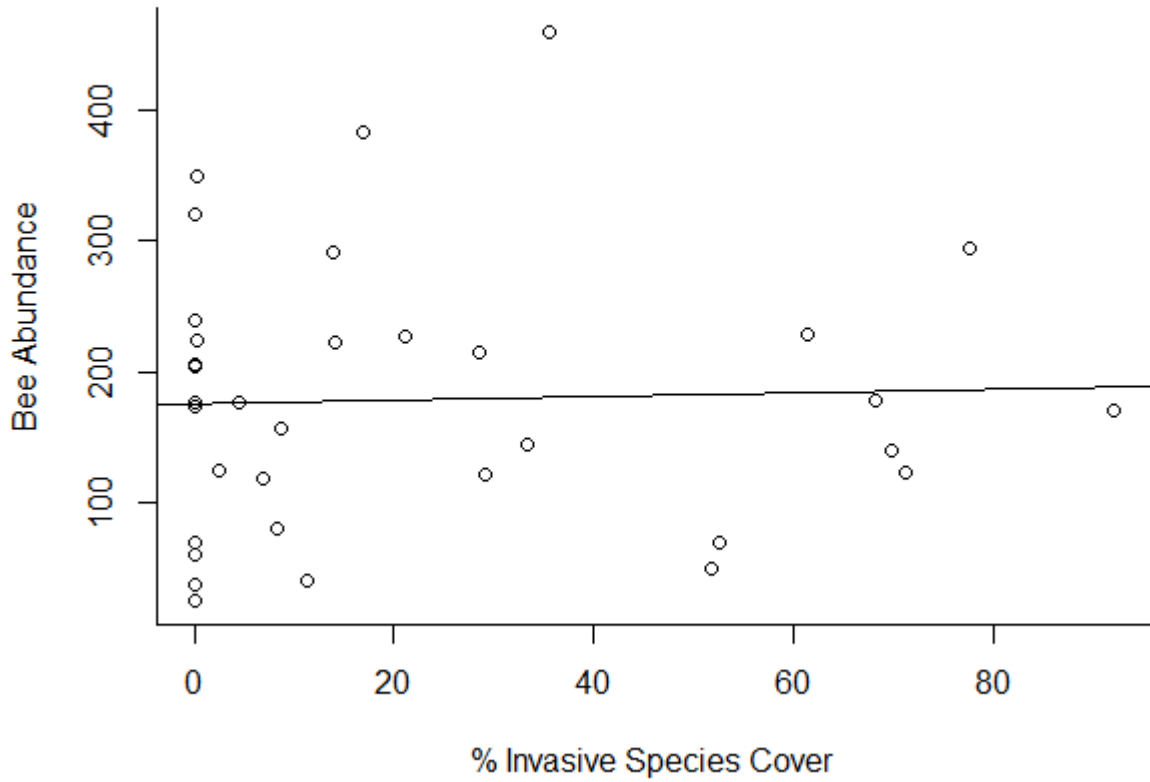
Figure 6. Native bee species richness as a function of bare ground percent cover in the four study parks in the Southern Plains Network for 2016 ($F_{(1,32)}$=4.998, p=0.03, R^2=0.1081).
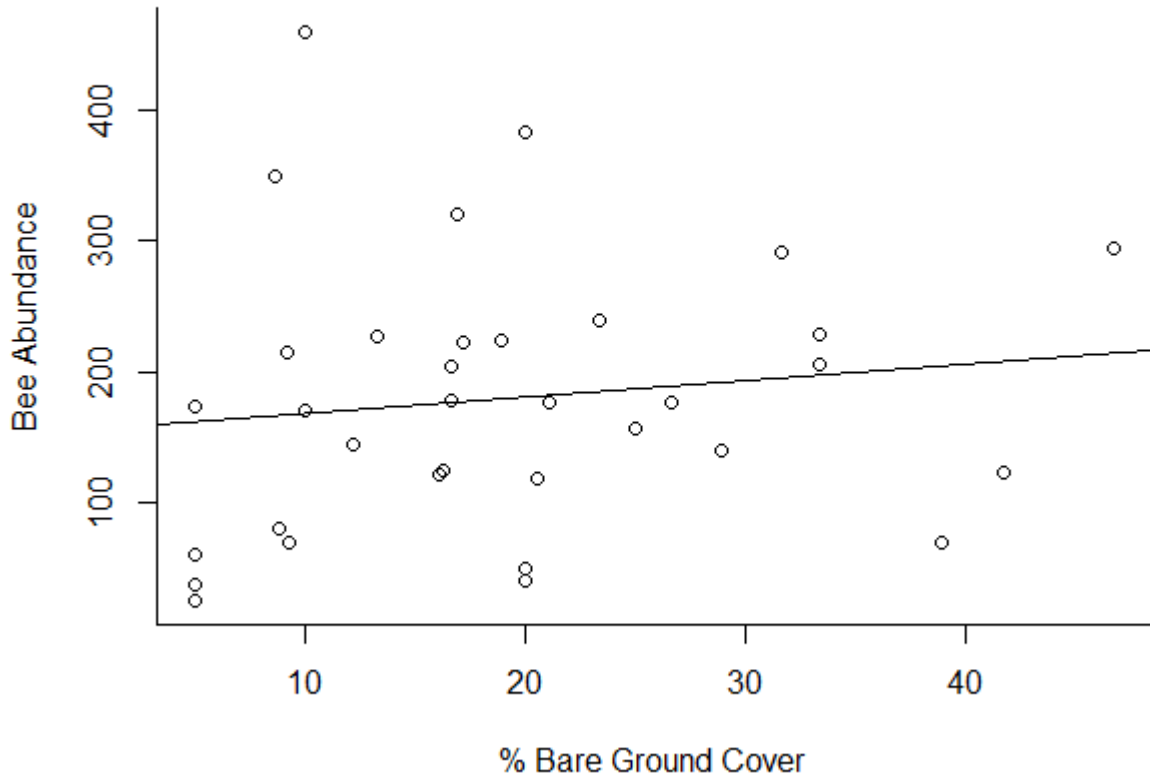
Figure 7. Native bee species richness as a function of native forb percent cover in the four study parks in the Southern Plains Network for 2016 (F(1,32)=0.2332, p=0.6325, R^2=-0.02379).

Figure 8. Native bee abundance along the invasive species gradient of combined *Kochia scoparia* and *Salsola tragus* percent cover in the four study parks in the Southern Plains Network for 2016 (F(1,32)=0.04287, p=0.8373, R^2=-0.02987).

Figure 9. Native bee abundance as a function of bare ground percent cover in the four study parks in the Southern Plains Network for 2016 (F(1,32)=0.589, p=0.4484, R^2=-0.01261).

Figure 10. Native bee abundance as a function of native forb percent cover in the four study parks in the Southern Plains Network for 2016 (F(1,32)=1.915, p=0.176, R^2=0.02697).
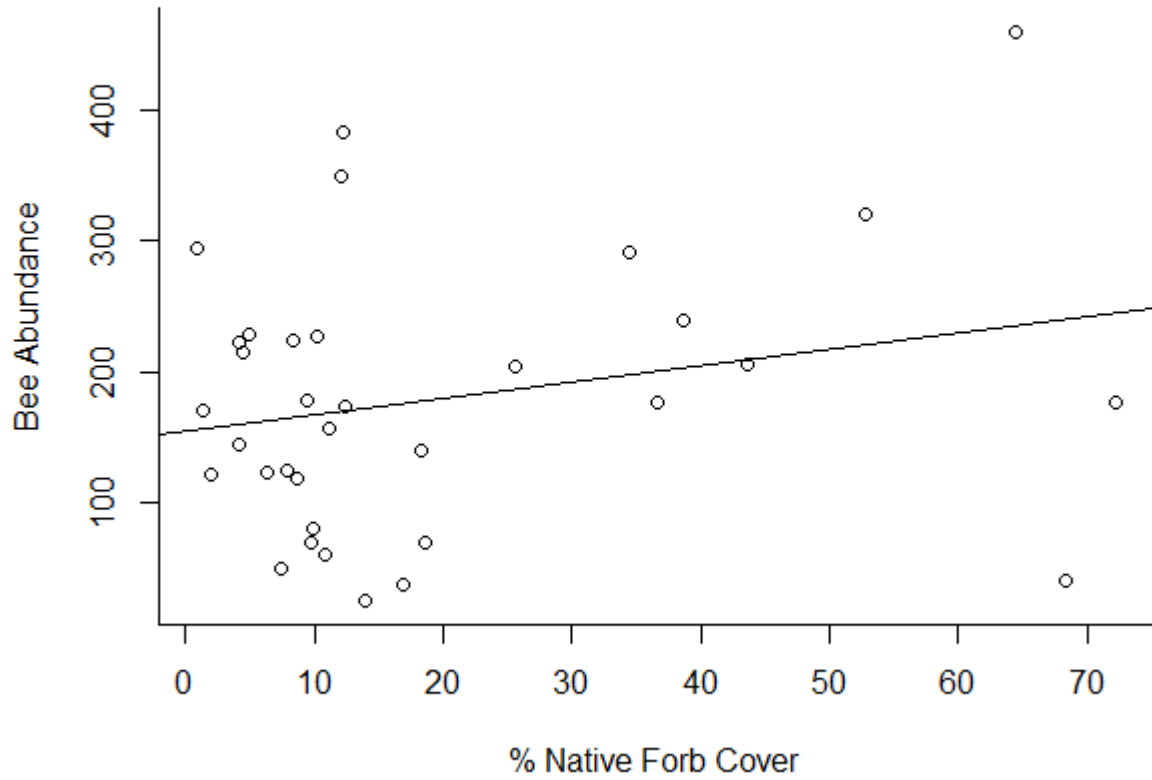
Figure 11. Native grass species richness as a function of the combined invasive species percent cover of *Kochia scoparia* and *Salsola tragus* in the four study parks in the Southern Plains Network for 2016 ($F(1,32)=17.42$, $p=0.00$, $R^2=0.3323$).
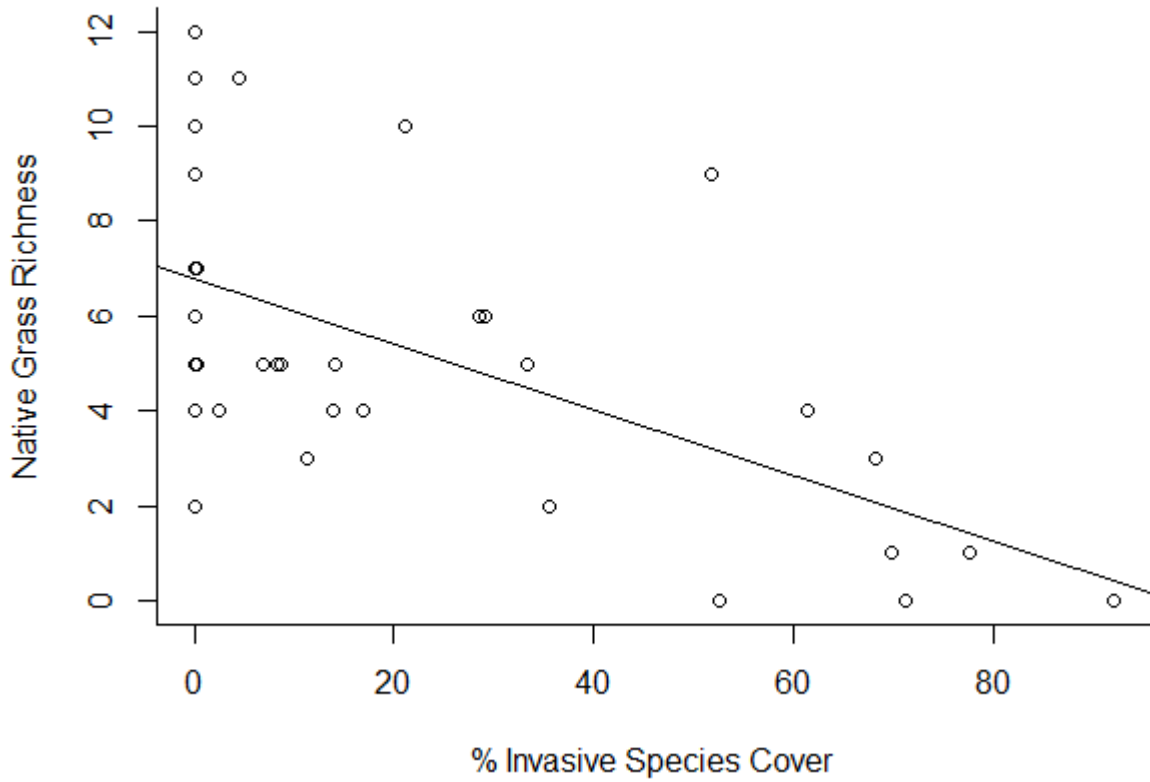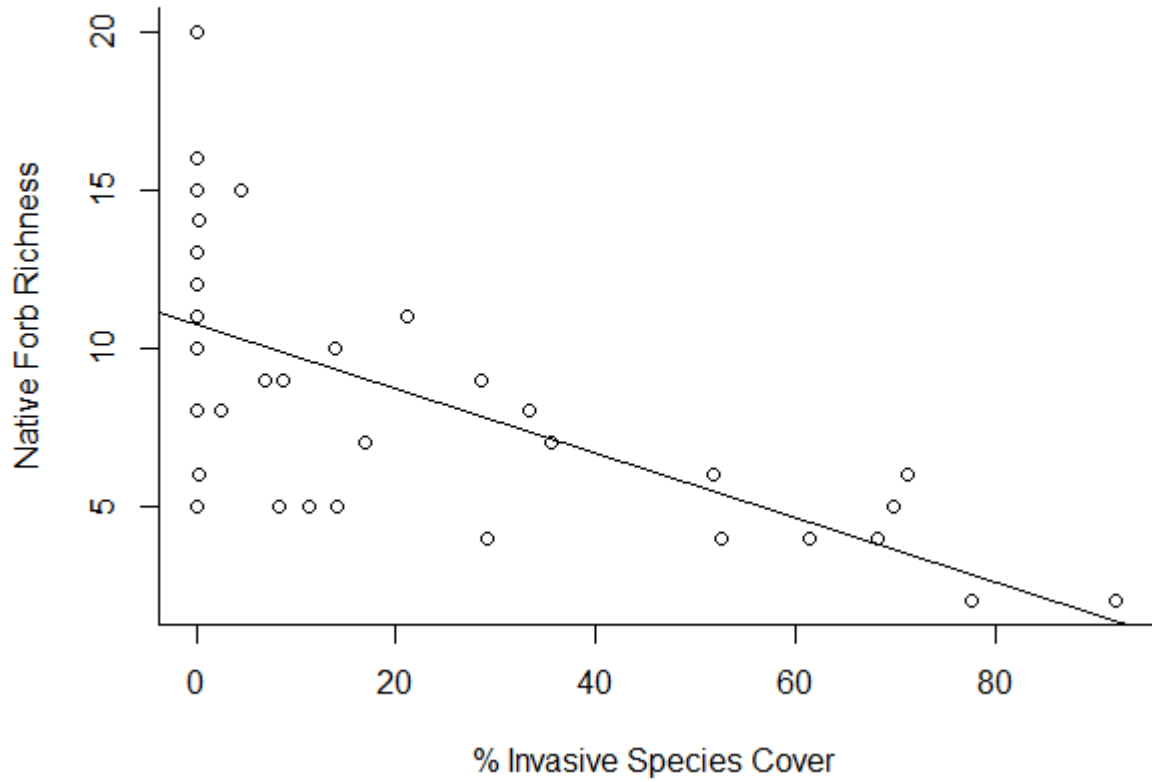
Figure 12. Native forb species richness as a function of the combined invasive species percent cover of *Kochia scoparia* and *Salsola tragus* in the four study parks in the Southern Plains Network for 2016 (F(1,32)=24.74, p=0.00, R^2=0.4185).

VITA

Kaitlin Mae O'Brien

Candidate for the Degree of

Master of Science

Thesis: EFFECTS OF INVASIVE PLANT SPECIES ON NATIVE BEE COMMUNITIES IN THE SOUTHERN GREAT PLAINS

Major Field: Integrative Biology

Biographical:

Education:

Completed the requirements for the Master of Science in Integrative Biology at Oklahoma State University, Stillwater, Oklahoma in May 2017.

Completed the requirements for the Bachelor of Science in Rangeland Ecology & Management at Texas A&M University, College Station, Texas in 2015.

Experience:

Graduate Research Assistant, Oklahoma State University, 2015-2017

Exotic Plant Monitoring Crew, Southern Plains Network, 2015-2017

Teaching Assistant, Texas A&M University, 2013-2015

Professional Memberships:

Student Member, Society for Range Management, 2011-Present

Student Member, Oklahoma Chapter of SRM, 2016-2017