NATIVE LEGUMES VERSUS *LESPEDEZA CUNEATA*:

IMPLICATIONS FOR ECOSYSTEM SERVICES

By

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2012

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
July 2019

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ACKNOWLEDGEMENTS

First and foremost, I must thank my adviser for the wonderful guidance and support that has been provided throughout my PhD experience. In addition to the research conducted in order to earn this degree, Dr. Kristen Baum has encouraged me to engage the public through meetings and conferences, take courses that expand my knowledge of my study system, and participate in both the university and local community. I also owe my gratitude to committee members Dr. Samuel Fuhlendorf, Dr. Karen Hickman and Dr. Gail Wilson for assisting me in designing data collection methods and analyses and for supporting and encouraging my growth.

During my time here at Oklahoma State University, I have also had wonderful mentors while volunteering, participating in research and serving as a graduate teaching assistant. I am sincerely grateful to the Dean and Associate Deans of the Graduate College: Dr. Sheryl Tucker, Dr. Brenda Smith, Dr. Jean Van Delinder, the Associate Vice President for Research Dr. Ron Van Den Bussche and Graduate Coordinators Dr. Matthew Lovern and Dr. Jennifer Grindstaff. I am also sincerely grateful to Dr. Matthew Bolek, Dr. Andy Dzialowski, Dr. Donald French, and Dr. Meredith Hamilton for their mentorship, patience and guidance which enabled me to engage and prepare effectively for courses I taught.

These projects which made up my dissertation, as well as all side projects I was able to participate in and complete, were also possible through the support of my family, and I am eternally grateful. I also want to express gratitude and appreciation to my friends and colleagues who have helped me talk out and express ideas, relax and take breaks, and who have pushed me to succeed in all of my endeavors. Finally, I would like to thank my trusty companions, Birdie and Wrendolyn, who have assisted me in the field portion of my research and who have shown me unconditional love, loyalty and dependability through this journey.

Name: JEREMY DANA KAPLAN

Date of Degree: JULY 2019

Title of Study: NATIVE LEGUMES VERUS *LESPEDEZA CUNEATA*: IMPLICATIONS FOR
ECOSYSTEM SERVICES

Major Field: INTEGRATIVE BIOLOGY

Abstract: Grasslands are the most threatened ecosystem worldwide due to habitat fragmentation and alteration, which have contributed to the spread of invasive plants. Fire is historically important in maintaining grasslands, and can reduce or eliminate some invasive plants, but facilitates the germination and spread of others. Invasive plants compete with natives and have the potential to impact ecosystem services (i.e., decomposition, soil C and N storage, pollination). *Lespedeza cuneata* is an invasive legume that reduces the abundance and diversity of native plants and can form monotypic stands. Many native legumes occur sympatrically with *L. cuneata*, including *Lespedeza virginica* and *Baptisia bracteata*. I evaluated if native versus invasive legume cover in different burn regimes influenced 1) litter decomposition and 2) invertebrate abundance and morphospecies richness, and if native versus invasive legume cover influenced 3) soil organic N (SON) and soil organic C (SOC), and 4) pollinator morphospecies richness and abundance. Sites were located within north-central Oklahoma in patch-burn managed rangelands. Findings suggest that decomposition and soil invertebrate morphospecies richness and abundance was highest in year of burn locations (versus two years since burn) and the highest level of *L. cuneata* cover. Decomposition was higher when microinvertebrates and macroinvertebrates were allowed access to litter, versus when only microinvertebrates were. SON and SOC (%) were positively correlated and lowest in areas with *B. bracteata* and increased as *L. cuneata* cover increased. Pollinator (Hymenoptera) richness was greater in locations with intermediate *L. cuneata* cover rather than in areas with more or less *Lespedeza* cover, including native *Lespedeza* cover. If abundance of decomposers and morphospecies richness of decomposers and pollinators is higher in locations dominated by *L. cuneata*, associated ecosystem services, including decomposition, soil C and N storage, and pollination, may contribute to its spread and the isolation of natives, further influencing grassland productivity and diversity. Additional research should evaluate these interactions with other invasive species and congeneric natives to identify factors that contribute to observed patterns across systems.

TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER I

DECOMPOSITION RATES AND LITTER AND SOIL INVERTEBRATE ASSEMBLAGES VARY WITH LEGUME COVER, YEARS SINCE BURN AND ACCESS BY DIFFERENT SIZED INVERTEBRATES

Abstract.

Grasslands are the most threatened ecosystem worldwide and invasive plants have contributed to grassland degradation. Fire is historically important in grassland systems where some invasive plants are reduced or eliminated by fire, while some respond positively. Legumes, a common forb in grasslands, require seed scarification that can be provided by prescribed fire. Thus, prescribed fire can facilitate the spread of some invasive legumes. Legumes influence soil dynamics and plant communities through nitrogen fixation and invertebrates can influence these patterns through ecosystem services, such as decomposition. Understanding how invasive legumes can modify grassland ecosystems by examining decomposition and invertebrate assemblages can give greater insight into the role of invertebrate detritivores and nutrient cycling through decomposition services. The principle goals of this project were to evaluate the effect of invasive species cover in the context of time since burn and season of burn on 1) decomposition rates and 2) the abundance and morphospecies richness of the invertebrate community between areas containing a commonly occurring native legume and an invasive legume. I evaluated litter and soil invertebrates and decomposition across a gradient of legume cover ranges (≥1-5%, and ≥25-75%) for invasive *Lespedeza cuneata* and a single plant cover of native *Baptisia bracteata*. Study sites were located within north-central Oklahoma in patch-burn managed rangeland where both species occur sympatrically. Mesh bags were used to assess litter invertebrates and decomposition, and soil cores were used to assess soil invertebrates. Findings suggest that legume cover, years since burn and the size distribution of invertebrates affect decomposition rates. Decomposition was highest and soil invertebrates were most abundant and had their highest morphospecies richness in locations burned that year and those with ≥25-75% *L. cuneata* cover. When macroinvertebrates were allowed access to mesh bags, decomposition was also higher than when access was restricted. Litter invertebrate abundance was positively correlated with litter morphospecies richness and soil invertebrate abundance was positively correlated with soil morphospecies richness. These findings suggest that decomposition and invertebrate abundance is higher in locations dominated by invasive *L. cuneata* rather than those containing native *B. bracteata* and in year of burn rather than two years post burn. If abundance and diversity of invertebrates and associated decomposition services are higher in recently burned locations and those dominated by invasive *L. cuneata*, associated ecosystem services may contribute to its spread and the isolation of natives.

Introduction.

Grasslands are the most threatened ecosystem worldwide with estimates of native tallgrass prairie being reduced to 1% of its original extent (Ricketts et al. 1999; Gauthier et al. 2003; Hines and Hendrix 2005; Hopwood 2008). In North America, the widespread use of grasslands for agriculture and livestock grazing, in addition to the effects of urbanization and other human activities, have led to dramatic losses in their extent and integrity. For temperate grasslands, invasive species are currently a major anthropogenic threat (Westbrooks 1998; Smith and Knapp 1999; Stohlgren et al. 1999a). Because of the historic importance of fire in the maintenance of grassland systems, the interactions between invasive species and fire are often of critical importance. In some cases, fire may eliminate or reduce nonnative invasive grasses (e.g., *Poa pratensis, Poa compressa, Bromus inermis*). However, other nonnative invaders (e.g., *Lespedeza cuneata*) may respond positively to fire. The interaction between fire and invasive species can be complicated by additional factors such as grazing, intensified agriculture, and pesticide application (Collins et al. 1995, 1998; Stohlgren et al. 1999b).

Fire and grazing occur in tandem in grassland ecosystems (Hobbs et al. 1991). Grazing can remove plant tissue from landscapes heterogeneously, which can increase spatial heterogeneity in fire behavior by increasing spatial variation (i.e., patchiness) in the amount of organic matter available for combustion (Hobbs et al. 1991). Thus, if grazers prefer forage in one patch over another, disparity of fuels will occur between those patches. This disparity results in less intense fire in grazed patches and more intense fire in ungrazed areas. Consequently, fire can reduce the spatial heterogeneity caused by grazing (Conrad and Poulton 1966; Norton-Griffiths 1979; Madany and West 1983; Zimmerman and Neuenschwander 1984). Many studies focus on how fire-grazing interactions influence vegetation communities and ecosystem services. However, fewer studies have focused on how fire-grazing interactions influence other consumer groups, such as detritivores (Whiles and Charlton 2006).

Alteration of the North American tallgrass prairie ecosystem, in combination with species introductions and losses over the last 150 years, suggest that tallgrass prairie and its soil biota demonstrate adaptions to periodic fire and grazing (Knapp and Seastedt 1986; Seastedt et al. 1988a), even though interactions among detritivores and plant communities lack the evolutionary history that exists for other temperate or tropical grassland systems (Seastedt et al. 1988a). In most ecosystems, including tallgrass prairie, the predominant herbivores and detritivores are arthropods (Whiles and Charleston 2006). Arthropods influence the cover, density and biomass of living and dead organic material and associated nutrient cycling (Naiman 1988; Seastedt 1984; Seastedt and Crossley 1984). Factors that regulate soil arthropod population dynamics and nutrient cycling in grassland ecosystems are inconsistent through studies (Todd et al. 1992), but soil arthropods are often more abundant in grazed prairie, even with reduction of root growth (Seastedt 1985; Seastedt et al. 1986). This interaction indicates that resource quality (i.e., nitrogen content) may influence the biomass of certain soil biota (Seastedt et al. 1988a, 1988b).

Fire-grazing interactions create a mosaic arrangement of resources for primary consumers, and therefore arthropod herbivore and detritivore impacts are expected to vary spatially and temporally and depending on the plant community. Aboveground arthropods (i.e., such as grasshoppers), generally do not control primary production and have subtle effects on plant communities with their most significant impacts seen on forbs (Wiegert 1965; Bunn et al. 1997; Bohart and David 2019). Belowground arthropods influence root dynamics and rhizosphere nutrient cycling, which may be particularly important for certain plants (e.g., legumes). Above and belowground invertebrates interact primarily through plant responses and detrital food-chain pathways. Therefore, arthropods are expected to vary within the tallgrass prairie depending on the available nutrients.

Legumes are a common forb in the tallgrass prairie, and influence soil dynamics and plant communities through nitrogen fixation via symbiotic root bacteria (Kaneko et al. 2002; Wu et al. 2016). Numerous legume species have been observed to increase in abundance (Lemon 1967; Adams and Anderson 1978; Niering and Dreyer 1989; Nagel et al. 1994) or remain unchanged (Curtis and Partch 1948; Kucera and Keolling 1964) following prescribed fire. Fire has been shown to positively affect germination of many legume species (Martin and Cushwa 1966), which possess a hard protective seed covering that requires scarification for germination (Sorensen and Holden 1974). Invertebrates may also influence the distribution and abundance of legumes and other plant species, such as by preferentially consuming the seeds of some species. Thus, both fire and invertebrates can influence legume establishment and secondary spread, especially in N stressed environments, and invasive legumes may have an advantage over native legumes through competitive traits. Understanding how invasive legumes can modify tallgrass prairie ecosystems by examining decomposition and invertebrate assemblages can give greater insight into the importance and role of soil and litter invertebrate detritivores and their role in nutrient cycling through decomposition services.

Objectives.

The principle goals were to evaluate the effect of invasive species cover in different burning regimes where time since burn and the season of burn may influence 1) decomposition rates and 2) the abundance and morphospecies richness of the invertebrate community. These goals were addressed by comparing decomposition rates and the invertebrate community between areas containing a commonly occurring native legume and different cover levels of an invasive legume. Litter bags were used to evaluate decomposition, and specimens collected from the litter bags and soil cores were used to evaluate the invertebrate community.

Materials and methods.

Study system.

Lespedeza cuneata is an herbaceous and woody, perennial legume, native to eastern Asia. This species was first introduced to the United States in 1896 and now occurs throughout the eastern and central United States (Cummings et al. 2007a). *Lespedeza cuneata* was originally cultivated and planted for erosion control and mine reclamation in the 1920s and 30s, and then began to be widely used as a pasture crop in the 1940s (Pitman 2006; Cummings et al. 2007a; EPPO 2018). As of surveys in 2009, *L. cuneata* was observed outside of cultivation throughout much of the United States (as far north as Ontario, Canada; south as Florida and Texas; west as Nebraska and Oklahoma and Texas panhandles; and throughout the majority of the east coast). The spread of *L. cuneata* is likely facilitated by seed coat scarification provided by prescribed fire. Young *L. cuneata* plants are palatable to livestock and readily grazed, but older plants produce tannins and become unpalatable (Guernsey 1977; Hoveland and Donnelly 1985). Yearling cattle tend to be less selective than mature cattle and intense, short periods of grazing by young livestock from June through mid-July can keep *L. cuneata* short (Altom et al. 1992; Cummings et al. 2007b; Gucker 2010), but older patches of *L. cuneata* are typically avoided over other forage. Thus, the accumulation of litter may differ among *L. cuneata* invaded areas based on the stage and extent of invasion, as well as fire-grazing interactions. Understanding the effects of *L. cuneata* on native species in grasslands in the context of different burn regimes has important implications for the conservation of remaining grassland remnants, as well as managed grasslands which provide habitat for many grassland specialist species.

Lespedeza cuneata can create monotypic stands in invaded areas, reducing plant community species richness and thereby influencing the composition of litter. Litter composition, due to varying tissue carbon (C) and N, influences decomposer communities and resulting decomposition (Wedin and Tilman 1990; Hobbie 1992). While both positive and negative interactions between litter quality and soil decomposers have been observed (Ayres et al. 2009; St. John et al. 2011; Perez et al. 2013), it remains unclear how such interactions affect decomposition (Lu et al. 2017). While some C compounds in legumes may reduce decomposition, high levels of N in litter tend to increase decomposition (Melillo et al. 1982). Invasive plants often maintain higher concentrations of leaf N (Vitousek et al. 1987; Vitousek and Walker 1989; Witkowski 1991; Baruch and Goldstein 1999; Nagel and Griffin 2001), compared to native species, and consequently are expected to decompose more rapidly and release more N to the soil. When N acquisition derived from decaying invasive plant species litter is greater than native plant-derived N, N availability at the soil surface and rates of nutrient cycling in invaded areas may increase (Vitousek and Walker 1989; Witkowski 1991). Thus, differences in leaf-level properties of invasive and native plants can have large impacts on ecosystem processes (Levine et al. 2003; Ashton at al. 2015).

Baptisia bracteata is an herbaceous, perennial native legume, which is confined to southeastern United States (Turner 2006). Typically occurring as a single isolated plant with 5 – 20 seeds per seedpod and a root system consisting of a stout taproot, *B. bracteata* prefers full sun and dry conditions, including open areas where there is reduced competition from taller vegetation. Seedlings are slow to mature, taking this plant several years to bloom. *Baptisia bracteata* can be observed in prairies and open woodland and prescribed fire is beneficial in maintaining populations of this plant. This species can be easily damaged by strong winds as its stem becomes more brittle as the summer progresses (Hilty 2018).

Study sites and treatments.

My research was conducted in north-central Oklahoma at Oklahoma State University's Stillwater Research Range (SRR), approximately 18 km west of Stillwater, OK. The SRR is located in the western section of the Cross Timbers ecoregion, which extends from southeastern Kansas to north-central Texas and is comprised of deciduous forest, savanna and tallgrass prairie; the SRR consists primarily of mixed and tallgrass prairie. An Oklahoma Mesonet (Brock et al. 1995) weather station located in the area records various climate measurements and shows annual precipitation averages 92.24 cm, with peak rainfall occurring in May and average temperatures range from 34.4°C in the summer to 1.1°C in the winter. Vegetation characteristic of tallgrass prairie remnants of the Cross Timbers ecoregion and commonly found in the SRR include dominant grasses (*Panicum virgatum*, *Sorghastrum nutans*, *Andropogon gerardi*, *Schizachyrium scoparium*, *Aristida purpurea*), dominant forbs (*Ambrosia psilostachya*, *Gutierrezia dracunculoides*), other forbs of prevalence (*Echinacea purpurea*, *Ratibida columnifera*, *Linum flavum*, *Triodanis perfoliata*, *Oenothera speciosa Convolvulus arvensis*, *Calendula arvensis*, *Erigeron annuus*, *Coreopsis palmate*, *Solidago rigida*, *Gutierrezia sarothrae*, *Solanum elaegnifolium* and *Grindelia squarrosa*) and dominant woody plants (*Quercus stellata*, *Quercus marilandica*, *Celtis* spp.) (Allred et al. 2010).

This study utilized patch-burn sites within the SRR, which range in size from 49 to 63 ha. Patch-burning (patch-burn grazing) involves the combined use of fire and grazing for ecological management goals by purposefully encouraging cattle to freely select the most recently burned part of a site. Grazing pressure is shifted when another section is burned, thus creating a shifting mosaic on the management unit (Cummings et al. 2007). Growing season prescribed fire (occurring in summer months) is conducted when warm-season herbaceous plants are actively growing, whereas dormant season prescribed fire (occurring in early spring months) is used to promote livestock production and is conducted just before spring green-up (Launchbaugh and Owensby 1978). SRR patch-burn sites are divided into 6 sections approximately equal in size and defined by burning regime. Two of six sections are burned each year: one in spring (February through March) and one in summer (July through

August). Within each patch-burn rangeland (each SRR site), I used the sections with the longest (two years since burn) and shortest (year of burn) times since burn, and included both spring (dormant season) and summer (growing season) burns for a total of four burn treatments at each site. Using the longest time since burn allowed *Lespedeza* plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom, while using the shortest time since burn allow for evaluation of invertebrate assemblages and decomposition post fire. Evaluating spring and summer burn sections allowed for assessment of how invertebrate assemblages and decomposition varies due to dormant or growing season burn treatments. Cattle are stocked at a constant rate in the SRR, consisting of 6.9 ha/animal.

I examined invertebrate assemblages and decomposition in areas that contained one native legume species and two *L. cuneata* cover ranges. *Lespedeza cuneata* cover ranges were designated as: ≥1-5% (low) and ≥25-75% (high), *L. cuneata* cover; a quadrat (0.25m x 0.25m) was used to estimate *Lespedeza* cover. *Baptisia bracteata* was selected as the native legume species. This species is a perennial legume that occurs sympatrically with *L. cuneata* throughout the tallgrass prairie region of the Great Plains and within the SRR. *Baptisia bracteata* tends to occur as isolated single plants, each with a single stem. Thus, areas containing *B. bracteata* were characterized by the presence of a single plant. Treatments within each section of each site included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/High cover (≥25-75%), and 3) *B. bracteata* single plant cover.

Vegetation surveys.

Within each sampling location, I conducted vegetation surveys in June of 2015 and 2016. At each location, I recorded percent cover (using a 0.25m x 0.25m quadrat) of forb (including a separate % cover for *L. cuneata* and *B. bracteata*) and grass.

Litter decomposition assessment using mesh bags and macro and microinvertebrate collection using mesh bags and soil cores.

Litter bags (180 x 180mm) of two mesh sizes (0.21 and 9.525mm) were used. The larger mesh bags (9.525mm mesh size) allowed entry by most macroinvertebrates, whereas the finer mesh size (0.21mm) excluded most meso- and macroinvertebrates. This approach allowed evaluation of the relative contribution of different sized invertebrates to litter decomposition. Bottoms of mesh bags were made from polyester broadcloth (approximately 55 micron mesh), which minimized loss of litter as invertebrates moved through the mesh and sifted through the plant litter (Sexton 2013). Mesh and broadcloth were stitched together using polyester core cotton covered thread to minimize separation.

During 2015 and 2016, 8 bags per mesh size were placed in each plot, separated by a minimum of 5m. Plant matter was collected in a nearby rangeland (composition of forbs and grass based on the vegetation surveys), air-dried, and homogenized to ensure an even distribution of petioles and/or leaf blades (which can influence decomposition rates) where each bag contained plant matter from the same collection (Sexton 2013). Ten grams of the homogenized sample (measured to the nearest 0.01g) was placed in each bag. Thus, assessment of decomposition was based on similar mesh litter bag contents in different legume cover ranges: 1) *L. cuneata*/High cover, 2) *L. cuneata*/Low cover, and 3) *B. bracteata* single plant cover. Bags were closed, placed in plots, and secured with U-shape stakes so that one side of each bag (broadcloth) was in contact with the soil. Mesh litter bags (one of each mesh size) were distributed and collected once every 3 months on a rolling basis where after each collection period ended, the next set of mesh litter bags was immediately placed in the field and collected 3 months later (i.e., each set of litter bags was in the field for 3 months; Table 1). Soil core samples were collected from each cover range at the time mesh litter bags were collected from the field. The contents of each mesh litter bag and soil core were processed in individual Berlese funnels (one per sample) for 3-5 days depending on sample moisture content. Within each Berlese funnel a 20-watt bulb suspended above the sample generated heat to dry the leaf litter or soil; invertebrates moved downward to avoid the heat and light, and were collected in a container filled with 70% EtOH to preserve the collected samples. After invertebrates were extracted from litter samples and the litter was dry, the remaining litter was separated by size of litter and debris using nested soil sieves (e.g., Loading Tray – Coarse – leaves, stems, large diameter vegetation – non-decomposed plant litter; Medium Tray - #5 [4000 µm/4.0 mm] – plant material pieces, seeds – decomposed plant litter; Fine Tray - #120 [125 µm/0.125 mm] – silt, duff) where each sieve level allowed for litter and debris to pass through or be blocked. Litter samples were then weighed (using the loading tray and medium tray) to estimate the proportion of lost biomass (measured as dry mass); leaf litter biomass was not mixed with invertebrate biomass. The fine tray allowed for evaluation of wind-blown debris that may have entered mesh bags over the collection period. The total weight of the contents of the mesh bag was used to evaluate how the ending dry mass deviated from the original 10g. Soil samples were not separated by particle size and only used to evaluate soil invertebrate abundance and morphospecies richness. Invertebrate samples (both litter and soil) were homogenized and individuals in one-third of each sample were identified to order and family (using Michener et al. 1994; Salsbury and White 2000; Triplehorn and Johnson 2005) and further separated into morphospecies based on morphologically distinct characteristics. Individual invertebrates were counted (actual counts, not estimates) using a stereo dissecting microscope (400x) and this information was used to estimate morphospecies richness and abundance to estimate their relative contribution to decomposition at each site.

Analyses.

Over six collection periods, a total of 432 mesh bags were collected from SRR sites under identical management conditions, representing three legume cover ranges (*L. cuneata*/Low cover [≥1-5%], *L. cuneata*/High cover [≥25-75%], and *B. bracteata* single plant cover), two times since burn (year of burn [0YB] and two years since burn [2YB]), two seasons of burn (spring and summer), and two mesh bag sizes (small and large). Over the same six collections a total of 216 soil cores were collected from the same SRR sites, representing the same legume cover ranges and fire regimes. Litter and soil invertebrate assemblages (morphospecies richness and individual abundance) and decomposition (measured as dry mass of litter and debris size) were evaluated between season of burn (spring and summer), years since burn (year of burn and two years since burn), legume species (*L. cuneata* and *B. bracteata*), legume species cover (*L. cuneata*/Low [≥1-5%], *L. cuneata*/High [≥25-75%], and *B. bracteata* [single plant, native legume sites]), and mesh bag size (Small and Large; Litter invertebrates only) using a repeated measures ANOVA and paired t-tests (significance noted from $p \leq 0.05$ level). Decomposition (measured as dry mass of litter and debris size) analysis included: dry mass of coarse and medium sized litter, fine debris and total contents by time since prescribed fire (year of burn and two years since burn), season of burn (spring and summer), mesh bag size (Small and Large), legume species (*L. cuneata* and *B. bracteata*), and legume species cover (*L. cuneata*/Low [≥1-5%], *L. cuneata*/High [≥25-75%] and *B. bracteata* [single plant, native legume sites]. Season of burn, years since burn, legume cover and litter and soil invertebrate abundance and morphospecies richness were evaluated using Pearson's r to assess the direction of significant correlations.

Results.

Litter invertebrates: Mesh leaf litter bags.

After 6 collections of leaf litter bags (Table 2), 9616 individuals were collected, averaging 22.26 individuals per leaf litter bag. Acari were the most prevalent taxa in leaf litter collections with Collembolans being the next most numerous (Table 2).

Season of burn by morphospecies richness and invertebrate abundance.

There was no significant relationship between season of burn and morphospecies richness (F [1,430] 1.347, p=0.246) and invertebrate abundance (F [1,430] 1.212, p=0.272) (Figure 1).

Years since burn by morphospecies richness and invertebrate abundance.

There was no significant relationship between years since burn and morphospecies richness (F [1,430] 2.019, p=0.156) and invertebrate abundance (F [1,430] 1.397, p=0.238) (Figure 2).

*Legume species (*B. bracteata *and* L. cuneata*) by morphospecies richness and invertebrate abundance.*

There was no significant relationship between legume species and morphospecies richness (F [1,430] 1.213, p=0.271) and invertebrate abundance (F [1,430] 0.778, p=0.378) (Figure 3).

Legume cover by morphospecies richness and invertebrate abundance.

There was no significant relationship between legume cover and invertebrate abundance (F [2,429] 2.58, p=0.077), although locations with ≥25-75% *L. cuneata* (M=29.78, SE=5.43) tended to have higher invertebrate abundance than locations with ≥1-5% *L. cuneata* (M=17.69, SE=2.76) and single plant cover of *B. bracteata* (M=19.31, SE=3.60). There was no significant relationship between legume cover and morphospecies richness (F [2,429] 0.761, p=0.468) (Figure 4).

Litter bag mesh size (accessibility by meso- and macroinvertebrates) by morphospecies richness and invertebrate abundance.

There was no significant relationship between litter bag mesh size and morphospecies richness (F [1,430] 2.205, p=0.138) and invertebrate abundance (F [1,430] 0.164, p=0.686) (Figure 5).

Soil invertebrates: Soil core samples.

After 6 collections of soil core samples (Table 3), 1853 individuals were collected, averaging 8.58 individuals per soil core. Acari were the most prevalent taxa in soil collections with Collembolans being the next most numerous (Table 3).

Season of burn by morphospecies richness and invertebrate abundance.

There was no significant relationship between season of burn and morphospecies richness (F [1,214] 0.336, p=0.563) and invertebrate abundance (F [1,214] 1.753, p=0.187) (Figure 6).

Years since burn by morphospecies richness and invertebrate abundance.

There was a significant relationship between years since burn and morphospecies richness (F [1,214] 6.961, p=0.009) and invertebrate abundance (F [1,214] 5.115, p=0.025), where there was higher morphospecies richness and invertebrate abundance in areas just burned than locations burned two years earlier (Figure 7).

There was a significant relationship between years since burn and Acari (F [1,214] 8.505, p=0.004) morphospecies richness where Acari morphospecies richness was higher in year of burn (M=3.82, SE=0.298) than in two years since burn (M=2.64, SE=0.277) locations. There was no significant relationship between years since burn and other taxa collected, including: Coleoptera (F [1,214] 0.039, p=0.844), Collembola (F [1,243] 1.584, p=0.210), Diptera (F [1,214] 0.263, p=0.609), Hymenoptera (F [1,214] 3.194, p=0.075), Nematoda (F [1,214] 2.135, p=0.145), Psocoptera (F [1,214] 1.014, p=0.315) and Thysanoptera (F [1,214] 0.115 p=0.735).

There was a significant relationship between years since burn and Acari (F [1,214] 7.521, p=0.007) abundance where Acari abundance was higher in year of burn (M=7.99, SE=1.005) than two years since burn (M=4.65, SE=7.171) locations. There was no significant relationship between years since burn and other taxa collected, including: Coleoptera (F [1,214] 0.470, p=0.494), Collembola, (F [1,214] 0.002, p=0.963), Diptera (F [1,214] 0.746, p=0.389), Hymenoptera (F [1,214] 2.408, p=0.122), Nematoda (F [1,214] 0.876, p=0.350), Psocoptera (F [1,214] 1.014, p=0.315) and Thysanoptera (F [1,214] 0.344, p=0.558).

*Legume species (*B. bracteata *and* L. cuneata*) by morphospecies richness and invertebrate abundance.*

There was no significant relationship between legume species and invertebrate abundance (F [1,214] 3.738, p=0.055), although there tended to be higher individual abundance in locations containing *L. cuneata* (N=144, M=9.69, SE=1.30) than locations containing *B. bracteata* (N=72, M=6.36, SE=0.77). There was no significant relationship between legume species and morphospecies richness (F [1,214] 2.628, p=0.106) (Figure 8).

There was a significant relationship between legume species and Coleoptera (F [1,214] 6.658, p=0.011) abundance where Coleoptera abundance was higher by *L. cuneata* (M=0.19, SE=0.04) than *B. bracteata* (M=0.04, SE=0.02). There was no significant relationship between legume species and other taxa collected, including: Acari (F [1,214] 1.785, p=0.183), Collembola (F [1,214] 2.924, p=0.089), Diptera (F [1,214] 0.093, p=0.761), Hymenoptera (F [1,214] 0.429, p=0.513), Nematoda (F [1,214] 2.925, p=0.089), Psocoptera (F [1,214] 0.506, p=0.478) and Thysanoptera (F [1,214] 0.172 p=0.679).

Legume cover by morphospecies richness and invertebrate abundance.

There was a significant relationship between legume cover and invertebrate abundance (F [2,213] 6.660, p=0.002), where there was higher invertebrate abundance in ≥25-75% *L. cuneata* locations than locations with ≥1-5% *L. cuneata* and single plant cover of *B. bracteata*. There was no significant relationship between legume cover and morphospecies richness (F [2,213] 2.710, p=0.069), although locations with ≥25-75% *L.*

cuneata (M=5.14, SE=0.49) tended to have higher morphospecies richness than locations with ≥1-5% *L. cuneata* (M=4.14, SE=0.40) and single plant cover of *B. bracteata* (M=3.79, SE=0.38) (Figure 9).

There was a significant relationship between legume cover and Acari (F [2,213] 3.689, p=0.027), Coleoptera (F [2,213] 3.337, p=0.037) and Collembola (F [2,213] 5.468, p=0.005) abundance. Acari abundance was higher in locations with ≥25-75% *L. cuneata* (M=8.67, SE=1.44) than locations with ≥1-5% *L. cuneata* (M=5.14, SE=0.73, p=0.019) and single plant cover of *B. bracteata* (M=5.15, SE=0.86, p=0.020), but there was no difference in Acari abundance in locations with ≥1-5% *L. cuneata* and single plant cover of *B. bracteata* (p=0.993). Coleoptera abundance was higher in locations with ≥25-75% *L. cuneata* (M=0.19, SE=0.05, p=0.020) and locations with ≥1-5% *L. cuneata* (M=0.18, SE=0.06, p=0.035) than in single plant cover of *B. bracteata* (M=0.04, SE=0.02), but there was no difference between locations with ≥1-5% *L. cuneata* and locations with ≥25-75% *L. cuneata* (p=0.832). Collembola abundance was higher in locations with ≥25-75% *L. cuneata* (M=2.78, SE=0.83) than locations with ≥1-5% *L. cuneata* (M=0.78, SE=0.21, p=0.005) and single plant cover of *B. bracteata* (M=0.71, SE=0.140, p=0.004), but there was no difference in Collembola abundance in locations with ≥1-5% *L. cuneata* and single plant cover of *B. bracteata* (p=0.922). There was no significant relationship between legume cover and other taxa collected, including: Diptera (F [2,213] 1.310, p=0.272), Hymenoptera (F [2,213] 1.182, p=0.309), Nematoda (F [2,213] 1.456, p=0.236), Psocoptera (F [2,213] 1.014, p=0.364) and Thysanoptera (F [2,213] 1.123, p=0.327).

There was a significant relationship between legume cover and Coleoptera (F [2,212] 3.703, p=0.026) morphospecies richness. Coleoptera morphospecies richness was higher in locations with ≥25-75% *L. cuneata* (M=0.19, SE=0.05) than in single plant cover of *B. bracteata* (M=0.04, SE=0.02, p=0.008), but there was no difference between locations with ≥1-5% *L. cuneata* (M=0.14, SE=0.05) and single plant cover of *B. bracteata* (p=0.089) or locations with ≥25-75% *L. cuneata* (p=0.329). There was no significant relationship between legume cover and other taxa collected, including: Acari (F [2,213] 2.021, p=0.135), Collembola (F [2,213] 1.413, p=0.246), Diptera (F [2,213] 1.310, p=0.272), Hymenoptera (F [2,213] 0.789, p=0.456), Nematoda (F [2,213] 1.298, p=0.275), Psocoptera (F [2,213] 1.014, p=0.364) and Thysanoptera (F [2,213] 1.039 p=0.356).

Invertebrate Assemblage Correlations.

Pearson's r revealed significant correlations between years since burn, legume cover, litter invertebrate abundance, litter morphospecies richness, soil invertebrate abundance and soil morphospecies richness. Years since burn was negatively correlated with soil invertebrate abundance (r=-0.153, p=0.025) and soil morphospecies richness (r=-0.177, p=0.009). Years since burn had no significant correlation with litter invertebrate abundance (r=-0.047, p=0.496) or litter morphospecies richness (r=0.022, p=0.744). Legume cover was positively correlated with soil invertebrate abundance (r=0.204, p=0.003). Legume cover had no significant correlation with soil (r=0.113, p=0.099) or litter (r=0.037, p=0.593) morphospecies richness or litter invertebrate abundance (r=0.029, p=0.675). Season of burn had no significant correlation with soil (r=0.040, p=0.563) or litter (r=0.045, p=0.513) morphospecies richness or soil (r=0.090, p=0.187) or litter (r=-0.040, p=0.562) invertebrate abundance. Soil invertebrate abundance was positively correlated with soil morphospecies richness (r=0.865, p<0.001) and litter invertebrate abundance was positively correlated with litter morphospecies richness (r=0.584, p<0.001). Soil individual abundance had no significant correlation with litter individual abundance (r=-0.080, p=0.244) or morphospecies richness (r=0.049, p=0.475). Soil morphospecies richness had no significant correlation with litter individual abundance (r=-0.102, p=0.135) or morphospecies richness (r=0.002, p=0.972).

Decomposition: Mesh leaf litter bags.

Years since burn by particle size dry mass.

Assessing sites of *L. cuneata* and *B. bracteata* grouped together, there was a significant relationship between years since burn and the dry mass of silt and duff (F [142,141.85] 0.39, p=0.032), medium sized plant litter (F [142,85.89] 36.004, p<0.001), and total dry mass of the contents from the mesh bag (F [142,82.42] 34.84, p<0.001) where the dry mass of each of these litter and debris sizes were significantly greater in areas just burned than in areas burned two years earlier. There was no significant difference in dry mass for coarse plant litter (F [142,139.216] 3.674, p=0.685) between year of burn and two years since burn (Figure 10). Analyzing *B. bracteata* separately from *L. cuneata*, there was a significant relationship between years since burn and medium sized plant litter (F [46,27.40] 12.26, p=0.001) and total dry mass of the contents from the mesh bag (F [46,25.56] 10.32, p=0.003) where the dry mass of each of these litter and debris sizes were significantly greater in areas just burned than in areas burned two years earlier. There was no significant difference in dry mass for silt and duff (F [46,37.738] 1.50, p=0.065) or coarse plant litter (F

[46,44.034] 3.124, p=0.677) between year of burn and two years since burn (Figure 10). However, coarse plant litter dry mass showed a significant relationship between plant species. Dry mass of coarse plant litter in the vicinity of *B. bracteata* had a significantly higher dry mass than those near *L. cuneata*, in both times since burn (Year of burn: (F [70,52.84] 0.023, p=0.016); Two years since burn: (F [142,103.936] 0.005, p=0.003). When *L. cuneata* and *B. bracteata* were grouped together, there was no significant relationship between years since burn and coarse plant litter (F [70,49.36] 0.014, p=0.062). Analyzing *L. cuneata* separately from *B. bracteata*, there was a significant relationship between years since burn and medium sized plant litter (F [94,56.74] 23.18, p<0.001) and total dry mass of the contents from the mesh bag (F [94,55.63] 23.81, p<0.001) where the dry mass of each of these particle sizes were significantly greater in areas just burned than in areas burned two years earlier. There was no significant difference in dry mass for silt and duff (F [94,91.252] 0.25, p=0.197) or coarse plant litter (F [94,92.252] 3.044, p=0.820) between year of burn and two years since burn (T-test for Equality of Means) (Figure 10).

Season of burn by particle size dry mass.

There was no significant relationship in the dry mass of silt and diff (F [1,430] 1.231, p=0.268), medium sized plant litter (F [1,430] 1.610, p=0.205), coarse plant litter (F [1,430] 0.556, p=0.456) and total dry mass of the contents from the mesh bag (F [1,430] 3.501, p=0.062) between spring and summer burns (Figure 11).

Litter bag mesh size by particle size dry mass.

When *L. cuneata* and *B. bracteata* were analyzed together, there was a significant relationship between litter bag mesh size and coarse plant litter (F [142,139.01] 5.67, p<0.001) and medium sized plant litter (F [142,129.92] 2.31, p=0.041) where the dry mass of coarse plant litter was greater coming from small mesh litter bags than large mesh litter bags and medium sized plant litter was greater coming from large mesh litter bags than small mesh litter bags. There was no significant difference in dry mass for silt and duff (F [142,141.188] 0.001, p=0.568) and total dry mass of the contents from the mesh bag (F [142,135.301] 1.871, p=0.593) between small and large mesh litter bags (Figure 12). When *B. bracteata* was analyzed separately from *L. cuneata*, there was a significant relationship between litter bag mesh size and coarse plant litter (F [46,38.96] 4.80, p=0.041) where dry mass for this litter size was significantly greater coming from small mesh litter bags than large mesh bags. There was no difference in the dry mass of silt and duff (F [46,33.942] 2.917, p=0.101), medium sized plant litter, (F [46,43.355] 0.012, p=0.781) and total dry mass of the contents from the mesh bag (F [46,40.617] 0.082, p=0.351) between small and large mesh litter bags (Figure 12).

When *L. cuneata* was analyzed separately from *B. bracteata*, there was a significant relationship between litter bag mesh size and coarse plant litter (F [94,92.59] 3.62, p<0.001) and medium sized plant litter (F [94,79.03] 3.14, p=0.030) where the dry mass of coarse plant litter was greater coming from small mesh litter bags than large mesh litter bags and medium sized plant litter was greater coming from large mesh litter bags than small mesh litter bags. There was no significant difference in dry mass of silt and duff (F [94,91.518] 1.693, p=0.613), and total dry mass of the contents from the mesh bag (F [94,75.580] 3.717, p=0.999) between small and large mesh litter bags (T-test for Equality of Means) (Figure 12).

Litter bag mesh size and years since burn by particle size dry mass.

In locations burned two years earlier, there was a significant relationship between litter bag mesh size and coarse plant litter (F [70,62.23] 9.28, p<0.001) and total dry mass of the contents from the mesh bag (F [70,61.91] 0.51, p=0.001) where dry mass was significantly greater coming from small mesh litter bags than large mesh bags. There was no significant relationship between mesh bag size and medium sized plant litter (F [70,70] 0.018, p=0.058), although dry mass tended to be greater coming from large mesh litter bags in locations burned two years earlier than small litter bags. There was no difference in dry mass for silt and duff (F [70,69.797] 0.192, p=0.893) between small and large mesh litter bags in locations burned two years earlier (Figure 13). In year of burn locations, there was a significant relationship between litter bag mesh size and coarse plant litter (F [70,69.90] 0.40, p=0.025) where the dry mass of coarse plant litter was greater coming from small mesh litter bags than large mesh litter bags. There was no significant difference in dry mass of silt and duff (F [70,67.767] 0.169, p=0.526), medium sized plant litter (F [70,63.494] 1.380, p=0.085) and total dry mass of the contents from the mesh bag (F [70,66.804] 1.364, p=0.766) between small and large mesh litter bags in locations burned that year (T-test for Equality of Means) (Figure 13).

Legume cover by particle size dry mass.

When year of burn and two years since burn were analyzed together, there was a significant relationship between coarse plant litter dry mass and legume species' cover ranges where coarse plant litter dry mass was significantly greater in single plant cover locations of *B. bracteata* than low (p=0.008) and high (p=0.011) cover ranges of *L. cuneata*. Dry mass of coarse plant litter was not significantly difference between low and high cover of *L. cuneata* (p=0.980). There was no significant difference in dry mass for silt and duff (p=0.773), medium sized plant litter (p=0.229) and total dry mass of the contents from the mesh bag (p=0.843) between legume species' cover ranges (Figure 14). When locations burned two years earlier were analyzed separately from locations burned that year, there was a significant relationship between medium sized plant litter and legume species' cover ranges, where high cover *L. cuneata* had significantly greater dry mass than single plant cover of *B. bracteata* (p=0.038). Dry mass of medium sized plant litter was not significantly different between low cover *L. cuneata* and single plant cover of *B. bracteata* (p=0.142) or low cover and high cover *L. cuneata* (p=0.878). There was no significant difference in dry mass of silt and duff (p=0.967), coarse plant litter (p=0.097) and total dry mass of the contents from the mesh bag (p=0.819) between legume species' cover ranges (Figure 14). When locations burned that year were analyzed separately from locations burned two years earlier, there was no significant relationship between legume cover and dry mass of any litter or debris size (silt and duff: p=0.589, medium sized plant litter: p=0.559, coarse litter: p=0.060, total dry mass of the contents from the mesh bag: p=0.981) (Post Hoc Tests of LSD) (Figure 14).

Discussion.

Decomposition was lowest in locations with the native legume in both times since burn, where dry mass of the remaining coarse plant litter in the leaf litter bags was heavier than locations with *L. cuneata* (Figures 10, 14). Decomposition was highest in year of burn locations for both legume species, where dry mass of medium sized plant litter (i.e., litter partially decomposed from the original coarse plant litter placed in the leaf litter bags) was heaviest (Figure 10). There was no difference between cover range and dry mass of any litter size and debris in year of burn locations, but decomposition was highest in ≥25-75% *L. cuneata* burned two years earlier, where the dry mass of medium sized plant litter was heavier than locations with single plant cover of *B. bracteata* (Figure 14). There was no difference in decomposition between season of burn (Figure 11). Soil invertebrates were more abundant and possessed higher morphospecies richness in recently burned locations (Pearson's r and Figure 7). Soil invertebrates were also more abundant in ≥25-75% *L. cuneata* rather than ≥1-5% *L. cuneata* and single plant *B. bracteata* (Pearson's r and Figure 9). Dry mass of coarse plant litter was heaviest in small mesh bags than large mesh bags, reflecting the contribution of meso- and macroinvertebrates to decomposition (i.e., they could access the litter in the large, but not the small mesh bags), in the presence of both legume species. When meso- and macroinvertebrates where allowed access to large mesh bags, medium sized plant litter was heaviest in the presence of *L. cuneata* (Figure 12 and 13). There were no significant differences for leaf litter invertebrates for any of the factors studied; season of burn (Figure 1), years since burn (Figure 2), presence of native versus invasive legumes (Figure 3), legume cover (Figure 4), or invertebrate size (small versus large mesh bags) (Figure 5). However, as litter invertebrate abundance increased, litter morphospecies richness increased. The same correlation was seen between soil invertebrate abundance and morphospecies richness (Pearson's r). There were no significant differences for soil invertebrates for season of burn (Figure 6) or presence of native versus invasive legumes (Figure 8).

Studies show that frequent fires are required to maintain the productivity of grasses and soil invertebrate density and biomass increase when spring fires occur once every 1-4 years (James 1982; Seastedt 1984a). As expected, surface-dwelling litter invertebrates are affected by fire more than soil-dwelling invertebrates, where soil biota 5 cm below the soil surface appear unaffected or even increase following fire (Seastedt 1988a). In this study, soil invertebrate abundance and morphospecies richness significantly increased following fire, showing higher soil invertebrate abundance and morphospecies richness in locations just burned (0YB) compared to locations burned two years earlier (2YB) (Figure 7). A significant relationship existed between time since burn and litter decomposition for both legume species, where the dry mass of medium sized plant litter and the total dry mass of the contents from the mesh bag, were significantly heavier in the locations just burned than those burned two years earlier (Figure 10). When grouping legume species, fine debris (silt and duff) contributed to a portion of the resulting total dry mass of the mesh bag contents (Figure 10), reflecting less decomposition in more recently burned areas and more decomposition in areas burned two years prior. However, many of the mesh litter bags placed in locations burned that year contained a heavier total dry mass after the collection period than when first deployed. There is less vegetation and impediment (i.e., plant, organic litter and debris) in recently burned areas, and therefore less obstruction to hinder the movement of plant litter, soil, and silt by wind, which may have contributed to the increased dry mass of the mesh bags in the recently burned areas (i.e., if material was blown into the bags throughout the collection period). Thus, the observed pattern of less decomposition in year of burn areas may have been biased by the movement of fine debris into the mesh bags; additional research is needed to evaluate this possibility. Litter invertebrate abundance and morphospecies richness did not differ based on years since burn (Figure 2). The season of burn (Spring: February-March; Summer: July-August) did not influence litter or soil invertebrate abundance or morphospecies richness (*Leaf litter*: Figure 1; *Soil*: Figure 6) or decomposition (Figure 11).

Comparing areas recently burned to areas burned two years earlier, differences in dry mass of different litter and debris sizes could depend on the collection start date relative to the date of the prescribed fire where mesh litter bags were located (Table 1). For example, mesh litter bags from the first collection were placed in the field in April of 2015. The most recently burned plot (year of burn) for that collection period was a spring burn in March of 2015; mesh litter bags were placed in those locations roughly one month after the spring burn. The next most recent burn (first collection) was a summer burn in August of 2014; mesh litter bags were placed in those locations roughly 8 months after the summer burn. Plant growth between summer and spring burns in year of burn locations (for the first collection) may have reduced the movement of silt, duff and medium sized plant litter in the summer year of burn sections with greater movement in the spring year of burn sections. When analyzing plant species separately (i.e., *B. bracteata* and *L. cuneata*; Figure 10), litter dry mass was greater in locations recently burned than those burned two years earlier for medium litter and the total dry mass of the contents from the mesh bag in areas with *B. bracteata* (Figure 10). The same trend was seen for each of these litter and debris sizes in plots that contained *L. cuneata* (Figure 10). When analyzing plant species together, the same trends were seen including heavier dry mass of fine debris (silt and duff) in year of burn locations. Thus, areas with the native and invasive legumes may have both experienced increased weight due to the movement of fine debris and medium litter, providing further support that fine debris and medium litter, contributed to the total dry mass of the mesh bag. With *L. cuneata* and *B. bracteata* both having similar weights at these litter and debris sizes, there seems to be no difference in decomposition. However, examining the difference in coarse litter weight between *L. cuneata* and *B. bracteata* provides more insight into litter decomposition over the collection period.

Coarse litter (leaves, stems, large diameter vegetation) had a significantly higher dry mass in locations with *B. bracteata* than locations with either *L. cuneata* cover range (Figures 10, 14). These trends were similar for year of burn and two years since burn treatments. Thus, there was more decomposition in locations with *L. cuneata* and less decomposition in locations with *B. bracteata* regardless of the time since burn. The cover and diversity of legumes enhance C and N pools where communities that have greater legume cover and diversity produce and use N more effectively (Oelmann et al. 2007). Leaf litter high in N concentration is favored by microorganisms and decomposition occurs more rapidly (Melillo et al. 1982). While *L. cuneata* is considered to contain relatively low levels of N (as g/kg) (Bransby et al. 1989) as an invasive legume, invasive plants generally maintain higher concentrations of leaf N (Vitousek et al. 1987; Vitousek and Walker 1989; Witkowski 1991; Baruch and Goldstein 1999; Nagel and Griffin 2001) and consequently decompose more rapidly and release more N to the soil than native species. Thus, invasion of legumes could lead to increased rates of decomposition and nutrient cycling in invaded areas (Vitousek and Walker 1989; Witkowski 1991).

Medium litter had a significantly higher dry mass in locations that contained a high cover of *L. cuneata* compared to *B. bracteata* locations (Figure 16). Although data were not collected regarding the specific contents that contributed to dry mass, seeds were visibly present in the medium litter from locations with a high cover of *L. cuneata* (J. Kaplan, personal observation). Thus, the dry mass of medium litter in high cover *L. cuneata* locations may also reflect *L. cuneata's* high seed production and increased decomposition of plant material at year of burn and two years since burn locations.

Previous research has shown that biodiversity, including genetic diversity, is positively associated with the facilitation of ecosystem services (Reynolds et al. 2012). Increased primary productivity and nutrient retention are ecosystem services associated with higher density and diversity of arthropods. The *resource concentration hypothesis* explains that herbivore arthropods should be more abundant in large patches of host plants, because they are more likely to find resources and stay longer in those patches; arthropod herbivory is expected to play a role in primary production among plant communities. In contrast, most experimental results find the number of herbivores per plant is generally lower in densely planted fields (Luginbill and McNeal 1958; Pimentel 1961; Way and Heathcote 1966; A'Brook 1978; Farrell 1976; Solomon 1981; Latheef and Ortiz 1983; Root and Kareiva 1984; Power 1987; Segarra-Carmona and Barobosa 1990; Thompson and Quisenberry 1995), with larger densities of arthropods associated with higher plant species richness than dense plant stands with one or a few plant species. The *resource diffusion hypothesis* suggests that the diffusion of resources, rather than dense stands, support higher abundance of arthropod herbivores.

Analysis of soil invertebrate collections favors the resource concentration hypothesis where there was higher abundance (specifically Acari, Coleopterans and Collembolans) collected in ≥25-75% *L. cuneata* rather than ≥1-5% *L. cuneata* or in single plant locations of *B. bracteata* (Figure 9). Similarly, there was also more decomposition in these areas (Figure 14). Legumes are susceptible to many Acari pests and 80% yield losses in many legume crops have been reported due to herbivory and damage through these invertebrates (Singh et al. 1990; Afun et al. 1991; Dreyer et al. 1994). Therefore, this may explain why Acari made up the majority (in terms of abundance of individuals) of leaf litter (Table 2) and soil (Table 3) collections and why decomposition was highest in ≥25-75% *L. cuneata* locations.

Coleopterans, despite accounting for a mere 1.62% of soil invertebrate abundance (Table 3), had a higher abundance in ≥25-75% *L. cuneata* locations compared to ≥1-5% *L. cuneata* or in single plant locations of *B. bracteata*. Many species of beetles in the family Chrysomelidae are agricultural pest insects and can cause damage legumes. Adults lay eggs on seeds and larvae consume these seeds as they develop and emerge from them as adults (Tuda et al. 2005).

Collembolans were a taxonomic group that was more abundant in ≥25-75% *L. cuneata* locations, rather than ≥1-5% *L. cuneata* or in single plant locations of *B. bracteata*. Presence of Collembolan decomposers increase total N concentration and N enrichment of grasses and legumes (Partsch et al. 2006). Thus, Collembolans can increase above ground plant productivity through effects on litter decomposition and nutrient mineralization which leads to increased plant nutrient acquisition. Below ground, root biomass is generally shown to decrease the presence of Collembolans, showing that the presence of

Collembolan decomposers can have impacts on plant root and shoot biomass (Partsch et al. 2006). However, it is not clear how Collembolans influence plant communities in the presence of legumes.

Lespedeza cuneata produces allelopathic chemicals that inhibit the germination and growth of many common grassland plants, such as big bluestem, Indiangrass, Kentucky blugrass, bermudagrass, fescue and ryegrass (Partsch et al. 2006). When examining if there was a difference between soil (Figure 8) and litter (Figure 3) invertebrate assemblages in the presence of different legume species (*L. cuneata* or *B. bracteata*), there was no significant difference between litter invertebrate abundance or morphospecies richness. Although not significant, trends indicate higher soil invertebrate abundance in locations containing *L. cuneata* rather than *B. bracteata* (Figure 8), suggesting that invertebrate assemblages are affected more by legume cover (*Leaf litter*: Figure 4; *Soil*: Figure 9) than legume species (*Leaf litter*: Figure 3; *Soil*: Figure 8); decomposition was highest in the presence of *L. cuneata* and in high cover locations of *L. cuneata* (Figure 10, 14). These results also indicate that legume cover may contribute more to the abundance of soil invertebrates than litter invertebrates. Legume cover was positively correlated with soil invertebrate abundance; the majority of individuals collected were Acari and Collembolans (Table 3).

A significant relationship existed between mesh bag size and decomposition with coarse litter decomposing less in small mesh bags than large mesh bags (Figures 12, 13). Coarse litter from small mesh bags likely weighed more due to macroinvertebrates (>2mm) being unable to access the contents of the litter bags. Microinvertebrates that can access small mesh bags may also decompose plant material at a slower rate compared to macroinvertebrates (Buckingham et al. 2015). This same trend occurred when separated by legume species (Figure 12). When legume species were analyzed together, a significant relationship existed between mesh bag size and decomposition where medium litter had heavier dry mass from large mesh bags than small mesh bags (Figure 12). While there was no difference in fine debris between mesh bag size, heavier dry mass of medium litter enclosed in large mesh bags reflected more decomposition over the three-month collection period. This same trend occurred by *L. cuneata*, but not by *B. bracteata* (Figure 12). Thus, the plant community and structure of the invertebrate community, specifically size distributions (where large mesh bags allow access to large-bodied invertebrates), can influence litter decomposition rates differently. Litter decomposition may therefore be influenced by macroinvertebrates in both *L. cuneata* and *B. bracteata* locations differently, where even though large mesh bags allow access to large-bodied invertebrates by both legumes similarly, litter enclosed in large mesh bags in *L. cuneata* locations decomposed more rapidly.

When considering burn regimes, coarse litter and the total dry mass from the contents of the mesh bag were significantly heavier from small mesh bags than large mesh bags in locations burned two years earlier (Figure 13). Coarse litter, but not the total contents from the mesh bags, also weighed more from small mesh bags than large mesh bags in year of burn locations (Figure 13). Thus, macroinvertebrates had a larger impact on decomposition than microinvertebrates (<2mm). Surface-dwelling litter invertebrates are expected to be negatively affected by fire, whereas soil-dwelling invertebrates may not, or may be less negatively affected depending on depth below the soil surface and fire intensity

(Seastedt 1988). Recently burned (burned this year) locations are expected to have a lower amount of surface-dwelling litter invertebrates compared to locations burned previously. Buckingham et al. (2015) found that macroinvertebrate exclusion following fire reduced decomposition by 34.7% and these detritivores were larger and less abundant following fire, possibly as a result of fire-induced changes in habitat structure. Interestingly, effects of fire severity on macroinvertebrate abundance and body size resulted in similarity throughout a range of fire severity tests, where no difference was observed in the rate of decomposition from macroinvertebrate detritivores (Buckingham et al. 2015).

The primary taxa collected from leaf litter (Table 2) and soil samples (Table 3) were Acari and Collembolans (Acari and Collembola combined abundance: *Leaf litter* = 86.45%; *Soil* = 90.23%), both of which were small enough to enter the small mesh litter bags. There was no significant relationship between mesh bag size and litter invertebrate abundance and morphospecies richness (Figure 5). Because most taxa collected (even aside from Acari and Collembolans) where small bodied, most invertebrates likely could access leaf litter in both the small and large mesh litter bags. It is important to note some large-bodied invertebrates may have been excluded from both mesh bag sizes, and that some invertebrates were located *underneath* the leaf litter bag (e.g., Coleopterans, personal observation, J. Kaplan), and therefore were not counted in the collections.

Conclusion and Future Directions.

Increased decomposition services from litter macroinvertebrate detritivores and soil invertebrates may contribute to higher decomposition rates in year of burn locations. Locations burned more recently are expected to have a lower amount of surface-dwelling litter invertebrate detritivores due to mortality from fire, lack of cover and increased desiccation, but soil biota below the surface are generally unharmed or increase in abundance post fire. Consequently, soil invertebrates were found to be more abundant in year of burn versus two years post burn locations, whereas there were no differences found for litter invertebrates. Decomposition services may also depend on the invertebrate community and their size distribution. When macroinvertebrates were allowed access to litter bags, decomposition was higher than when access was restricted; coarse litter from small mesh bags was heavier (i.e. less decomposition) than large mesh bags in both times since burn. However, there was no difference in litter invertebrate richness and abundance depending on mesh bag size. Acari and Collembola could access either mesh bag size and contributed to the majority of the collections; macroinvertebrates may contribute more to decomposition than microinvertebrates. Locations with a high cover *L. cuneata* had more decomposition compared to single plant cover of *B. bracteata*. Consequently, soil invertebrates were more abundant in high cover *L. cuneata* compared to low cover *L. cuneata* and single plant *B. bracteata*. However, there was no difference in litter invertebrate richness and abundance depending on legume cover. Abundance and morphospecies richness of litter and soil invertebrates and decomposition was not different depending on the season of burn. While factors investigated for leaf litter invertebrates did not show significant differences, as litter invertebrate abundance increased, litter morphospecies richness increased. The same correlation was seen between soil invertebrate abundance and morphospecies richness.

Additional research is needed to evaluate decomposition and invertebrate assemblages in grasslands with other invaders and congeneric natives in order to assess if decomposition and the invertebrate community differs among other plant communities and cover ranges. Including narrower and additional cover ranges, would allow further assessment of different stages of invasion. Additional research is needed to evaluate the influence of different burn regimes (e.g., cool season burns, different times since fire) and management practices on decomposition and invertebrate assemblages in invaded areas. Evaluation of these factors could provide valuable information for controlling non-natives.

Tables and figures.

Collection	Season of Burn	Years since Burn	Date of Prescribed Fire	Litter Bags Placed in Field	Litter Bags and Soil Collected from Field	Litter Bags and Soil Processed and Removed from Berlese Funnel
1	SP	0YB	Feb-Mar 15	Apr 15	Jul-Aug 15	
	SU		Aug-14			
	SP	2YB	Feb-13			
	SU		Sep-Oct 12			
2	SU	0YB	Jul-Aug 15	Aug 15	Nov-Dec 15	
	SP		Feb-Mar 15			
	SU	2YB	Oct- Nov 13			
	SP		Feb 13			
3	SU	0YB	Jul-Aug 15	Dec 15	Feb-Mar 16	Feb-Apr 16
	SP		Feb-Mar 15			
	SU	2YB	Oct-Nov 13			
	SP		Feb 13			
4	SP	0YB	Feb-Mar 16	Apr 16	Jul 16	
	SU		Jul-Aug 15			
	SP	2YB	Feb-Apr 14			
	SU		Oct-Nov 13			
5	SU	0YB	Jul-Aug 16	Aug 16	Nov 16	Nov-Dec 16
	SP		Feb-Mar 16			
	SU	2YB	Aug 14			
	SP		Feb-Apr 14			
6	SU	0YB	Jul-Aug 16	Dec 16	Mar 17	Mar-Apr 17
	SP		Feb-Mar 16			
	SU	2YB	Aug 14			
	SP		Feb-Apr 14			

Table 1. Summary of Collections (1-6) based on treatment [Season of Burn (SP = Spring; SU = Summer), Years since Burn (0YB = year of prescribed fire; 2YB = two years since prescribed fire)], Date of Prescribed Fire (month and year), month and year mesh litter bags were placed in field (Litter Bags Placed in Field); month and year mesh litter bags and soil core samples were collected from field (Litter Bags and Soil Collected from Field), month and year mesh litter bags and soil core samples were processed and removed from Berlese funnels (Litter Bags and Soil Processed and Removed from Berlese Funnel).

Litter Taxonomy	Abundance	% of Sample	Morphospecies
Acari	5201	54.09	48
Araneae	46	0.48	14
Coleoptera	568	5.91	21
Collembola	3112	32.36	21
Diptera	220	2.29	22
Hemiptera	8	0.08	3
Hymenoptera	20	0.21	9
Isopoda	1	< 0.01	1
Nematoda	13	0.14	1
Psocoptera	310	3.22	3
Tardigrada	1	< 0.01	1
Thysanoptera	56	0.58	5
Trichoptera	1	< 0.01	1
Unknown	11	0.11	11

Table 2. Litter samples showing invertebrate abundance, percent of sample and morphospecies richness. Invertebrates were collected from mesh litter bags placed at sites that were burned the same year (0YB; 216 total litter bags) and two years earlier (2YB; 216 total litter bags) and either burned in the spring (216 total litter bags) or summer (216 total litter bags at three cover ranges (≥1-5% and ≥25-75% invasive *L. cuneata* cover; single plant cover native *B. bracteata* cover). Litter bags were distributed and collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

Soil Taxonomy	Abundance	% of Sample	Morphospecies
Acari	1365	73.66	37
Coleoptera	30	1.62	10
Collembola	307	16.57	17
Diptera	36	1.94	9
Hymenoptera	27	1.46	2
Nematoda	45	2.42	1
Psocoptera	4	0.22	2
Thysanoptera	10	0.54	4

Table 3. Soil core samples showing invertebrate abundance, percent of sample and morphospecies richness. Invertebrates were collected from soil cores collected at sites that were burned the same year (0YB; 108 total soil cores) and two years earlier (2YB; 108 total soil cores) and either burned in the spring (108 total soil cores) or summer (108 total soil cores) at three cover ranges (≥1-5% and ≥25-75% invasive *L. cuneata* cover; single plant cover native *B. bracteata* cover). Soil cores were collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

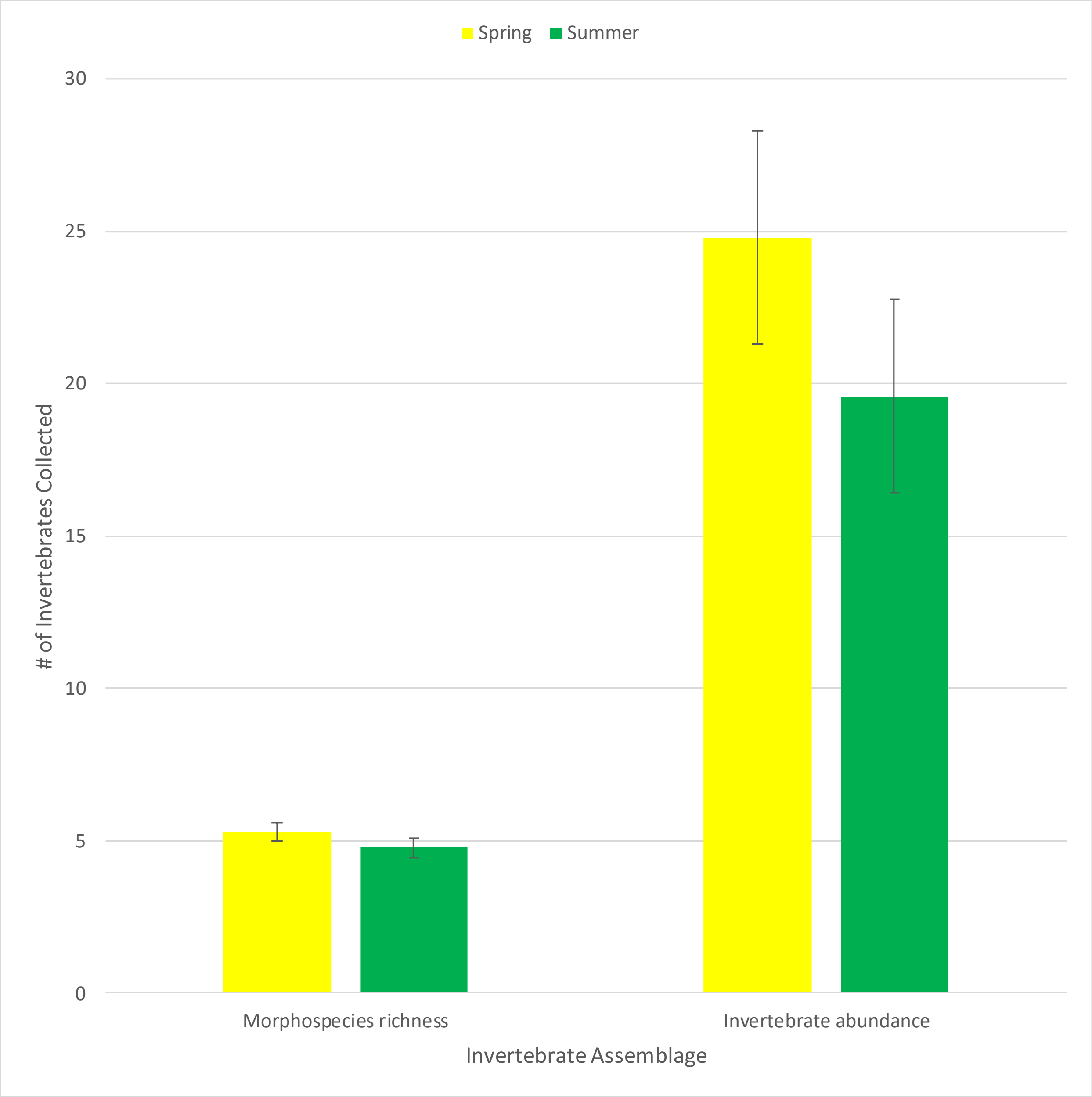

Figure 1. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of litter samples by season of burn. Two of six sections are burned each year: one dormant season spring burn (February through March) used to promote livestock production and is conducted just before spring green-up and one growing season summer burn (July through August) conducted when warm-season herbaceous plants are actively growing. Invertebrates were collected from mesh litter bags at sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

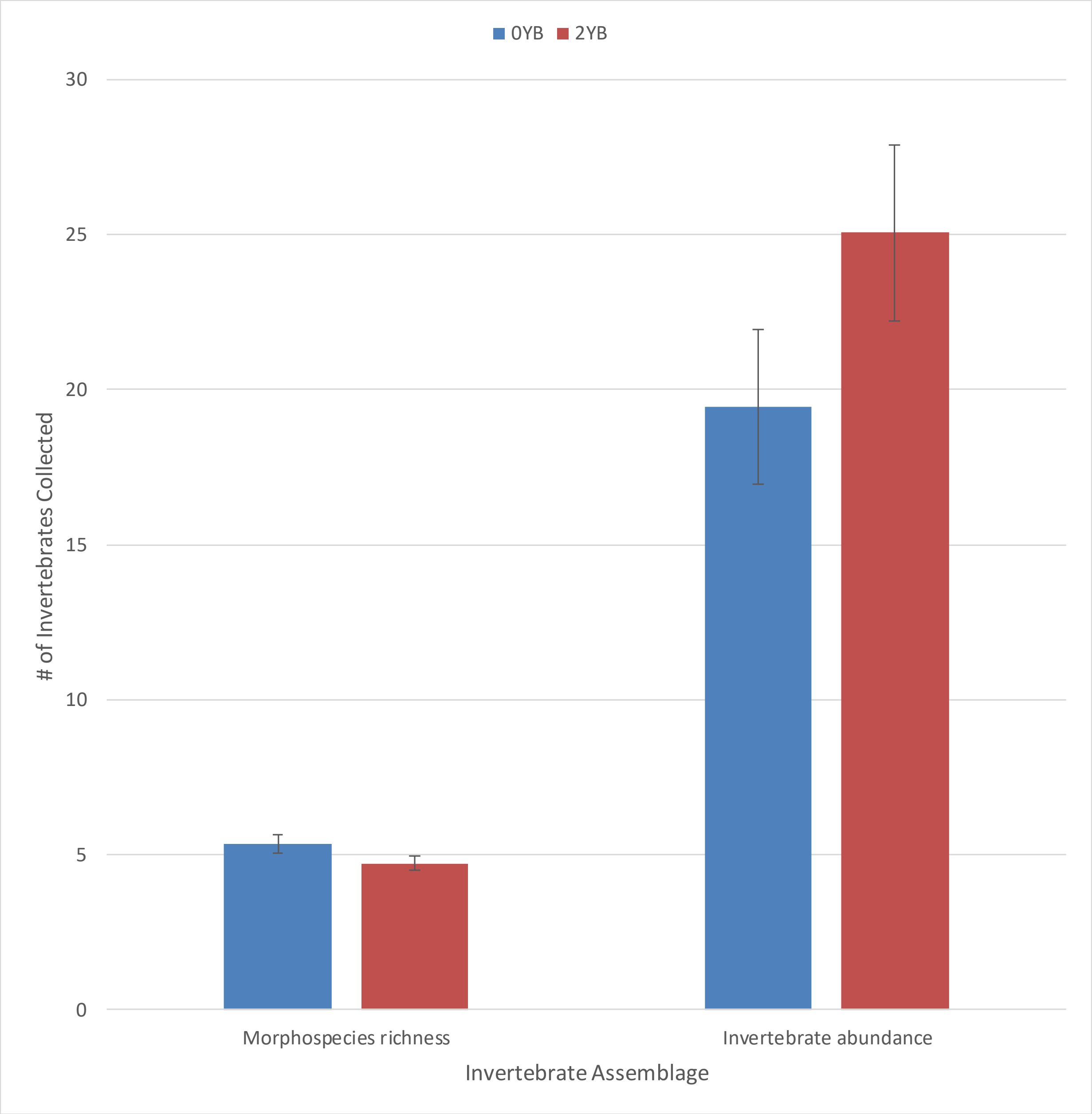

Figure 2. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of litter samples by years since burn. Two of six sections are burned each year. Longest time since burn (2YB) sections allow plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom, while using the shortest time since burn (0YB) allows for evaluation of invertebrate assemblages post fire. Invertebrates were collected from mesh litter bags at sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

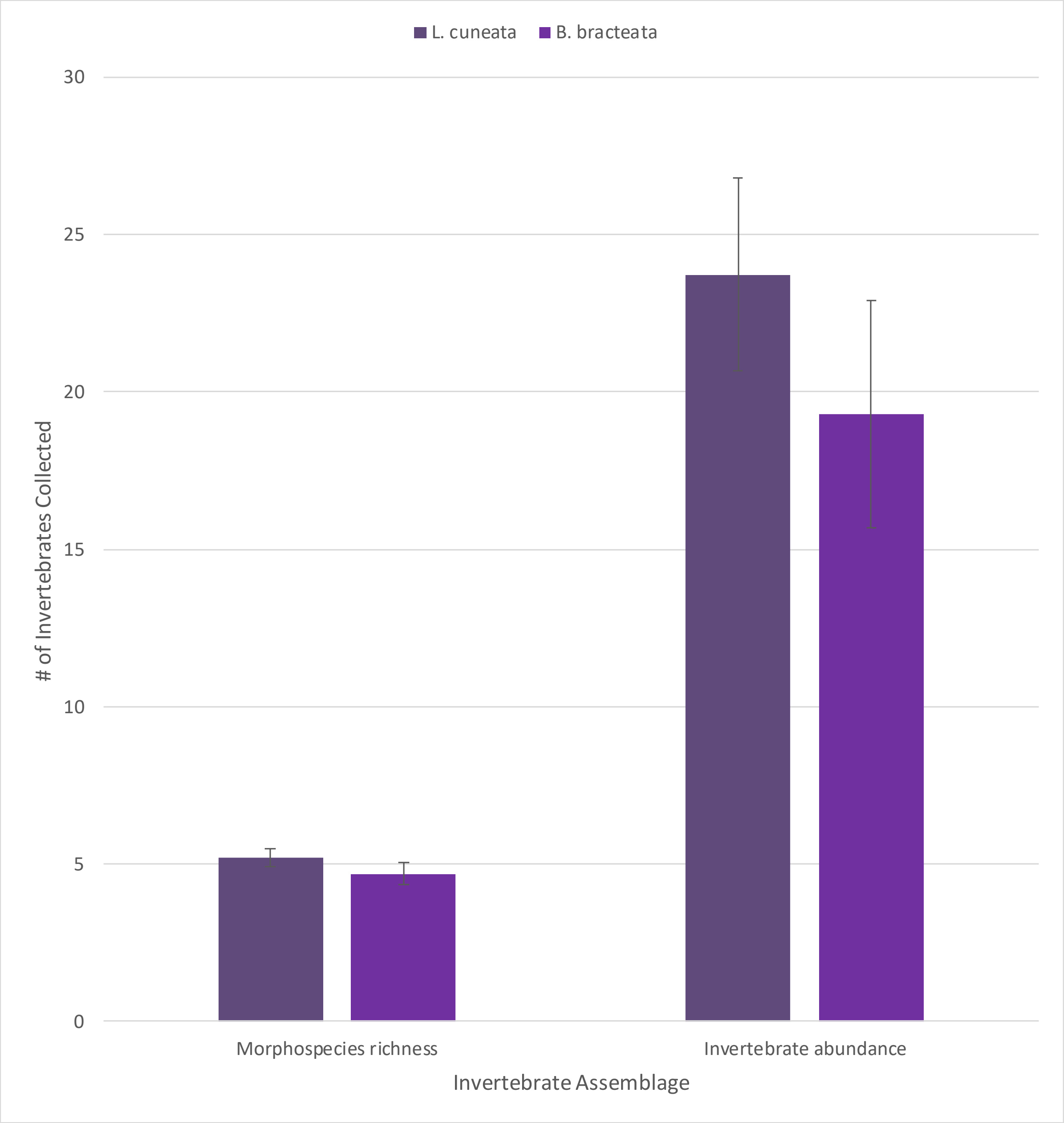

Figure 3. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of litter samples by legume species. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Invertebrates were collected from mesh litter bags at sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

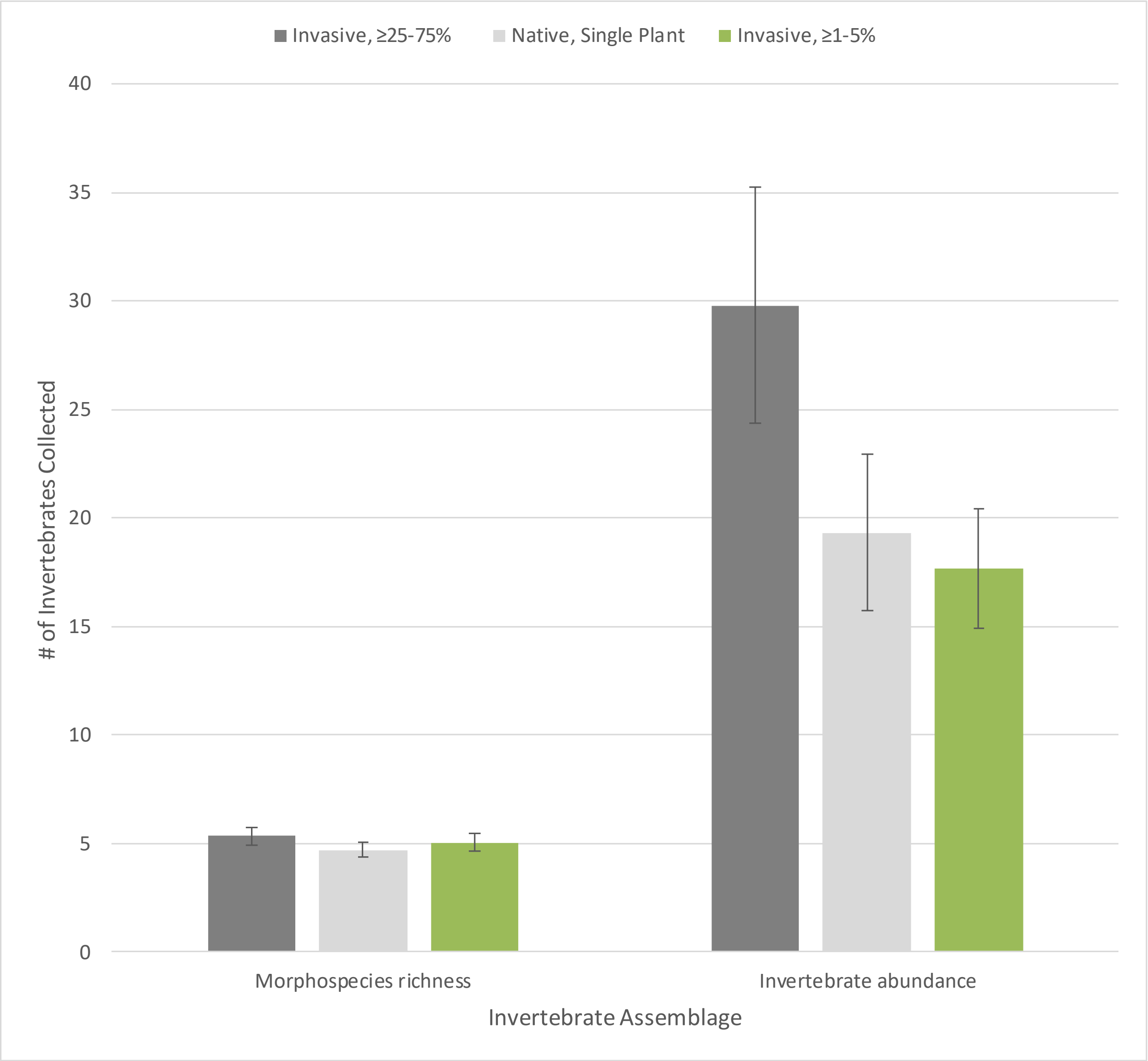

Figure 4. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of litter samples by legume cover. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Treatments within each section in the SRR included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/High cover (≥25-75%), and 3) *B. bracteata* single plant cover. Invertebrates were collected from mesh litter bags at sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

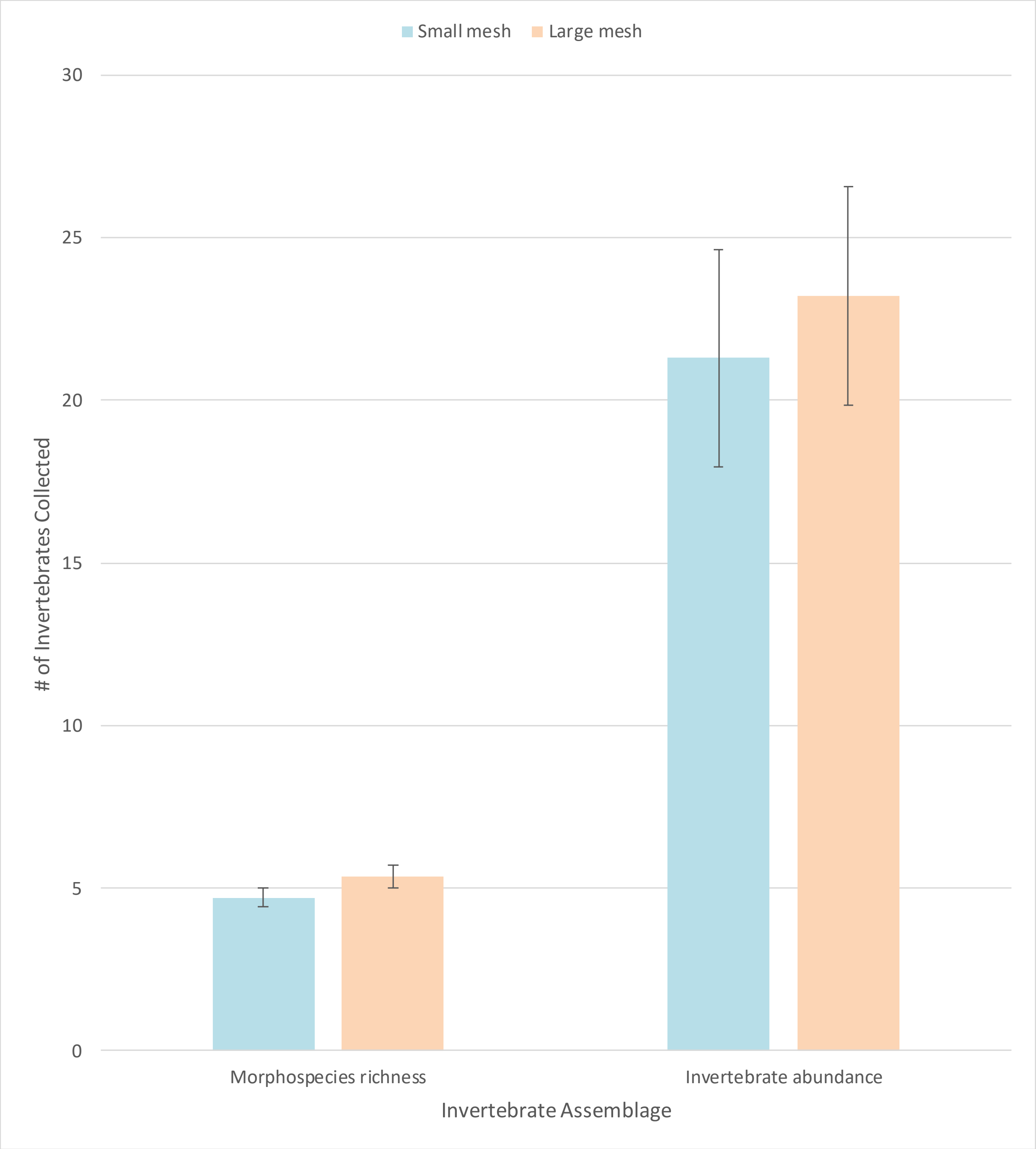

Figure 5. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of litter samples by litter bag mesh size. Large mesh bags allow entry by most meso- and macroinvertebrates, while the small mesh bags do not. Invertebrates were collected from mesh litter bags at sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

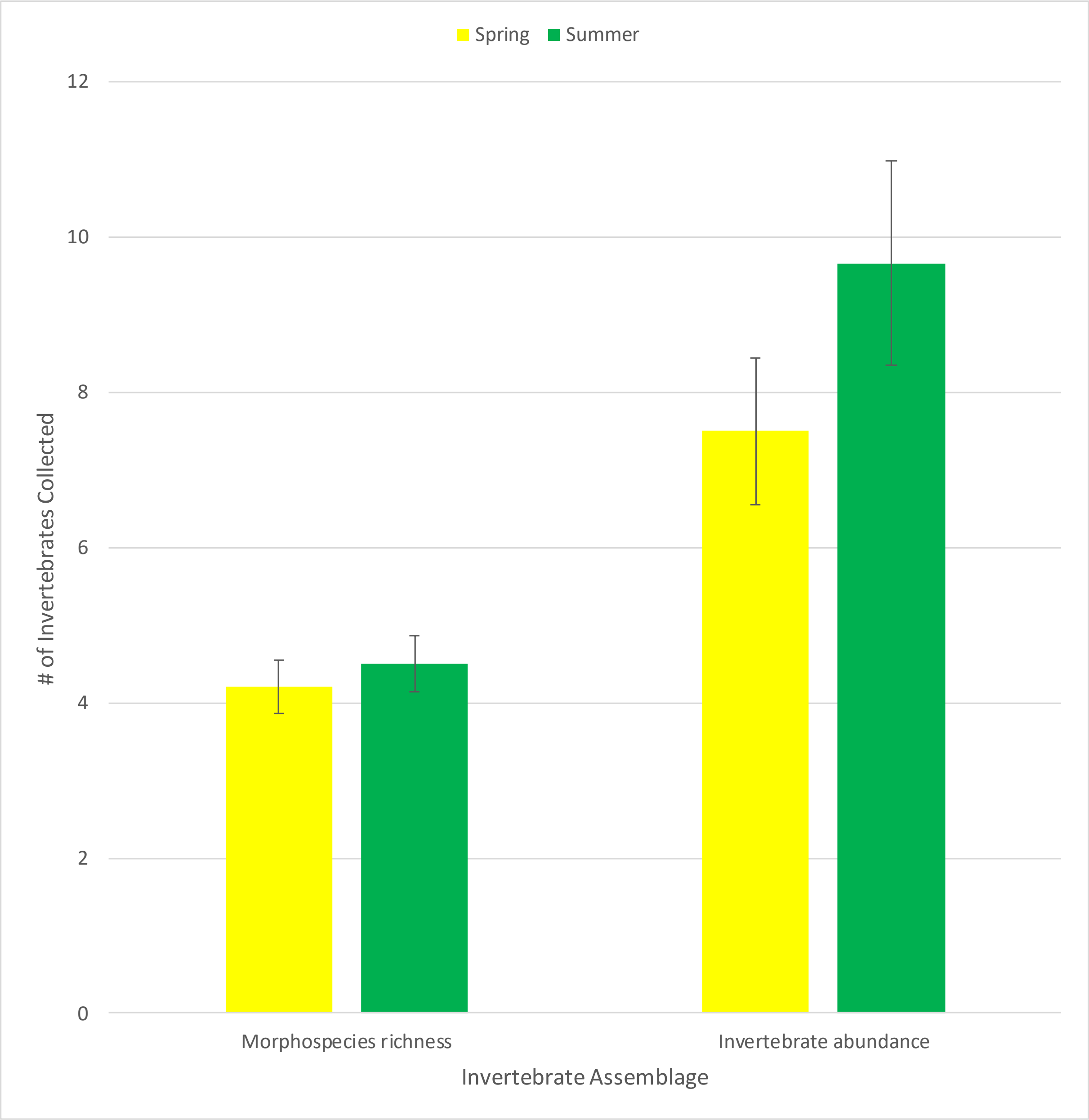

Figure 6. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of soil core samples by season of burn. Two of six sections are burned each year: one dormant season spring burn (February through March) used to promote livestock production and is conducted just before spring green-up and one growing season summer burn (July through August) conducted when warm-season herbaceous plants are actively growing. Invertebrates were collected from soil cores at sites that had similar treatments. Soil cores were collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

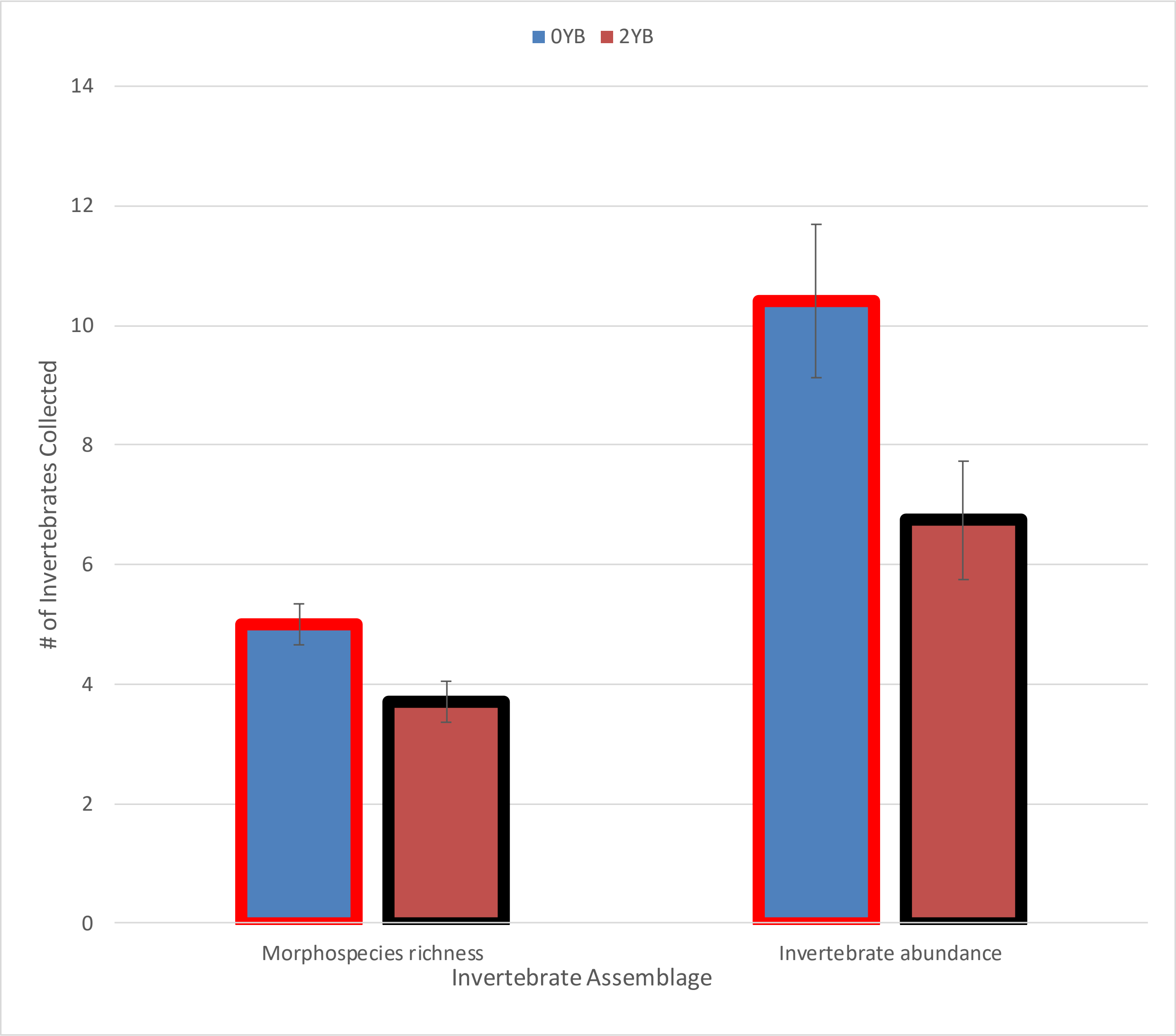

Figure 7. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of soil core samples by years since burn. Two of six sections are burned each year. Longest time since burn (2YB) sections allow plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom, while using the shortest time since burn (0YB) allows for evaluation of invertebrate assemblages post fire. Invertebrates were collected from soil cores at sites that had similar treatments. Soil cores were collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies. Years since burn showing invertebrate richness and abundance that are significantly (Repeated measures ANOVA $p<0.05$) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

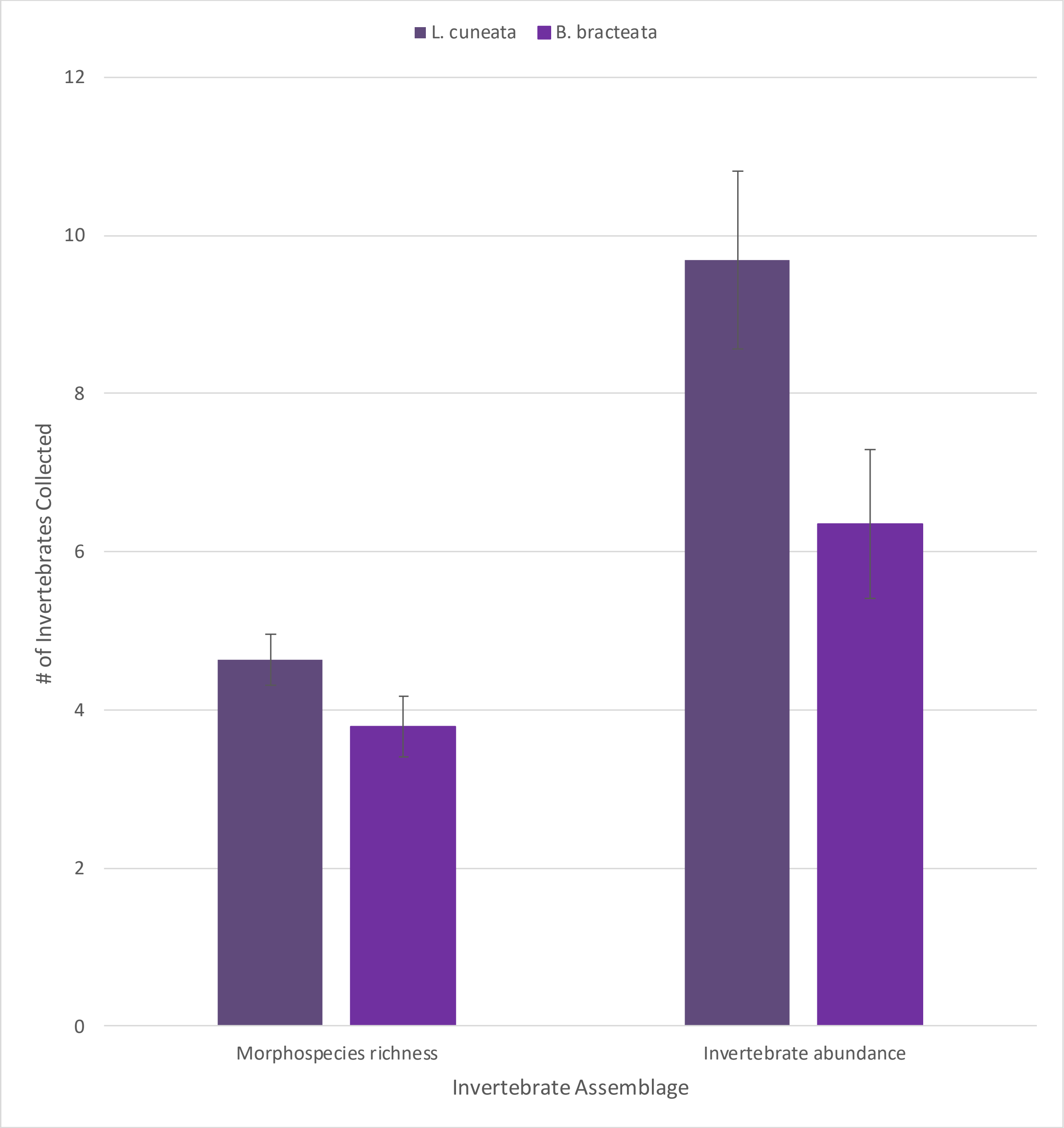

Figure 8. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of soil core samples by legume species. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Invertebrates were collected from soil cores at sites that had similar treatments. Soil cores were collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies.

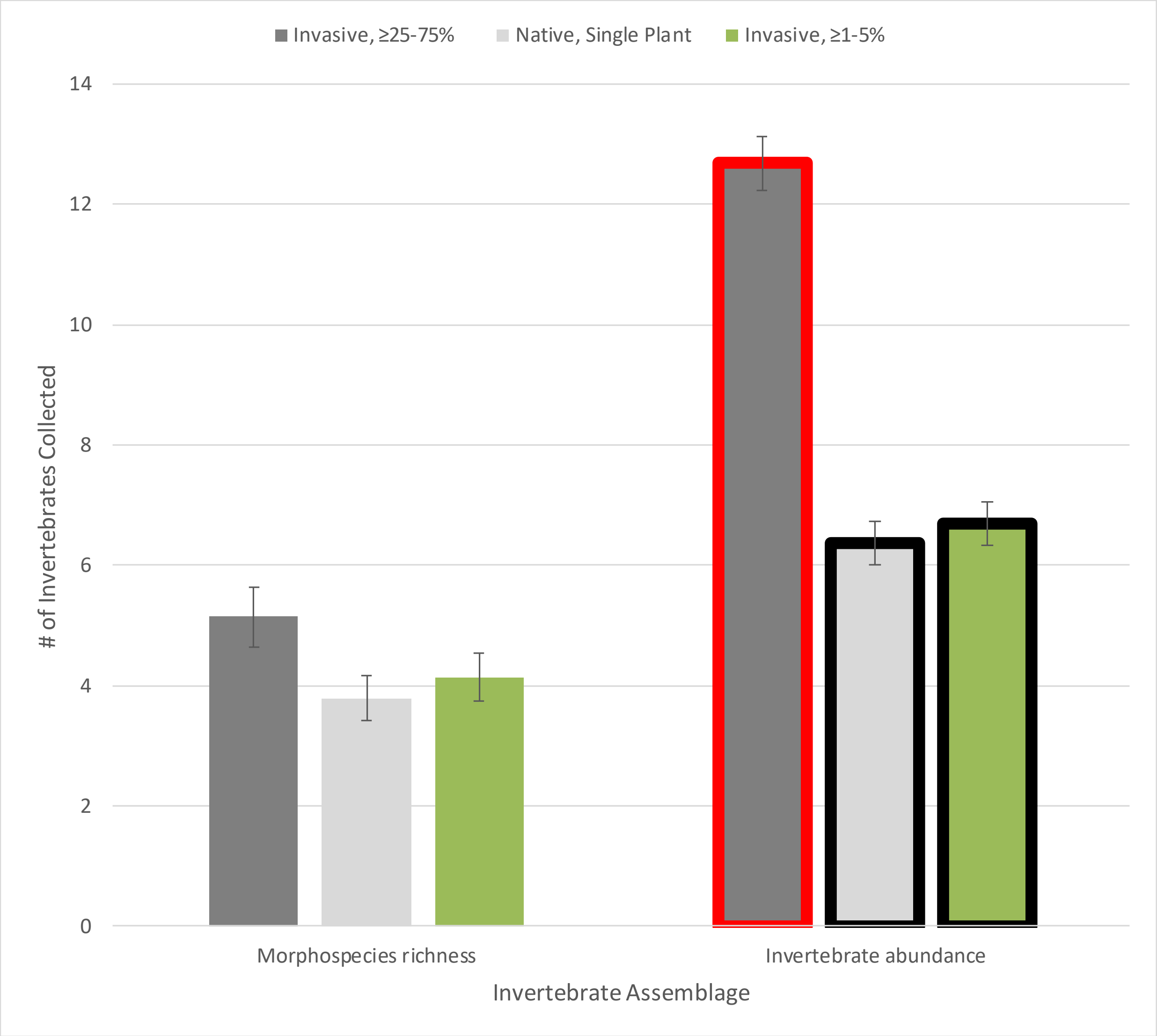

Figure 9. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) of soil core samples by legume cover. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Treatments within each section of each site included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/High cover (≥25-75%), and 3) *B. bracteata* single plant cover. Invertebrates were collected from soil cores at sites that had similar treatments. Soil cores were collected at three month intervals, dried, and processed through a Berlese funnel that separated invertebrates from substrate. Invertebrates were sorted and identified to order, family and morphospecies. Cover ranges showing invertebrate abundance that are significantly (Repeated measures ANOVA p<0.05) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

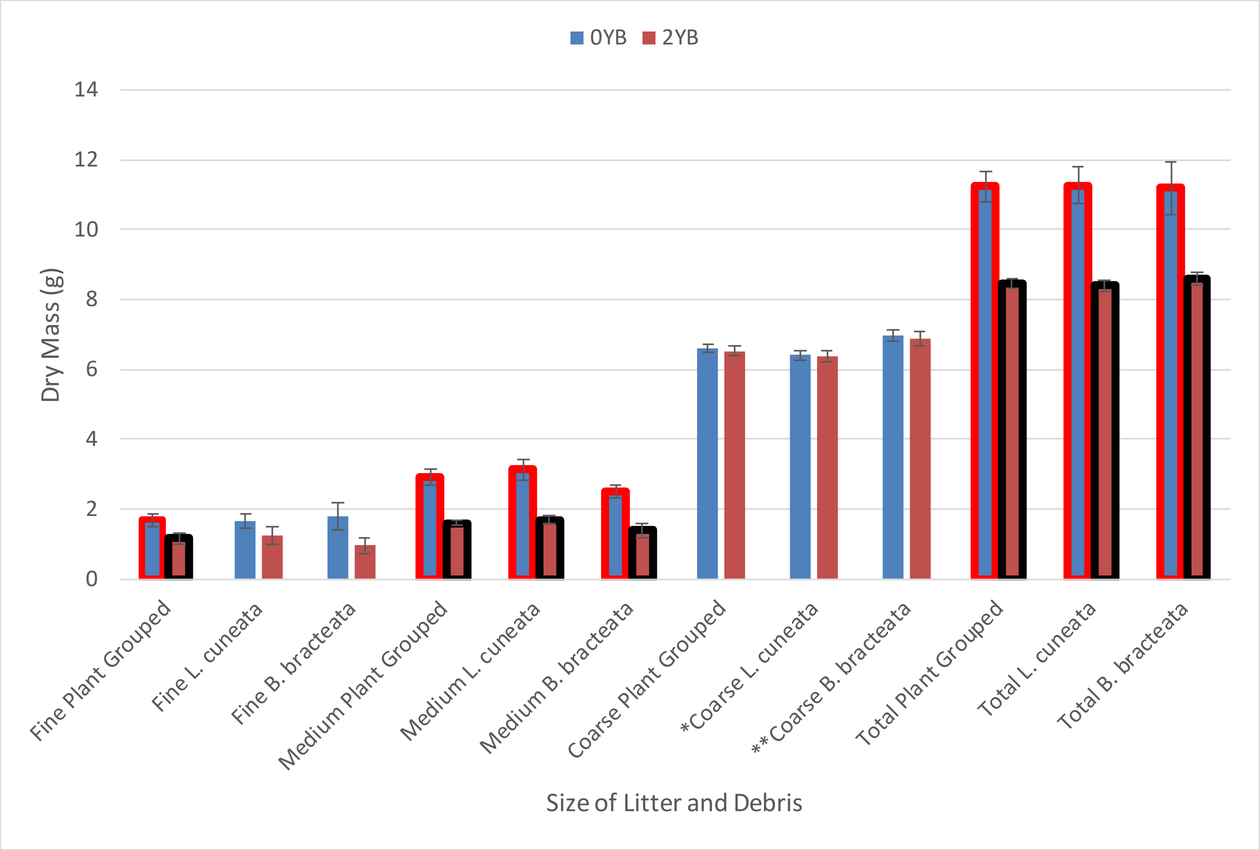

Figure 10. Dry mass (g) (mean ± SE) of decomposed (Medium) and non-decomposed (Coarse) litter, debris (Fine), and mesh bag contents (Total) by time since prescribed fire. Two of six sections are burned each year. Longest time since burn (2YB) sections allow plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom, while using the shortest time since burn (0YB) allows for evaluation of decomposition post fire. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Mesh litter bags were collected from sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through soil sieves to separate litter and debris by size, including coarse sieve where leaf litter was loaded, a medium sieve (#5 [4000 µm/4 mm]) that collected plant material pieces and seeds, and a fine sieve (#120 [125 µm/0.125 mm]) that collected silt and duff; Litter and debris biomass was not mixed with invertebrate biomass. Years since burn showing dry mass (g) of litter and debris that are significantly (Repeated measures ANOVA $p<0.05$) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower. Values *of* significance ($p<0.05$) between groups are denoted by ** versus those they are compared to (*).

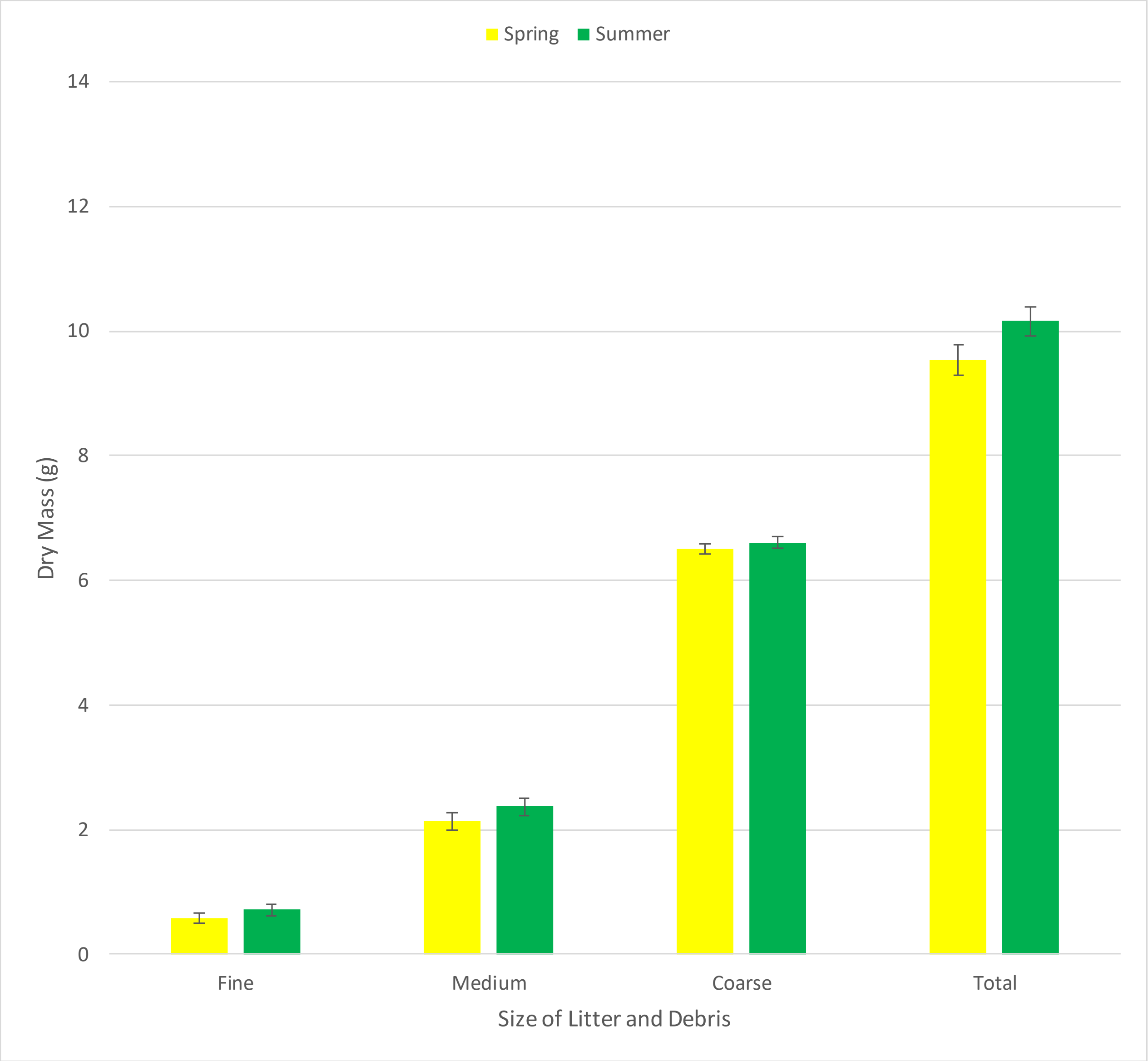

Figure 11. Dry mass (g) (mean ± SE) of decomposed (Medium) and non-decomposed (Coarse) litter, debris (Fine), and mesh bag contents (Total) by season of burn. Two of six sections are burned each year: one dormant season spring burn (February through March) used to promote livestock production and is conducted just before spring green-up and one growing season summer burn (July through August) conducted when warm-season herbaceous plants are actively growing. Mesh litter bags were collected from sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through soil sieves to separate litter and debris by size, including coarse sieve where leaf litter was loaded, a medium sieve (#5 [4000 µm/4 mm]) that collected plant material pieces and seeds, and a fine sieve (#120 [125 µm/0.125 mm]) that collected silt and duff; Litter and debris biomass was not mixed with invertebrate biomass.

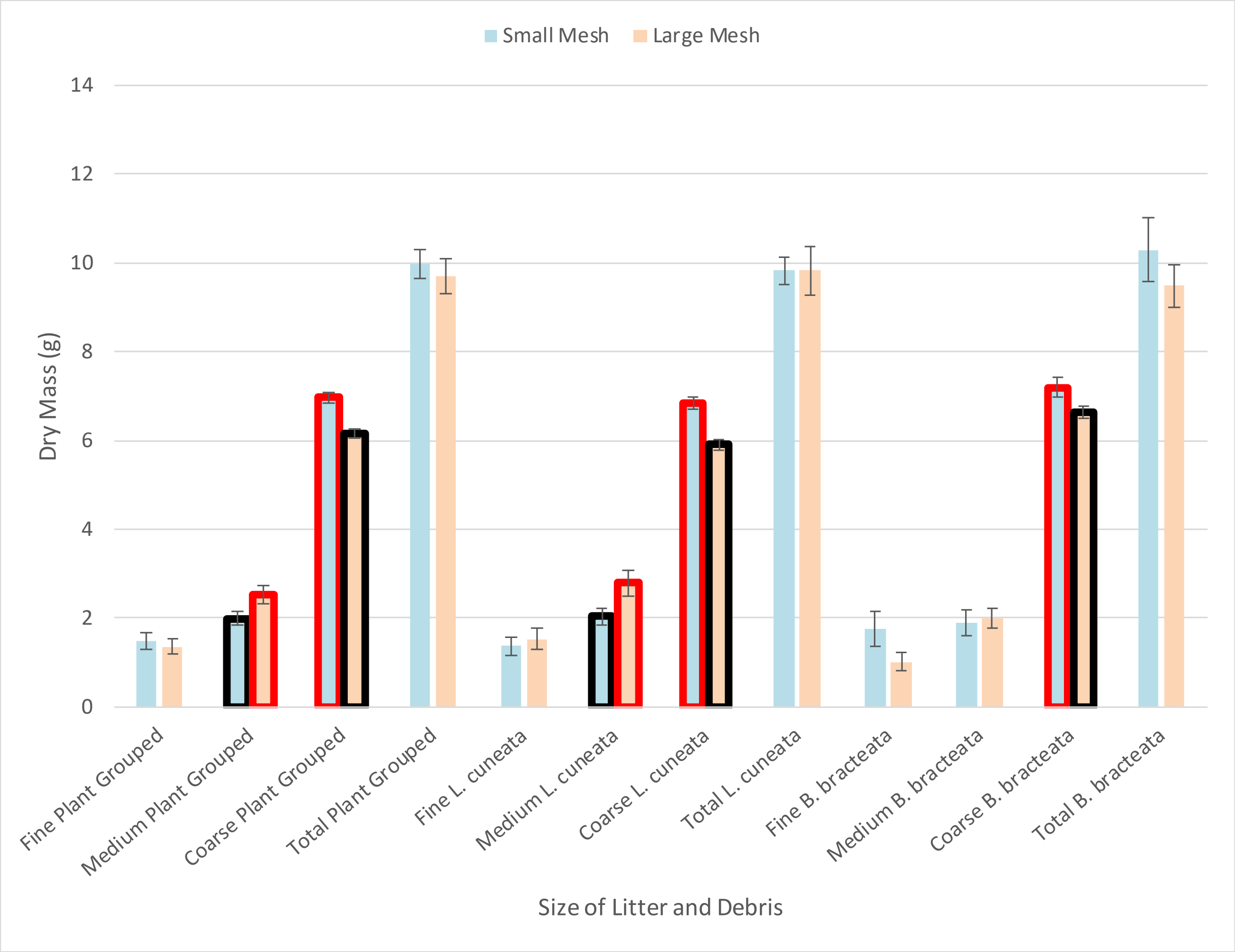

Figure 12. Dry mass (g) (mean ± SE) of decomposed (Medium) and non-decomposed (Coarse) litter, debris (Fine), and mesh bag contents (Total) by mesh bag size. Large mesh bags allow entry by most meso- and macroinvertebrates, while the small mesh bags do not. This approach allowed evaluation of the relative contribution of different sized invertebrates to litter decomposition. Mesh litter bags were collected from sites that had similar treatments. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Litter bags were distributed and collected at three month intervals, dried, and processed through soil sieves to separate litter and debris by size, including coarse sieve where leaf litter was loaded, a medium sieve (#5 [4000 µm/4 mm]) that collected plant material pieces and seeds, and a fine sieve (#120 [125 µm/0.125 mm]) that collected silt and duff; Litter and debris biomass was not mixed with invertebrate biomass. Years since burn showing dry mass (g) of litter and debris that are significantly (Repeated measures ANOVA $p<0.05$) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

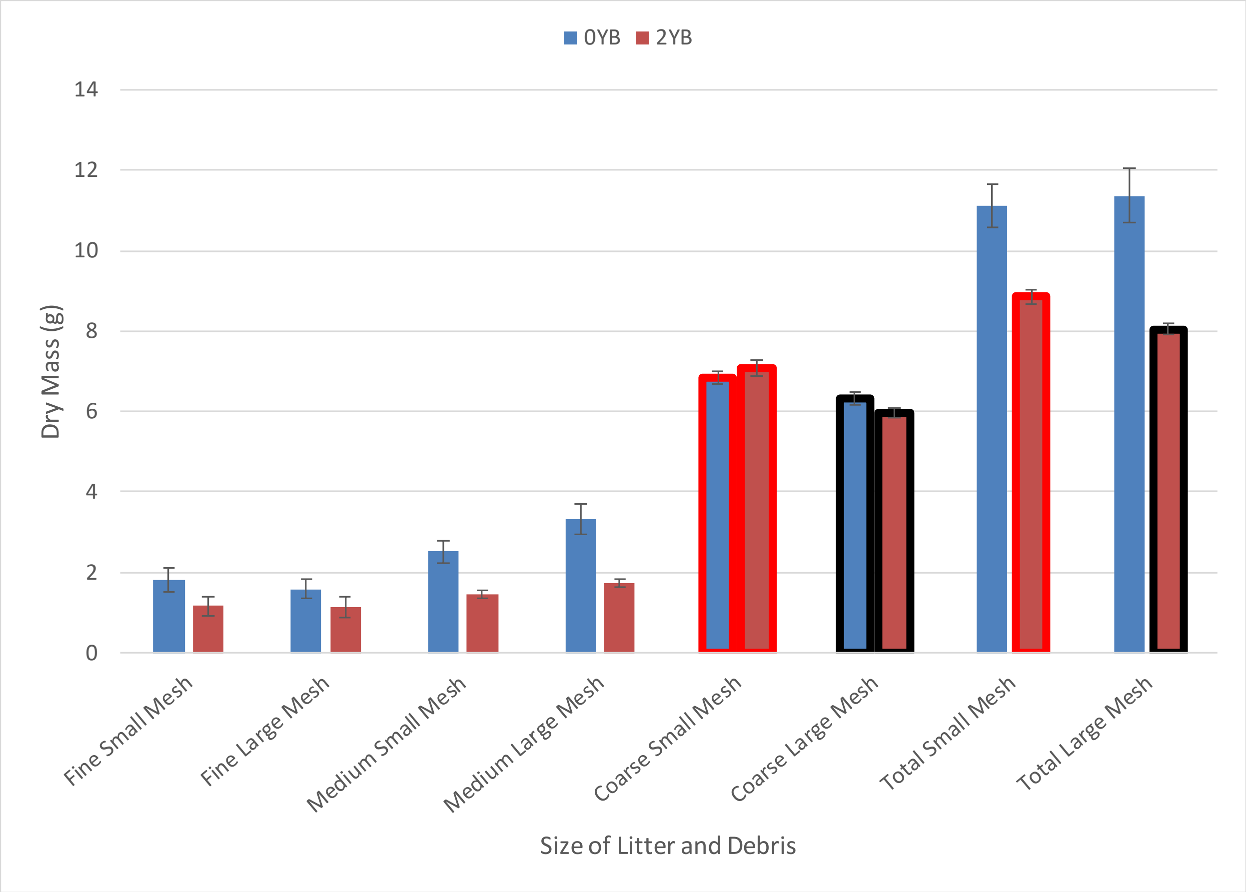

Figure 13. Dry mass (g) (mean ± SE) of decomposed (Medium) and non-decomposed (Coarse) litter, debris (Fine), and mesh bag contents (Total) by mesh bag size and time since fire. Two of six sections are burned each year. Longest time since burn (2YB) sections allow plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom, while using the shortest time since burn (0YB) allows for evaluation of decomposition post fire. Large mesh bags allow entry by most meso- and macroinvertebrates, while the small mesh bags do not. This approach allowed evaluation of the relative contribution of different sized invertebrates to litter decomposition. Mesh litter bags were collected from sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through soil sieves to separate litter and debris by size, including coarse sieve where leaf litter was loaded, a medium sieve (#5 [4000 µm/4 mm]) that collected plant material pieces and seeds, and a fine sieve (#120 [125 µm/0.125 mm]) that collected silt and duff; Litter and debris biomass was not mixed with invertebrate biomass. Years since burn showing dry mass (g) of litter and debris that are significantly (Repeated measures ANOVA $p<0.05$) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

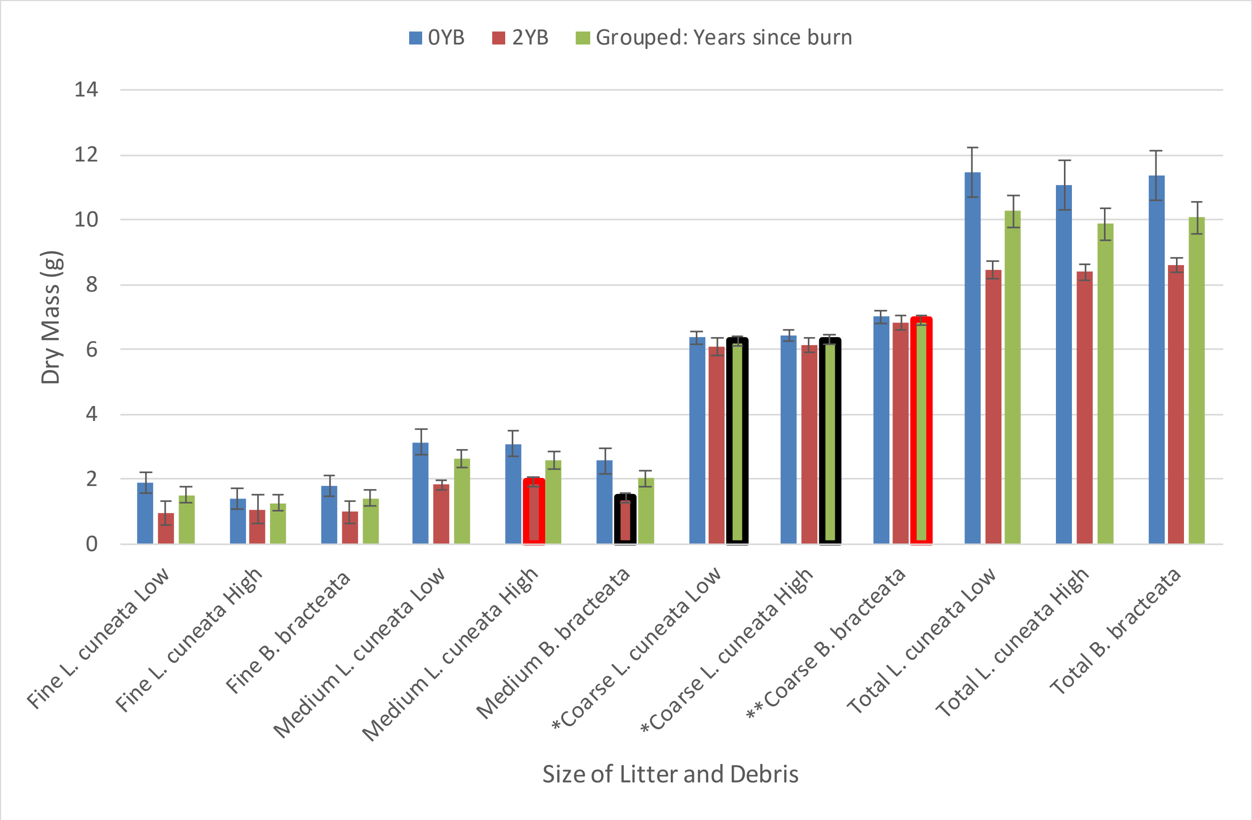

Figure 14. Dry mass (g) (mean ± SE) of decomposed (Medium) and non-decomposed (Coarse) litter, debris (Fine), and mesh bag contents (Total) by time since prescribed fire. Two of six sections are burned each year. Longest time since burn (2YB) sections allow plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom, while using the shortest time since burn (0YB) allows for evaluation of decomposition post fire. Native *B. bracteata* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Treatments within each section in the SRR included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/High cover (≥25-75%), and 3) *B. bracteata* single plant cover. Mesh litter bags were collected from sites that had similar treatments. Litter bags were distributed and collected at three month intervals, dried, and processed through soil sieves to separate litter and debris by size, including coarse sieve where leaf litter was loaded, a medium sieve (#5 [4000 µm/4 mm]) that collected plant material pieces and seeds, and a fine sieve (#120 [125 µm/0.125 mm]) that collected silt and duff; Litter and debris biomass was not mixed with invertebrate biomass. Years since burn showing dry mass (g) of litter and debris that are significantly (Repeated measures ANOVA p<0.05) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

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CHAPTER II

INVASIVE *LESPEDEZA CUNEATA* AND NATIVE *BAPTISIA BRACTEATA*: IMPLICATIONS FOR ORGANIC NITROGEN AND ORGANIC CARBON IN TALLGRASS PRAIRIE SOILS

Abstract.

Habitat fragmentation and alteration of grasslands have contributed to the spread of invasive plant species. Invasive legumes decrease plant biodiversity and species richness and outcompete native forbs and grasses. Native legumes promote biodiversity and increase native biomass, while facilitating ecosystem services in grasslands. Plant community composition, including the coverage of legumes, strongly affects soil C and N storage. The purpose of this study was to evaluate if soil organic N (SON) and soil organic C (SOC) varied with invasive versus native legume cover. I evaluated the percent of SON and SOC in soil cores across a gradient of legume cover ranges (≥1-5% [low], >5-25% [moderate], and >25-75% [high]) for invasive *Lespedeza cuneata* and a single plant cover of native *Baptisia bracteata*. Study sites were located in rangelands in north-central Oklahoma where both species occur sympatrically. Findings suggest that SON and SOC (%) are significantly and positively correlated. SON and SOC (%) were lowest in areas with *B. bracteata* and increased as *L. cuneata* cover increased. However, SON and SOC (%) were not different between locations with *B. bracteata* and low cover *L.*

cuneata cover ranges. Overall, the presence of legumes increased SON and SOC (%) simultaneously, but not synchronously, as indicated by fluctuations in the C:N ratio. This study found that soil C and N storage was highest in high cover *L. cuneata* locations, possibly through increasing legume cover and associated soil C and N inputs. Because invasive legumes outcompete native plants and increase SON and SOC (%), locations dominated by invasive legumes may utilize available nutrients while isolating native plants, further altering ecosystem services, such as soil C and N storage, productivity and diversity in grasslands.

Introduction.

Fire and grazing commonly occur in tandem in grassland ecosystems where fire-grazing interactions play a profound role in processes that drive nutrient cycling (Hobbs et al. 1991) and influence the distribution of nitrogen (N) by mediating losses and additions to the N budget in soils. Thus, grazing by large herbivores conserves N sources that would be otherwise lost through fire. Studies that focus on the effects of herbivore grazing on ecosystem N dynamics (Brockman et al. 1971; Woodmansee 1978; Stillwell and Woodmansee 1981; Coppock et al. 1983a; Coppock et al. 1983b; Lambert et al. 1985; Schimel et al. 1986; Agrawal and Tiwari 1987; Detling 1988; Jaramillo and Detling 1988; McNaughton et al. 1988; Jarvis et al. 1989) have typically navigated away from discussing fire as a grazing interaction that influences N and nutrient dynamics (Cook 1939; Norman and Wetselaar 1960; Kucera and Ehrenreich 1962; Lloyd 1971; Christensen 1976; Wells et al. 1979; Woodmansee and Wallach 1981; Boerner 1982; Schimel 1982; Hobbs and Schimel 1984; Robertson and Rosswall 1986; D'Antonio and Vitousek 1992). However, understanding fire and grazing requires understanding their interactions (Hobbs et al. 1991).

Grazing by large herbivores removes vegetation from the landscape unevenly, increasing heterogeneity of plant tissue across the landscape. Fire behavior is affected by the heterogeneity and spatial variation (i.e. patchiness) of plant tissue due to the amount of organic matter (OM) available for combustion (Hobbs et al. 1991). If grazers prefer forage in one location over another, a disproportionate amount of fuel will occur between those areas, resulting in less intense fire in more intensively grazed patches and more intense fire in ungrazed ones. Consequently, fire can reduce the spatial heterogeneity caused by grazing (Conrad and Poulton 1966; Norton-Griffiths 1979; Madany and West 1983; Zimmerman and Neuenschwander 1984).

Prescribed fire also play a prevailing role in shaping plant community structure and composition of tallgrass prairie. Annual burning in late spring often results in an observable reduction of species diversity and heterogeneity of perennial grasses (Abrams and Hulbert 1987; Gibson 1988; Collins 1992) while simultaneously reducing woody encroachment (Ansley and Castellano 2006; Higgins et al. 2007; Twidwell 2013a; Twidwell 2013b). Annual burning reduces the available soil N through combinations of oxidation, volatilization, ash transport, leaching and erosion (Ojima et al. 1994). Even low intensity fires can reduce N by 54-75% (Raison et al. 1985). Some nutrient dynamics are unaffected by fire (i.e., K, CA and Mg ions) and some tend to decrease (i.e., N and S) following fire (Hough 1981). Although the relationship between fire and soil nutrients is complex, fire intensity is usually the most critical factor affecting post-fire dynamics, with greater nutrient losses occurring with higher fire intensity. For example, N begins volatizing out of OM at only 200°C (Neary et al. 1999). Reduced N can therefore alter competitive interactions among grasses and forbs (Seastedt et al. 1991), further shaping the plant community and subsequent future plant community dynamics. In contrast, burning infrequently increases forb abundance and diversity for several years post fire, followed by a decrease in abundance in subsequent years (Gibson 1988; Collins 1992).

Although fire can diminish nutrient pools, nutrient availability and soil fertility often increase following fire, since fire chemically converts nutrients bound in dead plant tissue and the soil surface to more available and usable forms. Fire can also indirectly increase mineralization rates through impacts on soil microorganisms (Schoch and Binkley 1986). The abundance of microorganisms (specifically arthropods) is typically reduced with increased fire frequency. One study showed that mites and springtails were reduced (25%) by periodic fires, but that reduction increased to 75-80% when fires occurred annually (Brand 2002; Dress and Boerner 2004). These studies attributed these reductions to decreased habitat (i.e., litter mass loss); many of these organisms live in decomposing leaf litter and most of the litter is lost in fire. The impact of these microorganism reductions for the decomposition of new leaf litter has not been thoroughly addressed.

Soil organic carbon (hereafter referred to as SOC) is the largest active C pool in terrestrial ecosystems (Muller et al. 2017). It was originally thought that the majority of SOC originated directly from plant residues, but more recent research shows plant-derived C enters the SOC pool indirectly through microorganisms within soil zones (Kogel-Knabner 2002; Liang and Balser 2011; Miltner et al. 2011). Soil microorganisms encompass organisms < 150-200 µm (i.e., predominantly fungi and bacteria, but also archaebacteria, algae, protozoa, rotifers, tardigrades, mites and small nematodes) (Swift et al. 1979; Coleman and Wall 2006). These soil microorganisms accomplish most enzymatic processes in soil and preserve nutrients in microbial biomass (i.e. microbial tissue) (Jenkinson and Ladd 1981), and microorganisms alter their metabolic state between extensive periods of vegetation dormancy and growth. Living microorganisms account for less than 5% of SOC (Dalal 1998), but these organisms account for decomposition processes of C pools concentrated in soils. Microbial cells eventually die and contribute to 50-80% SOC (van Veen et al. 1984;

Jenkinson et al. 1992; Liang and Balser 2011; Simpson et al. 2007). Plant cover, diversity, and soil type are also important contributors to primary productivity and storage of SOC and soil organic N (hereafter referred to as SON) (Catovsky et al 2002; Fornara and Tilman 2008; Steinbeiss et al 2008; Schmidt et al. 2011). Thus, it is necessary to evaluate the impacts of plant species community composition, diversity, and cover on SOC and SON storage (Wu et al. 2016).

Legumes are a common forb in the tallgrass prairie, and influence soil dynamics and plant communities through nitrogen fixation via symbiotic root bacteria (Kaneko et al. 2002; Wu et al. 2016). Fire-grazing interactions contribute to the heterogeneous distribution of N throughout the tallgrass prairie landscape. Frequency and intensity of prescribed fire have been reported to increase the abundance of some legumes (Lemon 1967; Adams and Anderson 1978; Niering and Dreyer 1989; Nagel et al. 1994), whereas others are not affected (Curtis and Partch 1948; Kucera and Keolling 1964). Fire has been shown to positively affect germination of many legume species (Martin and Cushwa 1966), which possess a hard protective seed covering that requires scarification for germination (Sorensen and Holden 1974) and prescribed fire stimulates seedling emergence (Woods et al. 2009). Thus, fire could enhance legume establishment and secondary spread, especially in N stressed environments. It could be assumed that higher abundance of legumes may yield more soil OM (hereafter referred to as SOM), and thus increased SOC. As legumes increase with fire, localized areas around these plants now have increased C input (including increased N pools) and organic substrate to support immobile, dormant microorganisms.

Legume cover, diversity, and composition can significantly affect grassland productivity and efficiency of C and N storage in soils (Spehn et al. 2002; Fornara and Tilman 2008). Legumes also promote biodiversity, ecosystem processes (Spehn et al. 2002), plant productivity (Marquard et al. 2009), and N availability (Oelmann et al 2011) while serving as drivers of primary productivity, C sequestration, N accumulation and mineralization (Lambers et al. 2004; Fornara and Tilman 2008). Diversity and plant composition can also be affected by increasing (Ferreira et al. 2014; Shang et al. 2014; Parras-Alcantara et al. 2015; Wasak and Drewnik 2015 and Novara et al. 2016) or reducing C and N in soil through respiration, volatilization, and leaching (Catovsky et al. 2002; De Deyn et al. 2008; Phoenix et al. 2008). Both diversity of legumes and functional composition of grasslands control N pools where communities that are more diverse use N more effectively (Oelmann et al. 2007). Soil C and N pools are enhanced by the presence and biomass of legumes, whereas the species richness of other forbs and grasses do not affect soil C and N (De Deyn et al. 2009). However, plant diversity has been observed to promote soil C and N uptake, allowing complementarity in use of resources (Cong et al. 2014; Lange et al. 2015). Therefore, plant diversity can promote N transformations that may include N mineralization and nitrification (Mueller et al. 2013). In many of these studies, researchers hint that plant diversity, composition and fire dynamics (i.e., frequency and intensity) control C and N in soil (Fornara and Tilman 2008; Roa-Fuentes et al. 2015; Hu et al. 2016), but the influence of legumes in native grasslands is poorly understood (Wu et al. 2016). Invasive legumes may have an advantage over native legumes and could modify nutrient pools. Understanding how SOC and SON vary with invasive and native legume cover can provide important insight on the influence of invasive plants and management practices.

Objectives.

The goal of this study was to evaluate if SON and SOC (%) vary with invasive versus native legume cover. To address this goal, I used soil cores to assess SON and SOC (%) across a range of invasive legume cover compared to areas with a native legume that tends to occur as single, isolated plants.

Materials and methods.

Study system.

Lespedeza cuneata is an herbaceous and woody, perennial legume, which occurs throughout the eastern and central United States. Native to eastern Asia, this non-indigenous weed was first introduced to the United States in 1896 (Cummings et al. 2007). *Lespedeza cuneata* was originally cultivated and planted for erosion control and mine reclamation, and then widely used as a pasture crop starting in the 1940s (Pitman 2006; Cummings et al. 2007; EPPO 2018). As of surveys in 2009, *L. cuneata* was observed outside of cultivation throughout much of the United States. *Lespedeza cuneata* produces up to 6000 seeds per plant/year, which require seed coat scarification for germination (Sorensen and Holden 1974). Prescribed fire facilitates seed coat scarification and stimulates seedling emergence (Woods et al. 2009). Prescribed fire can also act as a potential management strategy to control *L. cuneata* (Hoveland et al. 1970; Hoveland et al. 1971) while minimizing the impacts to native legumes and the ecosystem (Schutzenhofer and Knight 2007; Gurevitch et al. 2011) Prescribed fire in the fall, before seed dispersal, reduces *L. cuneata* seed set and viability, lowering successful secondary dispersal and establishment events by controlling the seed bank before seeds become incorporated into the soil during the freeze-thaw process in the winter and before germination begins in the spring. Prescribed fire is also used to reduce encroachment of woody species in grasslands and is considered an important component of historical disturbance regimes in the Great Plains (Wong et al. 2012) but also contributes to the spread of this invasive legume.

Baptisia bracteata is an herbaceous, perennial legume, which is confined to southeastern United States (Turner 2006). Typically occurring as a single isolated plant with 5 – 20 seeds per seedpod and a root system consisting of a stout taproot, *B. bracteata* prefers full sun and dry conditions, including open areas where there is reduced competition from taller vegetation. Seedlings are slow to mature, taking this plant several years to bloom. *Baptisia bracteata* can be observed in prairies and open woodland and prescribed fire is beneficial in maintaining populations of this plant. This species can be easily damaged by strong winds as its stem becomes more brittle as the summer progresses (Hilty 2018).

Study sites and treatments.

My research was conducted in north-central Oklahoma at Oklahoma State University's (OSU) Stillwater Research Range (SRR), approximately 18 km west of Stillwater, OK. The SRR is located in the western section of the Cross Timbers ecoregion, which extends from southeastern Kansas to north-central Texas and is comprised of deciduous forest, savanna and tallgrass prairie. The SRR consists primarily of native vegetation, including mixed and tallgrass prairie and is managed with livestock grazing and prescribed fire. An

Oklahoma Mesonet (Brock et al. 1995) weather station located in the area records various climate measurements and shows annual precipitation averages 92.24 cm, with peak rainfall occurring in May and average temperatures range from 34.4°C in the summer to 1.1°C in the winter. Vegetation characteristic of tallgrass prairie remnants of the Cross Timbers ecoregion and commonly found in the SRR include dominant grasses (*Panicum virgatum*, *Sorghastrum nutans*, *Andropogon gerardii*, *Schizachyrium scoparium*, *Aristida purpurea*), dominant forbs (*Ambrosia psilostachya*, *Gutierrezia dracunculoides*), other forbs of prevalence (*Echinacea purpurea*, *Ratibida columnifera*, *Linum flavum*, *Triodanis perfoliata*, *Oenothera speciosa*, *Convolvulus arvensis*, *Calendula arvensis*, *Erigeron annuus*, *Coreopsis palmata*, *Solidago rigida*, *Gutierrezia sarothrae*, *Solanum elaeagnifolium*, *Grindelia squarrosa*) and dominant woody plants (*Quercus stellata*, *Quercus marilandica*, *Celtis* spp.) (Allred et al. 2010).

This study utilized patch-burn sites within the SRR, which range in size from 49 to 63 ha. Patch-burning (patch-burn grazing) involves the combined use of fire and grazing for ecological management goals by purposefully encouraging cattle to freely select the most recently burned part of a site. Grazing pressure is shifted when another section is burned, thus creating a shifting mosaic on the management unit (Cummings et al. 2007). Growing season prescribed fire (occurring in summer months) is conducted when warm-season herbaceous plants are actively growing, whereas dormant season prescribed fire (occurring in early spring months) is used to promote livestock production and is conducted just before spring green-up (Launchbaugh and Owensby 1978). SRR patch-burn sites are divided into 6 sections approximately equal in size and defined by burning regime. Two of six sections are burned each year: one in spring (February through March) and one in summer (July through August). Within each patch-burn rangeland (each SRR site), I used the section with the longest time since burn (two years since a spring burn). Using the longest time since burn allowed *Lespedeza* plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom. Cattle are stocked at a constant rate in the SRR, consisting of 6.9 ha/animal.

I examined SON and SOC in areas containing one native legume species and three *L. cuneata* cover ranges. *Lespedeza cuneata* cover ranges were designated as: ≥1-5% (low), >5-25% (moderate) and >25-75% (high); a quadrat (0.25m x 0.25m) was used to estimate *Lespedeza* cover. *Baptisia bracteata* was selected as the native legume species. This species is a perennial legume that occurs sympatrically with *L. cuneata* throughout the tallgrass prairie region of the Great Plains and within the SRR. *Baptisia bracteata* tends to occur as isolated single plants, each with a single stem. Thus, areas containing *B. bracteata* were characterized by the presence of a single plant. Treatments within each site included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/Moderate cover (>5-25%), 3) *L. cuneata*/High cover (>25-75%), and 4) *B. bracteata* single plant cover.

Soil samples.

In October of 2017, SON and SOC (%) were assessed by collecting three soil cores (5 cm diameter x 10 cm depth), separated by a minimum of 5m, from each of the four treatment plots (plant cover ranges) from each of the SRR sites, for a total of 9 replicate samples from each cover range. Leaf litter and OM were removed prior to collection to ensure that cores only contained soil. Soil core samples were analyzed by OSU's Soil, Water and Forage Analytical Laboratory (SWFAL). SOC data were estimated as SOM/1.724, where average SOM is composed by the stoichiometric percentage of 58% C (100/58= 1.72) (Nelson and Sommers 1996).

Analyses.

I used a repeated measures ANOVA and paired T-tests to determine if SON and SOC (%) differed between areas containing *B. bracteata* and the three *L. cuneata* cover ranges. A Pearson correlation (Pearson's r) was used to evaluate the extent (between -1 and 1) of linear relatedness between SON and SOC (%).

Results.

SON and SOC (%) by cover.

SON (F[3,32] = 11.483, $p<0.001$) was significantly lower than SOC (%; F[3,32] = 7.440, $p=0.001$) and a significant and positive correlation occurred between SON and SOC (%) and cover range ($r = 0.988$) (Pearson's r; 2-tailed; significant at the $p=0.01$ level); SON and SOC (%) was lowest in areas with single plant *B. bracteata* and increased as *L. cuneata* cover increased (Figure 1). SON and SOC (%) was significantly higher between certain cover ranges and not others; >5-25% and ≥1-5 ($p=0.008$; $p=0.031$), >25-75% and ≥1-5 ($p=0.003$; $p=0.014$), >5-25% and single plant *B. bracteata* ($p<0.001$; $p=0.001$), and >25-75% and single plant *B. bracteata* ($p<0.001$; $p<0.001$), respectively. SON and SOC (%) was not different between cover ranges for single plant *B. bracteata* and ≥1-5% ($p=0.085$; $p=0.150$) and >5-25 and >25-75% ($p=0.660$; $p=0.738$), respectfully (Tukey LSD) (Figure 1).

Discussion.

A positive and significant relationship existed between legume cover and SOC and SON (%) (Figure 1). Past studies have also demonstrated significant correlations between legume status (i.e., presence versus absence, legume species, density and diversity; Hobbs et al. 1991), soil properties and increased SOC and SON (%). Wu et al. (2017) found that aboveground legume biomass was a good predictor of soil C and N storage, while belowground legume biomass was a relatively poor predictor. However, the authors may not have adequately sampled belowground biomass because they used a 9 cm-diameter root auger (i.e. mature *L. cuneata* plants develop a 0.9 – 1.2m woody taproot that extends laterally). Visual observations by Wu et al. (2017) suggested aboveground total plant community biomass increased as legume density increased.

SOC and SON (%) were significantly and positively correlated (r = 0.988) across all legume cover ranges and soil organic C:N was calculated as 10:1; soil organic C:N was lowest by single plant *B. bracteata* and increased as *L. cuneata* cover increased (Figure 1). Deng et al. (2013) and Wu et al. (2017) also found that SOC=10SON in other grassland ecosystems; in the presence of legumes, SOC content was approximately 10 times as much as SON storage, which is more than in the absence of legumes (presumably due to nitrogen fixation by legumes). The 10-fold difference between SOC and SON may be due to greater inputs and fewer outputs for SOC compared with SON (Wu et al. 2017). Legumes increase net primary production, utilizing part of the SON storage and increasing SOC content (Fornara and Tilman 2008), leading to greater C sequestration than N sequestration; soil C and N accumulation depend on enhanced C and N inputs returned to the soil from the plant community.

The percent of SON and SOC was lowest in areas with *B. bracteata* and increased as *L. cuneata* cover increased. However, SON and SOC (%) was not different between locations with *B. bracteata* and low cover *L. cuneata* and moderate and high cover *L. cuneata* (Figure 1). SON and SOC (%) was significantly higher in moderate and high *L. cuneata* cover, than low *L. cuneata* cover ranges and significantly higher in moderate and high *L. cuneata* cover, than single plant cover *B. bracteata* (Figure 1). Wu et al. (2017) observed similar results where SOC increased in the presence of legumes, thereby increasing SOM and SON and the soil organic C:N ratio. The presence of native legumes (i.e. invasive legumes may form monotypic stands) increases plant diversity, enhancing rhizosphere C inputs into microbial communities which results in amplified microbial activity and soil C storage (Lange et al. 2015) but microbial activity results in loss of C through respiration. Wet N derived from the symbiosis of legume root nodules and rhizobia, rather than through inputs of dry atmospheric N, is qualitatively important in building up SOM and soil C storage (Resh et al. 2002; Christopher and Lal 2007).

Legumes and symbiotic free-living N-fixing bacteria stimulate mineralization of organic plant material and nutrients and promoting mycorrhizal growth. Releasing fixed N by legumes increases soil N pool availability for uptake by non-legume forbs and grasses and can result in qualitative differences (i.e., floral composition, vegetation stratification, phenology, vitality, vigor, life form and sociability) in plant community composition (Bezemer and Jones 1998; Awmack and Leather 2002; Kardol et al. 2006; van Der Heijden et al. 2008). Decreased soil NO_3 levels created by non-legume forbs and grasses may cause legumes to fix more N, enhancing soil N supply rates and supporting non-legume forb and grass growth (Fornara and Tilman 2008). Sustaining soil N supply and decreasing N losses and leaching (Hooper et al. 2005; Oelmann et al. 2007; De Deyn et al. 2009) may also be driven by higher species richness, diversity and cover of legumes (Scherer-Lorenzen et al. 2003; Oelmann et al. 2007). Higher diversity grasslands show importance of a larger, more extensive root biomass throughout the soil layers where legumes drive deep soil N to the top surface of the soil, resulting in N uptake by grasses and non-legume forbs (Wu et al. 2017). Atmospheric N and regular fire can also cause legumes to flourish in N-stressed conditions through N fixation and seed scarification (Sorensen and Holden 1974).

Habitat fragmentation and alteration of grasslands have contributed to the spread of invasive plant species where invaders often outcompete natives and decrease heterogeneity. Therefore, impacts through native versus invasive legume species presence can produce very different results depending on life history characteristics. Native legumes promote biodiversity and increased biomass of natives, while providing functional redundancy and facilitation of ecosystem resistance, resilience and service to grassland natives (Zhao et al. 2014). Invasive legumes (in particular, *L. cuneata*) have the opposite effect, by decreasing plant biodiversity and species richness and outcompeting native forbs and grasses (Vavra et al. 2007; Vila et al. 2015). Through opportunistic traits such as early emergence, rapid growth and high seed production, invading plants can form isolated monocultures while increasing homogeneity and fragmentation (Vila et al. 2010; Wolkovich and Cleland 2014). Eddy and Moore (1998) found that *L. cuneata* reduced the biomass of native forbs and grasses by 92% and native species richness from 27 to 8 species within 5 to 7 years of invasion in Kansas sites. It is expected that management with *L. cuneata*-specific considerations would prevent or at least reduce such a large loss of native biodiversity, species richness and accumulated native biomass.

Conclusions and future directions.

Density of legumes strongly affects SOC and SON storage where the presence of legumes increases SOC and SON simultaneously, but not synchronously. Both native and invasive legumes increase SOC and SON. However, other research has shown that invasive legumes decrease species richness and diversity, which may reduce ecosystem complexity, resistance and resilience (Zhao et al. 2014). A combination of legume and non-legume forbs and grasses may increase ecosystem functionality by mediating soil C and N storage, productivity and diversity in grassland ecosystems. Future research should focus on evaluating the impacts of community plant species composition, diversity and cover on SOC and SON storage in native grassland soils to provide important information about ecosystem services and function.

Figures.

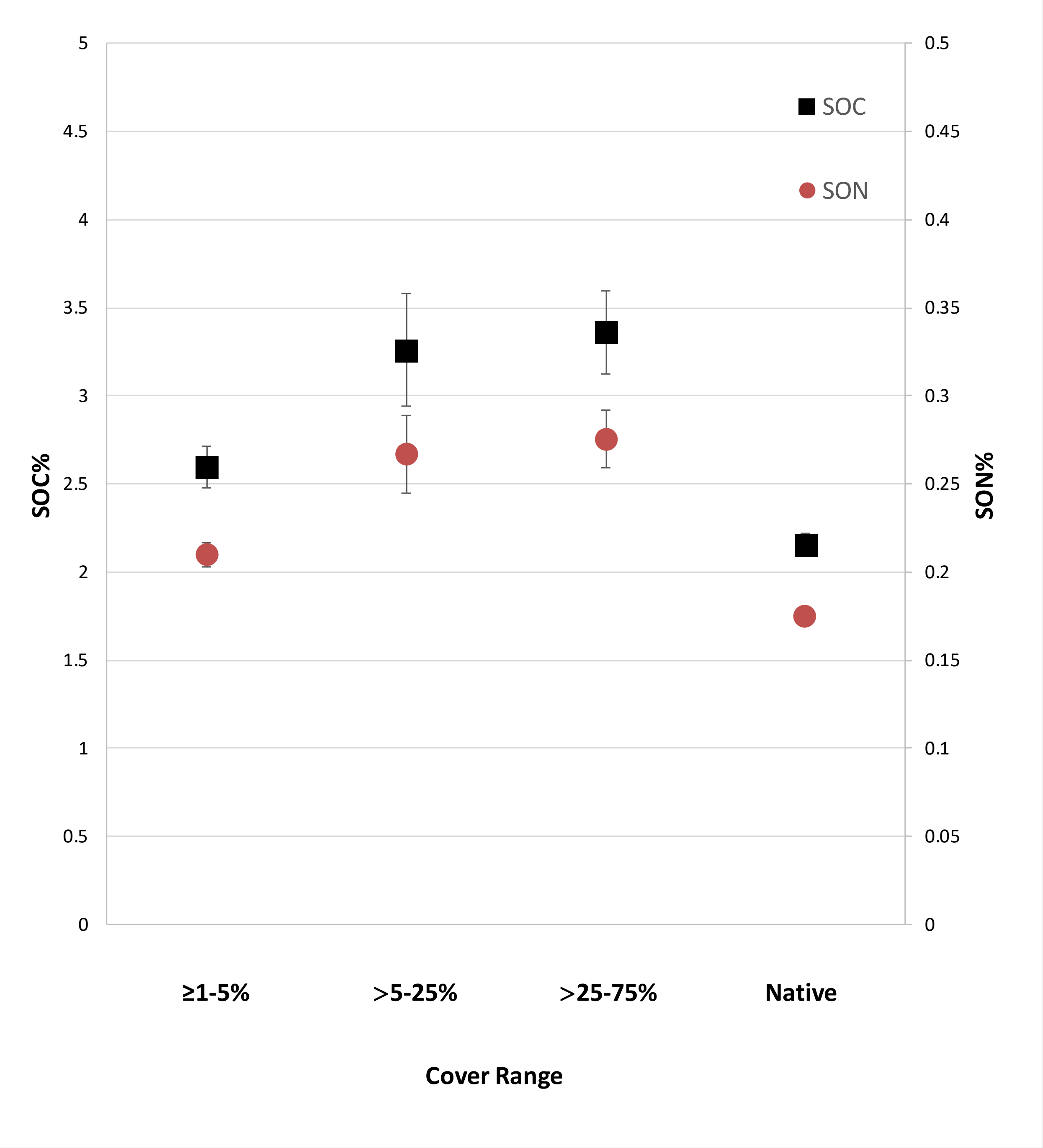

Figure 1. Means ± SE of soil organic carbon (SOC; %) and soil organic nitrogen (SON; %) for plots with low cover (≥1-5%), moderate cover (>5-25%), and high cover (>25-75%) *L. cuneata*, as well as single plant *B. bracteata* (native) cover. Soil cores were collected from the field at sites that were burned two years earlier (36 soil cores from SRR sites [3 replicates within each cover range]). SON (%) was positively correlated with SOC (%; r = 0.988) across cover ranges.

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CHAPTER III

POLLINATOR ABUNDANCE AND RICHNESS ACROSS COVER RANGES OF INVASIVE *LESPEDEZA CUNEATA* AND NATIVE *LESPEDEZA VIRGINICA*

Abstract.

Decline of native invertebrate pollinators and decreases of native flowering forbs is of growing concern worldwide. In the southern Great Plains of the United States, grasslands are one of the most important ecosystems for providing resources for pollinators, but have also experienced extensive loss and fragmentation and are considered one of the most threatened ecosystems in the world. Non-native and invasive plant species can alter remaining grassland remnants, although it is not clear how invasive plants affect pollinator populations and communities. Over two years, pan traps placed at ground level were used to evaluated pollinator species richness and abundance across a gradient of cover ranges (≥1-5%, >5-25%, and >25-75%) for invasive *Lespedeza cuneata* and a typically observed cover range (10-15%) of native *Lespedeza virginica*. Study sites were located within north-central Oklahoma in patch-burn managed rangelands where both species occur sympatrically. Findings suggest that morphospecies richness declines as *Lespedeza* cover increases; invertebrate abundance increased as morphospecies richness increased, but invertebrate abundance did not

differ with *Lespedeza* species or cover. Hymenoptera morphospecies richness was greatest in locations with moderate cover of *L. cuneata* rather than in normal cover of *L. virginica*. This study suggests that pollinator richness is higher in locations dominated by invasive *L. cuneata* rather than locations containing native *L. virginica*. If pollinator richness and associated pollination services are also higher in these areas, then increased genetic variability between *L. cuneata* populations may contribute to its spread and the isolation of natives.

Introduction.

Grasslands are the most threatened ecosystem worldwide with estimates of native tallgrass prairie being reduced to 1% of its original extent (Gauthier et al. 2003; Hines and Hendrix 2005; Hopwood 2008). Remaining tallgrass prairie remnants are prone to invasion by non-native plant species, which results in further habitat degradation (Hejda et al. 2009; Twidwell et al. 2012). Species diversity has also declined in these prairie remnants, including both plants and animals. Pollination services are critical in maintaining native grassland plant diversity, which in turn provides habitat for pollinators (Ashman et al. 2004; Westphal et al. 2008). Declines in pollinators are associated with the decrease of many native flowering forb populations (Westphal et al. 2008; Potts et al. 2010). Invasive plants may therefore have negative implications for pollinator assemblages through lowering plant diversity and modifying ecosystem services.

Declines in native bee and other invertebrate pollinators are attributed to habitat loss, fragmentation and degradation, intensified agriculture and pesticide application, invasive species and loss of native forb communities (Klein et al. 2007; Potts et al. 2010; Vanbergen 2013; Mogren et al. 2016). Fire suppression, which can modify grazing practices, also contributes to grassland degradation, leading to encroachment of woody plant species (Howe 1994; Fuhlendorf et al. 2008) and a decline of native bee communities (Martin et al. 2015). Prescribed fire implemented to reduce encroachment of woody plant species can also facilitate the establishment and spread of some invasive plants that rely on fire for seed scarification needed for germination and seedling emergence (i.e. *Lespedeza cuneata*; Cushwa et al. 1968). Further, the improper use of management practices (i.e. fire regimes that are too frequent, heavy stocking rates, broad-scale herbicide use) and the introduction of exotic plant species for soil stabilization, livestock forage, or unintentionally, have aided in the homogenization and degradation of native grassland fragments (McKinney 2006; Qian and Ricklefs 2006). Few studies have focused on the impact of invasive plant species on pollinator populations and communities in grassland ecosystems (Potts et al. 2010). Understanding how invasive plants impact native bees and other invertebrate pollinators may provide important information for managing habitat for pollinators and understanding the impact of invasive non-native plants on grassland ecosystems.

Invasive species and their native congeners provide unique opportunities to explore both ecological and evolutionary dynamics where they occur sympatrically; invaders can decrease (Barret-Segretian 2005; Thomason 2005) or increase the relative abundance of congeners (D'Antonio and Hobbie 2005; Traveset and Richardson 2006). Invasive species can also alter community dynamics through gene flow and isolation (Bossdorf et al. 2005; Dlugosch and Parker 2008). These modifications can alter plant-pollinator interactions throughout the landscape, with important implications for the structure and function of the overall community (Lee 2002; Cox 2004; Prentis et al. 2008).

Pollination of native plants can be competitively or facultatively impacted by co-flowering invasive species, which often depends on the landscape context (Bjerknes et al. 2007; Munoz and Cavieres 2008; Sargent and Ackerly 2008). Morales and Traveset (2009) report that many invasive species successfully compete with natives for pollination services through the use of denser or more colorful floral displays or due to more attractive floral rewards compared to native congeners. One study reported a decrease in visitation rate, pollination services and seed set in *Lythrum alatum* after the arrival of the invader *Lythrum salicaria*, which was attributed to the invader having a more densely packed and vibrant floral display (Brown and Mitchell 2001; Brown et al. 2002). A similar study conducted by Chittka and Schurkens (2001) in Germany reported that insect pollinators preferred the invasive *Impatiens glandulifera* to its native congeners due to a higher rate of sugar production (Comba et al. 1999; Corbet et al. 2001). Both cases resulted in reduced seed set for the native congener. Woods et al. (2012) suggests the importance of considering contextual factors that influence potential competitive or facultative effects invasive plants can have on insect pollination services of native plants, such as the degree of dependence on pollinators, the amount of shared pollinator species, the timing, showiness and coloration of flowering, similarity in flower morphology and color, relatedness of invasives to their native congeners, as well as population size and structure throughout the landscape (Bjerknes et al. 2007; Munoz and Cavieres 2008; Morales and Traveset 2009). Thus, contextual factors shape plant community dynamics and work concurrently or independently to modify the community.

Objectives.

The goal of this study was to evaluate if abundance and morphospecies richness of invertebrate pollinators vary with invasive versus native legume cover. To address this goal, I used pan traps to assess the abundance and morphospecies richness of the invertebrate pollinator community across a range of invasive legume cover compared to areas with a typically observed cover range of a congeneric native legume.

Methods.

Study system.

Lespedeza cuneata is an herbaceous and woody, perennial legume, which occurs throughout the eastern and central United States. Native to eastern Asia, this non-indigenous weed was first introduced to the United States in 1896 (Cummings et al. 2007). Legumes are a common forb in the tallgrass prairie and influence plant communities through nitrogen fixation via symbiotic root bacteria (Kaneko et al. 2002; Wu et al. 2016). *Lespedeza cuneata* does not flower during the first growing season, but typically flowers and sets seed at the end of the second growing season (Wong et al. 2012). The spread of *L. cuneata* is likely facilitated by seed coat scarification, which is required for germination (Woods et al. 2009) and prescribed fire stimulates seedling emergence. Prescribed fire is considered an important component of historical disturbance regimes in the Great Plains and is used to reduce encroachment of woody species in grasslands (Wong et al. 2012). However, prescribed fire in the fall, prior to seed dispersal, can reduce *L. cuneata* seed set and viability, reducing successful secondary dispersal and establishment events (Bell and Koerner 2009).

Propagative flexibility (Rejmanek et al. 2005) in reproductive strategy is likely an important contributing factor in the establishment and secondary spread of *L. cuneata* (Groisman et al. 2005). The reproductive strategies of *Lespedeza* species are similar and involve the production of two flower types: cleistogamous and chasmogamous. Cleistogamous flowers permit self-pollination, aid in long-distance colonizing efforts, provide reproductive assurance when pollinators are limited and facilitate more rapid genetic variation among plant populations. Chasmogamous flowers facilitate mixed-mating or outcrossing (out-pollination) that can maintain high genetic variability throughout the landscape (Allard et al. 1972; Novak et al. 1991; Daehler 1998; Pappert et al. 2000; Lambrinos 2001; Levin 2003; Barrett et al. 2008).

The *Lespedeza* species of interest in this study included the native *L. virginica* and the non-native *L. cuneata*. Both species are sympatrically occurring perennial legumes throughout the tallgrass prairie region of the Great Plains. *Lespedeza cuneata* and *L. virginica* share similar flower morphology, size and coloration, and overlap in peak flowering period from late July through late September. Chasmogamous flowers of *Lespedeza* species open in the morning and typically last a day before wilting. Cleistogamous flowers occur in an interspersed pattern throughout the plant ramets, and are very much reduced (Woods et al. 2009; Woods et al. 2012). Native *Lespedeza* species have been known to hybridize with other natives (Woods 2006; Woods et al. 2012), however hybridization does not occur with *L. cuneata* plants due to a difference in chromosomal number (*L. cuneata* chromosomal number is n = 19 and North American native *Lespedeza* is n = 10; Clewell 1966). *Lespedeza* species are fire adapted and require seed coat scarification for germination and fire stimulates seedling emergence (Clewell 1966; Cushwa et al. 1968). Individual, mature *Lespedeza* plants consist of multiple ramets emerging from a common base, which together comprise an individual plant.

Study sites and treatments.

My research was conducted in north-central Oklahoma at Oklahoma State University's Stillwater Research Range (SRR), approximately 18 km west of Stillwater, OK. The SRR is located in the western section of the Cross Timbers ecoregion, which extends from southeastern Kansas to north-central Texas and is comprised of deciduous forest, savanna and tallgrass prairie. The SRR consists primarily of native vegetation, including mixed and tallgrass prairie and is managed with livestock grazing and prescribed fire. An Oklahoma Mesonet (Brock et al. 1995) weather station located in the area records various climate measurements and shows annual precipitation averages 92.24 cm, with peak rainfall occurring in May and average temperatures range from 34.4°C in the summer to 1.1°C in the winter. Vegetation characteristic of tallgrass prairie remnants of the Cross Timbers ecoregion and commonly found in the SRR include dominant grasses (*Panicum virgatum*, *Sorghastrum nutans*, *Andropogon gerardii*, *Schizachyrium scoparium*, *Aristida purpurea*), dominant forbs (*Ambrosia psilostachya*, *Gutierrezia dracunculoides*), other forbs of prevalence (*Echinacea purpurea*, *Ratibida columnifera*, *Linum flavum*, *Triodanis perfoliata*, *Oenothera speciosa*, *Convolvulus arvensis*, *Calendula arvensis*, *Erigeron annuus*, *Coreopsis palmata*, *Solidago rigida*, *Gutierrezia sarothrae*, *Solanum elaeagnifolium*, *Grindelia squarrosa*) and dominant woody plants (*Quercus stellata*, *Quercus marilandica*, *Celtis* spp.) (Allred et al. 2010).

This study utilized patch-burn sites within the SRR, which range in size from 49 to 63 ha. Patch-burning (patch-burn grazing) involves the combined use of fire and grazing for ecological management goals by purposefully encouraging cattle to freely select the most recently burned part of a site. Grazing pressure is shifted when another section is burned, thus creating a shifting mosaic on the management unit (Cummings et al. 2007). Growing season prescribed fire (occurring in summer months) is conducted when warm-season herbaceous plants are actively growing, whereas dormant season prescribed fire (occurring in early spring months) is used to promote livestock production and is conducted just before spring green-up (Launchbaugh and Owensby 1978). SRR patch-burn site are divided into 6 sections approximately equal in size and defined by burning regime. Two of six sections are burned each year: one in spring (February through March) and one in summer (July through August). Within each patch-burn rangeland (each site), I used the section with the longest time since burn (two years since a spring burn). Using the longest time since burn allowed *Lespedeza* plants the longest recovery time since the last burn and for any newly recruited plants (germinated in response to the fire) to bloom. Cattle are stocked at a constant rate in the SRR, consisting of 6.9 ha/animal.

I examined invertebrate pollinator morphospecies richness and abundance in areas containing one native *Lespedeza* species and three invasive *L. cuneata* cover ranges. *Lespedeza cuneata* cover ranges were designated as: ≥1-5% (low), >5-25% (moderate), and >25-75% (high) *L. cuneata* cover. Areas containing a native legume were characterized by 10-15% *L. virginica* cover, which is a typical cover range in the SRR (personal observation, J. Kaplan); a quadrat (0.25m x 0.25m) was used to estimate *Lespedeza* cover. *Lespedeza virginica* is typically observed to grow in patches much less dense and with less coverage when compared to its invasive congener, *L. cuneata*. Thus, treatments included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/Moderate cover (>5-25%), 3) *L. cuneata*/High cover (>25-75%), 4) *L. virginica* 'normal' cover (10-15%).

Pan trap sampling for pollinators.

In August of 2017 and 2018, pan traps were used to assess the abundance and morphospecies richness of the invertebrate pollinator community within plots identified for

Lespedeza cover treatments. Pan traps are considered the most objective method for assessing the bee community because there is no observer bias (Gezon et al. 2015). Pan traps were arranged in clusters of three (one white, florescent blue and florescent yellow) and spaced approximately 5m apart in a triangular formation at ground level. Pan traps mimic flowers and these colors have been previously identified as attracting a diverse bee community (Leong and Thorp 1999; Cane et al. 2000; Stephen and Rao 2005; Toler et al. 2005; Roulston et al. 2007; Vrdoljak and Samways 2011). One set of three pan traps were arranged at each cover treatment plot within each site, with a 15m buffer of the appropriate legume cover treatment around the pan trap array. Pan traps were placed in the field before 0900 hours CDST and collected before 0900 hours CDST the following day. Thus, pan traps had 24 hours of exposure in the field. Upon collection from the field, contents of pan traps were stored in 8oz deli cups, and then washed and stored in 70% ethanol until preparation for identification.

Invertebrate pollinator abundance and morphospecies richness.

Invertebrates collected in pan traps were inspected under a stereo dissecting microscope (400x) and identified to lowest taxonomic rank (to order, family and genus, respectively; using Michener et al 1994; Salsbury and White 2000; Triplehorn and Johnson 2005) and further separated into morphospecies based on morphologically distinct characteristics. Morphospecies were used for species richness and abundance analyses where invertebrates were identified as pollinators or non-pollinators.

Analyses.

I used a repeated measures ANOVA and paired T-test to determine if invertebrate pollinator abundance and morphospecies richness varied between areas containing *L. virginica* and three *L. cuneata* cover ranges. Pollinator abundance and morphospecies richness of each order was used for analysis. Hymenopterans had a relatively large presence in pan trap samples, so Formicidae and Halictidae were also included in a separate analysis. Although pan traps may not effectively sample non-pollinator invertebrates, Collembolans (identified as non-pollinators) had a relatively large presence in pan trap samples, so non-pollinator orders were analyzed separately. A Pearson correlation (Pearson's r) was used to evaluate the extent (between -1 and 1) of linear relatedness between plant type (invasive or native), cover range, species richness (total morphospecies) and abundance.

Results.

Across two years, 1037 individuals were collected. Hymenoptera were the most prevalent taxa (N=550) and large numbers of Formicidae (N=445) and Halictidae (N=105) accounted for over half of collected invertebrates. Collembola (N=100), Diptera (N=214) and Hemiptera (N=118) represented another 432 individuals, while Araneae (N=3), Coleoptera (N=18), Lepidoptera (N=18) and Thysanoptera (N=16) were present, but sparse.

Lespedeza cover and species: Pollinator morphospecies richness.

There was a significant relationship between *Lespedeza* cover and total morphospecies richness (F [3,8] 4.35, p=0.043) and morphospecies richness of certain invertebrate taxa, including Formicidae (F [3,8] 13.424, p=0.002) and Hymenoptera (F [3,8] 6.73, p=0.014). Total morphospecies richness of pan trap samples were highest in *L. virginica* locations. Formicidae and Hymenoptera were most prevalent in moderate cover *L.*

cuneata compared to locations with *L. virginica* and other *L. cuneata* cover ranges (Table 1, Figure 1).

Total morphospecies richness was significantly different between *L. virginica* and high cover *L. cuneata* (p=0.008) where morphospecies richness was higher in areas with *L. virginica*. There was no difference between *L. virginica* and low (p=0.126) and moderate (p=0.323) cover *L. cuneata*, low and high (p=0.108) cover *L. cuneata* and low and moderate (p=0.532) cover *L. cuneata*. Hymenopteran morphospecies richness was highest in moderate cover *L. cuneata* than low (p=0.014) or high (p=0.004) cover *L. cuneata* or locations with *L. virginica* (p=0.006). There was no difference between *L. virginica* and low (p=0.616) and high (p=0.737) cover *L. cuneata* and low and high (p=0.409) cover *L. cuneata*. Formicidae morphospecies richness was highest in moderate cover *L. cuneata* compared to low (p=0.002) or high (p=0.003) cover *L. cuneata* or locations with *L. virginica* (p<0.001). There was no difference between *L. virginica* and low (p=0.237) and high (p=0.126) cover *L. cuneata* and low and high (p=0.681) cover *L. cuneata* (Table 1, Figure 1).

There was no significant relationship between *Lespedeza* cover and Coleoptera (F [3,8] 0.222, p=0.878), Diptera (F [3,8] 3.15, p=0.086), Halictidae (F [3,8] 3.088, p=0.090), Hemiptera (F [3,8] 1.143, p=0.389), Lepidoptera (F [3,8] 1.200, p=0.370) and Thysanoptera (F [3,8] 1.286, p=0.344) morphospecies richness (Table 1, Figure 1).

Lespedeza cover and species: Non-pollinator morphospecies richness.

There was a significant relationship between *Lespedeza* cover and morphospecies richness of Collembola (F [3,8] 7.68, p=0.01). Collembolan morphospecies richness was significantly higher in *L. virginica* locations than in moderate (p=0.032) and high (p=0.002) cover *L. cuneata* and higher in low than high (p=0.006) cover *L. cuneata*. There was no difference between *L. virginica* and low (p=0.511) cover *L. cuneata* and low and moderate (p=0.104) cover *L. cuneata* (Table 1, Figure 1).

There was no significant relationship between *Lespedeza* cover and Araneae (F [3,8] 0.333, p=0.802 morphospecies richness (Table 1, Figure 1).

Lespedeza cover and species: Pollinator abundance.

There was no significant relationship between *Lespedeza* cover and total invertebrate abundance (F [3,8] 3.44, p=0.072), Coleoptera (F [3,8] 3.44, p=0.072), Diptera (F [3,8] 3.60, p=0.065), Formicidae (F [3,8] 1.082, p=0.410), Halictidae F [1,10] 3.681, p=0.062), Hemiptera (F [3,8] 2.978, p=0.096), Hymenoptera (F [3,8] 1.292, p=0.342), Lepidoptera (F [3,8] 0.667, p=0.596) and Thysanoptera (F [3,8] 1.477, p=0.292) abundance (Table 1, Figure 2).

Lespedeza cover and species: Non-pollinator abundance.

There was a significant relationship between *Lespedeza* cover and Collembola abundance (F [3,8] 4.78, p=0.034). Collembola abundance was significantly higher in *L. virginica* locations compared to high cover *L. cuneata* (p=0.005). There was no difference between *L. virginica* and low (p=0.084) or moderate (p=0.065) cover *L. cuneata* and low and moderate (p=0874) and moderate and high (p=0.139) cover *L. cuneata* (Table 1, Figure 2).

There was no significant relationship between *Lespedeza* cover and Araneae (F [3,8] 0.333, p=0.802) abundance (Table 1, Figure 2).

Correlations: Plant type, cover range, morphospecies richness and abundance.

Pearson's r revealed significant correlations (2-tailed; significant at the p=0.01 level) between *Lespedeza* cover range, morphospecies richness and invertebrate abundance. Morphospecies richness was negatively correlated with *Lespedeza* cover (r=-0.681, p=0.015) and positively correlated with invertebrate abundance (r=0.715, p=0.009). There was no significant correlation between invertebrate abundance and *Lespedeza* cover (r=-0.522, p=0.082). There was no significant correlation between *Lespedeza* species and invertebrate abundance (r=-0.523, p=0.081) and morphospecies richness (r=-0.558, p=0.059).

Discussion.

Morphospecies richness was negatively correlated with *Lespedeza* cover (Pearson's r, Table 1, Figure 1). Thus, there were fewer morphospecies as *Lespedeza* cover increased. Morphospecies richness was highest in locations with *L. virginica* (10-15% cover) and lowest in locations with the highest cover of *Lespedeza* (*L. cuneata* >25-75%) (Pearson's r, Table 1, Figure 1). As morphospecies richness increased, invertebrate abundance also increased (Pearson's r). However, invertebrate abundance did not differ based on *Lespedeza* cover (Pearson's r, Table 1). Morphospecies richness and invertebrate abundance did not differ with *Lespedeza* species (Pearson's r, Table 1).

Based on morphology, *Lespedeza* flowers are expected to attract short-tongued invertebrates (i.e., certain flies and bees), so visitation by long-tongued invertebrates (i.e., certain flies, bees and Lepidopterans) would not be expected (Bohart and David 2019). Conversely, as seen in Woods et al. (2009), some flowers with exposed nectar, like *Lespedeza* (more specifically *L. cuneata*), attract certain long-tongued bees like *Apis mellifera* (Woods et al. 2012), but are particularly well-suited for short-tongued bees like

Halictidae (Bohart and David 2019). Despite Woods et al. (2012) findings, *Apis mellifera* were not found in this study, although it is well documented that pan traps are not expected to capture honey bees (Cane et al. 2001).

Hymenoptera and Formicidae had greater morphospecies richness in locations with moderate *L. cuneata* cover compared to *L. virginica* cover (10-15%) and although not significant, a similar trend occurred with Halictidae (Table 1, Figure 1). Woods et al. (2009) observed *L. cuneata* to have a similar pollinator visitation rate relative to native congeners, on a per flower basis. These observations indicate that higher visitation per plant of the invasive is due to its relatively high floral density where *L. cuneata* produces five times as many seeds per plant and more than twenty times the amount of chasmogamous flowers per plant in relation to *Lespedeza* congeners (Woods et al. 2009). In this study, *L. cuneata* moderate cover (>15-25%) was similar to *L. virginica* cover (10-15%). However, based off of Woods et al. (2009) observations, invasive *L. cuneata* would likely have a greater number of ramets per plant and greater density of flowers per ramet than *L. virginica*, which would result in a floral display that averages at least twenty times that of native *Lespedeza* congeners (i.e., *L. capitata, L. violacea* and *L. virginica*). With an increase in seed production and chasmogamous flower density per plant, *L. cuneata* was shown to benefit more from chasmogamous (assumingly insect-pollinated) flowers than its native congeners (Woods et al. 2009).

High densities and coverages typically associated with invasive plants relative to natives may support a higher abundance of pollinators, where they are more likely to find resources and stay longer. Insect pollinators (i.e. Hymenoptera) were found to have the greatest morphospecies richness in moderate cover (>5-25%) *L. cuneata* plots (Table 1, Figure 1), and although not statistically significant, also tended to have the greatest abundance in these plots, which are similar in cover to the normal cover (10-15%) *L. virginica* plots (Table 1, Figure 2). *Lespedeza* cover and Hymenoptera morphospecies richness suggest native *Lespedeza* may attract more insect pollinators if its floral density was similar to that of *L. cuneata* (Table 1, Figure 1); pollinator abundance at *L. virginica* locations resembles that in low cover *L. cuneata* (Table 1, Figure 2). Hymenoptera morphospecies richness increased between low and moderate locations, but did show a decline in Hymenoptera morphospecies richness as *L. cuneata* cover increased to >25-75%, perhaps reaching a threshold for the attraction of more insects. In these instances, Hymenoptera were at their lowest richness (Figure 1) and abundance of all cover ranges sampled (Table 1, Figure 2). Other plausible explanations include that pan traps may have been less visible because of high *L. cuneata* cover, the placement of pan traps (ground-level versus elevated within the vegetation canopy) (Harris et al. 2017; McCravy and Ruholl 2017), or that flowering forbs outcompeted the pan traps for bees (Cane et al. 2000; Mayer 2005; Roulston et al. 2007; Wilsons et al. 2008; Baum and Wallen 2011). When examining Hymenoptera taxa collected, Formicidae morphospecies richness was lower in high cover *L. cuneata* locations and tended to have higher morphospecies richness (Figure 1) and abundance in moderate cover *L. cuneata* locations (Table 1, Figure 2). Data from this study was similar to Woods et al. (2009) where *L. cuneata* and *L. virginica* were shown to generally share a similar insect community, besides a few non-pollinator morphospecies collected; invertebrate abundance was not significantly different depending on the

Lespedeza congener (Table 1, Figure 2). While *L. virginica* (10-15%) had greater morphospecies richness (Table 1, Figure 1), moderate cover of *L. cuneata* had the highest morphospecies richness of the *L. cuneata* cover ranges (Table 1, Figure 1).

The most prominent flying insect pollinator overall was the family Halictidae. While Halictids were not significantly more abundant based on *Lespedeza* species or cover (Table 1), they accounted for 10.1% of collected individuals. Not only are the bodies of these sweat bees well-suited for exposing the anthers of *Lespedeza* flowers, which deposit pollen directly onto their abdomens, but sweat bees are also generalist foragers, visiting a wide array of nectar sources. Halictids typically nest in bare soil located in sunny locations in areas of minimum tilling and insecticide use (Buckley et al. 2016), so likely had access to nest sites within the SRR.

Formicidae morphospecies richness was greater in locations with moderate *L. cuneata* cover compared to normal cover of *L. virginica* (Table 1, Figure 1). Given the social structure of ant colonies, it was not surprising that if a pan trap contained ants, it generally contained quite a few. Ants collected from pan traps were wingless and must crawl into flowers, and may prefer flowers positioned close to the stem due to ease of access (USDA Forest Service, Ant Pollination; Hickman 1974). Despite collecting nectar, ants are not considered important pollinators, but may transfer some pollen among flowers (but see Hickman 1974). Overall, cross pollination among ant species is understudied, but additional research is needed to evaluate their potential role in providing pollination services.

While morphospecies richness was highest in locations with the native congener (Table 1, Figure 1), incidental insects (i.e. Collembola*;* not regarded as pollinators;

Triplehorn and Johnson 2005; Gibb 2014) contributed to this richness along with others that feed on plant parts or are predators of flower visitors and not necessarily plant pollinators (i.e. some Diptera such as Asilidae, Muscidae, Drosophilidae [Kevan 2008; Bohart and David 2019]) (Table 1, Figure 1), although some may still contribute to the movement of pollen. Diptera tended to be more abundant by *L. virginica* than *L. cuneata* (Table 1, Figure 2). Drosophilidae and Muscidae adults feed on flowers with exposed nectar but are not considered important pollinators, whereas their larvae often develop inside living plant tissue and can harm the plant. Asilidae are predatory flies that feed on many insect orders (Bohart and David 2019).

Insect visitation and pollination services may be important for genetic variation among invasive *L. cuneata* and native congeners. Studies on *Lespedeza* species in North American prairies indicate patterns of genetic diversity; Cole and Biesboer (1992) found low heterozygosity in widespread native *L. capitata*, yet strong genetic variability, consistent with self-pollination. When mimicking outcrossing with *L. capitata* and a threatened *Lespedeza* congener, *L. leptostachya*, outcrossing still proved important in maintaining viable populations while contributing to further genetic variability and gene flow. Sundberg et al. (2002) found considerable genetic variability in invasive *L. cuneata* plants collected from different populations, suggesting outcrossing contributes to greater genetic diversity within and among populations or due to a history of non-native introductions, or both. Other possible reasons for this difference include that native *Lespedeza* species occur at lower densities (not usually forming dense monocultures within a community) and because they occur less frequently throughout the landscape. Pollinators may visit numerous chasmogamous flowers in a single stopover to a plant, and pollination between chasmogamous flowers on the same plant may be possible. Because both self- and cross-pollination of cleistogamous and chasmogamous flowers lead to successful reproduction in *Lespedeza* species, and because chasmogamous flowers may also aid in self-pollination, limiting access to or altering the coverage of chasmogamous flowers may negatively impact reproductive success, which could have important implications for limiting the spread of *L. cuneata*.

Conclusion and future directions.

Morphospecies richness declined as *Lespedeza* cover increased; invertebrate abundance increased as morphospecies richness increased, but invertebrate abundance did not differ with *Lespedeza* species or cover. Morphospecies richness and invertebrate abundance did not differ among *Lespedeza* species when cover was similar. Hymenoptera morphospecies richness was greater in locations containing moderate cover of *L. cuneata* than in normal cover of *L. virginica*. Thus, while non-pollinator invertebrate abundance and richness (Collembolan) was higher in native *Lespedeza* plots, insect pollinators (Hymenoptera) had higher richness in plots with moderate cover of invasive *Lespedeza*. If pollinator visitation rates are higher in locations dominated by *L. cuneata*, this may further contribute to increased genetic variability and gene flow between *L. cuneata* populations. Future research could evaluate if the abundance and species richness of invertebrate pollinators differ between areas with other native *Lespedeza* species (e.g., *L. violacea*, *L. capitata*, *L. stuevei*) and areas with invasive *L. cuneata*. Additional research is also needed to evaluate the potential role of Formicidae in providing pollination services. Supplementary evaluation of pan trap placement (ground-level versus elevated within the vegetation canopy) may attract a different variety of invertebrate pollinators between *Lespedeza* congeners when pan traps are more visible.

Tables and figures.

Collection	*Lespedeza* Cover	Mean	SE (±)
Invertebrate Abundance	*L. virginica* 10-15%	47.00	5.01
	L. cuneata ≥1-5%	28.67	2.49
	L. cuneata >5-25%	41.83	10.66
	L. cuneata >25-75%	21.67	3.67
Morphospecies Richness*	*L. virginica* 10-15%	36.00^{1}	1.89
	L. cuneata ≥1-5%	30.33	1.83
	L. cuneata >5-25%	32.50	3.25
	L. cuneata >25-75%	24.33^{2}	2.13
Araneae Abundance	*L. virginica* 10-15%	0.17	0.17
	L. cuneata ≥1-5%	0.00	0.00
	L. cuneata >5-25%	0.17	0.17
	L. cuneata >25-75%	0.17	0.17
Araneae Morphospecies Richness	*L. virginica* 10-15%	0.17	0.17
	L. cuneata ≥1-5%	0.00	0.00
	L. cuneata >5-25%	0.17	0.17
	L. cuneata >25-75%	0.17	0.17
Coleoptera Abundance	*L. virginica* 10-15%	2.67	1.45
	L. cuneata ≥1-5%	0.67	0.17
	L. cuneata >5-25%	1.17	0.17
	L. cuneata >25-75%	0.67	0.44
Coleoptera Morphospecies Richness	*L. virginica* 10-15%	0.67	0.44
	L. cuneata ≥1-5%	0.67	0.17
	L. cuneata >5-25%	1.00	0.29
	L. cuneata >25-75%	0.67	0.44
Collembola Abundance*	*L. virginica* 10-15%	8.17^{1}	1.92
	L. cuneata ≥1-5%	4.17	1.20
	L. cuneata >5-25%	3.83	1.74
	L. cuneata >25-75%	0.50^{2}	0.29
Collembola Morphospecies Richness*	*L. virginica* 10-15%	3.50^{1}	0.58
	L. cuneata ≥1-5%	3.00	0.76
	L. cuneata >5-25%	1.67^{12}	0.33
	L. cuneata >25-75%	0.33^{2}	0.17
Diptera Abundance	*L. virginica* 10-15%	17.33	3.71
	L. cuneata ≥1-5%	8.33	3.25
	L. cuneata >5-25%	5.83	3.63
	L. cuneata >25-75%	4.17	0.83

Diptera Morphospecies Richness	*L. virginica* 10-15%	6.00	0.29
	L. cuneata ≥1-5%	2.83	0.93
	>5-25%	2.50	1.32
	>25-75%	3.33	0.73
Hemiptera Abundance	*L. virginica* 10-15%	3.17	0.60
	L. cuneata ≥1-5%	4.67	0.17
	>5-25%	7.83	1.69
	>25-75%	4.00	1.52
Hemiptera Morphospecies Richness	*L. virginica* 10-15%	2.33	0.17
	L. cuneata ≥1-5%	2.83	0,17
	>5-25%	3.27	0.73
	>25-75%	3.33	0.88
Hymenoptera Abundance	*L. virginica* 10-15%	12.83	4.60
	L. cuneata ≥1-5%	10.33	1.92
	>5-25%	58.17	41.25
	>25-75%	9.33	3.83
Hymenoptera Morphospecies Richness*	*L. virginica* 10-15%	4.33^2	0.93
	L. cuneata ≥1-5%	4.83^2	0.88
	>5-25%	7.83^1	0.44
	>25-75%	4.00^2	0.00
Formicidae Abundance	*L. virginica* 10-15%	9.50	5.57
	L. cuneata ≥1-5%	7.33	2.21
	>5-25%	50.83	40.92
	>25-75%	6.50	3.01
Formicidae Morphospecies Richness*	*L. virginica* 10-15%	2.00^2	0.29
	L. cuneata ≥1-5%	2.50^2	0.29
	>5-25%	4.33^1	0.33
	>25-75%	2.67^2	0.29
Halictidae Abundance	*L. virginica* 10-15%	5.00	1.50
	L. cuneata ≥1-5%	2.83	1.17
	>5-25%	7.00	0.29
	>25-75%	2.67	0.93
Halictidae Morphospecies Richness	*L. virginica* 10-15%	2.67	0.60
	L. cuneata ≥1-5%	2.17	0.60
	>5-25%	3.17	0.44
	>25-75%	1.17	0.17
Lepidoptera Abundance	*L. virginica* 10-15%	1.17	0.33
	≥1-5%	0.50	0.29
		0.67	0.44

	L. cuneata >5-25% >25-75%	0.67	0.33
Lepidoptera Morphospecies Richness	*L. virginica* 10-15%	1.00	0.29
	L. cuneata ≥1-5%	0.50	0.29
	>5-25%	0.50	0.29
	>25-75%	0.33	0.17
Thysanoptera Abundance	*L. virginica* 10-15%	0.83	0.83
	L. cuneata ≥1-5%	0.00	0.00
	>5-25%	0.00	0.00
	>25-75%	1.83	1.17
Thysanoptera Morphospecies Richness	*L. virginica* 10-15%	0.33	0.33
	L. cuneata ≥1-5%	0.00	0.00
	>5-25%	0.00	0.00
	>25-75%	0.50	0.29

Table 1. Invertebrate abundance (mean ± SE) and morphospecies richness (mean ± SE) from pan trap samples by order (including Hymenopteran family: Formicidae and Halictidae), *Lespedeza* species and cover. Native *L. virginica* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Treatments within each section of each site included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/Moderate cover (>5-25%), 3) *L. cuneata*/Moderate cover (>25-75%), and 4) *L. virginica* 10-15%) cover. Invertebrates were collected from pan traps (yellow, blue and white) that were placed in the field for 24 hours at sites that had similar treatments. Invertebrates were sorted and identified to order, family and morphospecies. Values *of* significance ($p<0.05$) based on a repeated measures ANOVA are denoted by * for abundance and morphospecies richness. Significant differences ($p<0.05$) of pair-wise comparisons of abundance and morphospecies richness within each species and cover category are denoted by ^{1} for significantly higher and ^{2} for significantly lower.

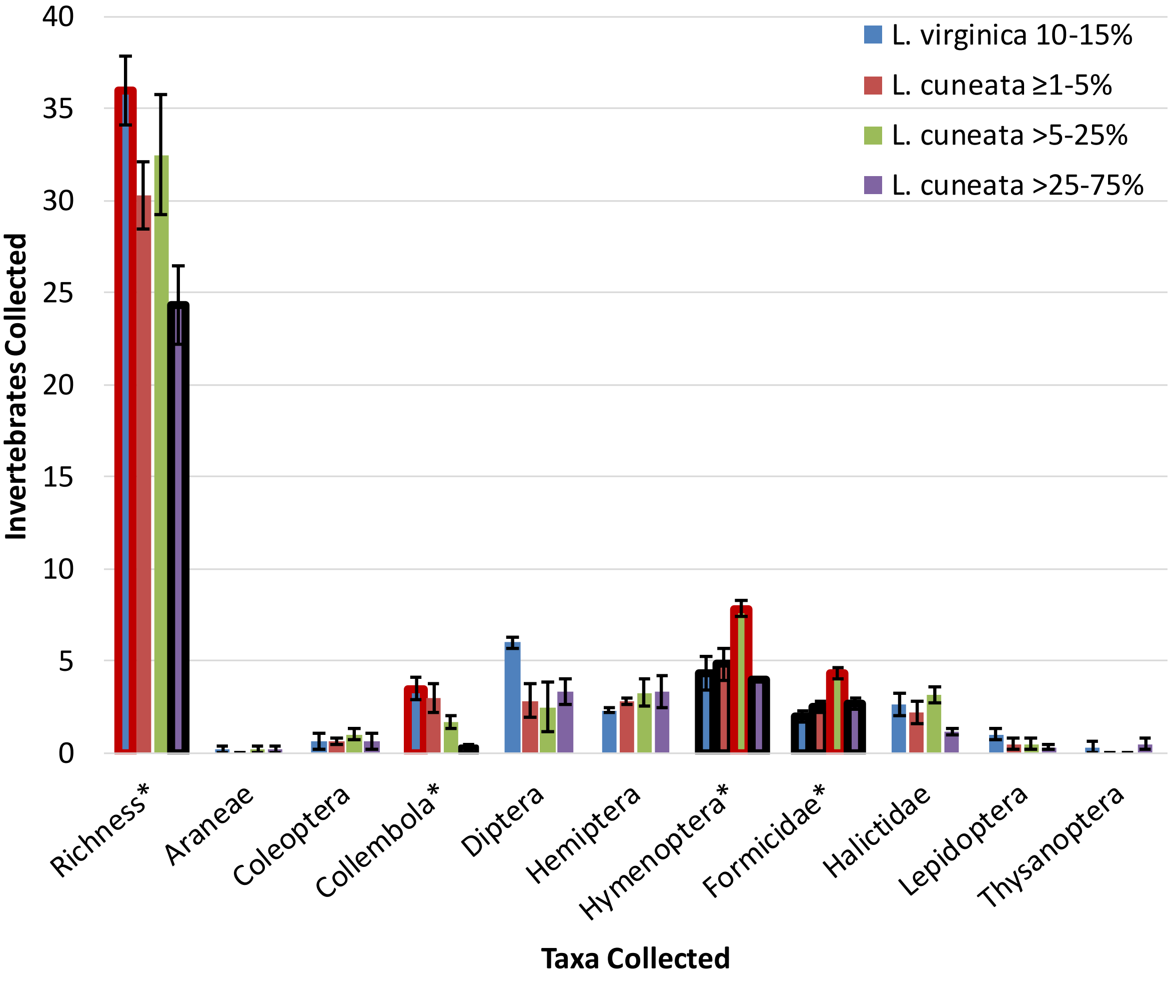

Figure 1. Invertebrate morphospecies richness (mean ± SE) from pan trap samples by order (including Hymenopteran family: Formicidae and Halictidae), *Lespedeza* species and cover. Native *L. virginica* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Treatments within each section of each site included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/Moderate cover (>5-25%), 3) *L. cuneata*/Moderate cover (>25-75%), and 4) *L. virginica* 10-15%) cover. Invertebrates were collected from pan traps (yellow, blue and white) that were placed in the field for 24 hours at sites that had similar treatments. Invertebrates were sorted and identified to order, family and morphospecies. Values *of* significance (p<0.05) based on a repeated measures ANOVA are denoted by * for morphospecies richness. Cover ranges showing morphospecies richness that are significantly (p<0.05) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

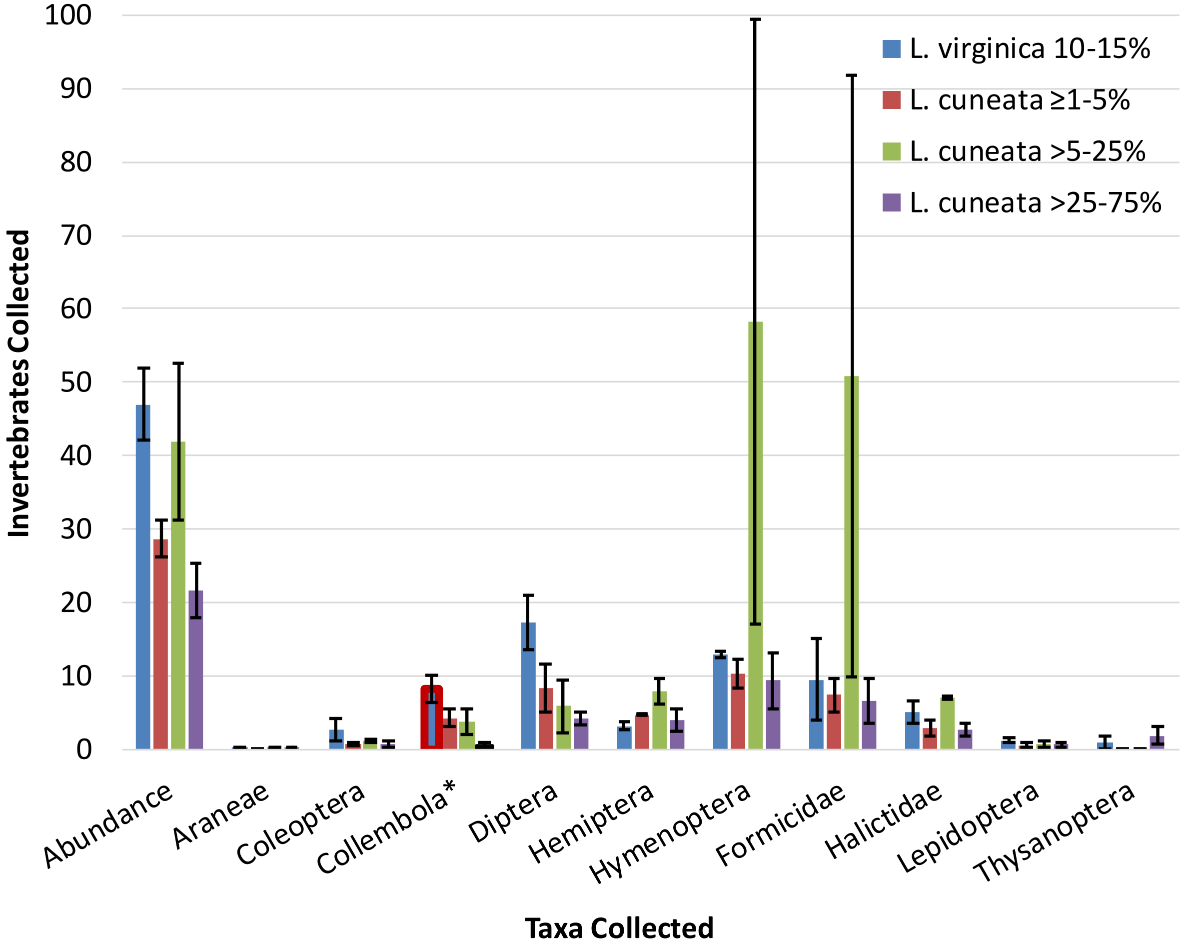

Figure 2. Invertebrate abundance (mean ± SE) from pan trap samples by order (including Hymenopteran family: Formicidae and Halictidae), *Lespedeza* species and cover. Native *L. virginica* and invasive *L. cuneata* are sympatrically occurring perennial legumes found throughout the tallgrass prairie region of the Great Plains and within the SRR. Treatments within each section of each site included 1) *L. cuneata*/Low cover (≥1-5%), 2) *L. cuneata*/Moderate cover (>5-25%), 3) *L. cuneata*/Moderate cover (>25-75%), and 4) *L. virginica* 10-15%) cover. Invertebrates were collected from pan traps (yellow, blue and white) that were placed in the field for 24 hours at sites that had similar treatments. Invertebrates were sorted and identified to order, family and morphospecies. Values *of* significance ($p<0.05$) based on a repeated measures ANOVA are denoted by * for invertebrate abundance. Cover ranges showing invertebrate abundance that are significantly ($p<0.05$) higher are denoted by a red outline versus those they are compared to (black outline) that are significantly lower.

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VITA

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