Spiders in California's grassland mosaic: The effects of native and non-native grasses on spiders, their prey, and their interactions

by

Kirsten Elise Hill

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Abstract

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Found in nearly all terrestrial ecosystems, small in size and able to occupy a variety of hunting niches, spiders' consumptive effects on other arthropods can have important impacts for ecosystems. This dissertation describes research into spider populations and their interactions with potential arthropod prey in California's native and non-native grasslands. In meadows found in northern California, native and non-native grassland patches support different functional groups of arthropod predators, sap-feeders, pollinators, and scavengers and arthropod diversity is linked to native plant diversity.

Wandering spiders' ability to forage within the meadow's interior is linked to the distance from the shaded woodland boundary. Native grasses offer a cooler conduit into the meadow interior than non-native annual grasses during midsummer heat. Juvenile spiders in particular, are more abundant in the more structurally complex native dominated areas of the grassland. Potential prey species and abundance differ along the trajectory from woodland boundary to meadow interior and may have consequences for the survival of juvenile spiders that reside primarily near the woodland boundary.

Spiders' ability to influence the eating habits of potential prey species is regulated by temperature and grassland characteristics. In experimental wolf spider enclosures, cooler habitats in which spiders were present evidenced lower herbivory by large chewing invertebrates. Herbivory differed across a gradient of temperature and sunlight but newly restored plants in exposed and warmer soil faced higher rates of herbivory than established plants; herbivory may be better mediated by spider activity in cooler environments.

Introduction

“The last word in ignorance is the man who says of an animal or plant, "What good is it?" If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.”
– Aldo Leopold, Round River: From the Journals of Aldo Leopold

Through their abundance and activity, arthropods are integral to the balance of many terrestrial ecosystems. As the animal base of many food webs, their abundance and activity is a key to functioning of food webs. I choose to study arthropods in California’s grasslands because currently little is known how they have been affected by sweeping changes; landscapes once dominated by perennial grasses are now deluged with non-native annual grasses. I choose to focus on wandering spiders within the grasslands because their abundance and activity has been used in other systems as a measure ecosystem health (Gerlach et al 2013). As dominant arthropod predators, they can be sensitive to desiccation and temperature is often critical in determining their distributions (Almquist 1973, Bonte et al 2006). In this changed ecosystem, their activity, distribution, and abundance throughout the grasslands may indicate their adaptation, or lack thereof, to the relatively novel introduced annual grasses.

One hypothesis, widely applied for understanding trophic cascades in invaded systems, is the enemy release hypothesis. This hypothesis states that invading plants (or other types of invaders) are released from natural (herbivore or other) enemies that control their populations in their native range (Keane et al. 2002). The enemy release hypothesis postulates that these invaders spread rapidly, grow taller and/or larger than they would in their home range, and out-compete less resource-flexible native species within their own range because they are freed from parasites, herbivores or other attackers that would generally keep the population in check. These invaders are also flexible enough in their resource requirements that they can continue to spread into a greater array of habitats. California’s non-native annual grasses may be freed from herbivore enemies through lack of native herbivore host switching, annual grasses also have a comparatively short life cycle; they senesce before many arthropod herbivore populations reach peak activity abundance in mid-summer. Native perennials support the remaining herbivore load for the greater portion of the year. Another dilemma for invertebrates may be created when annual plants senesce in the summer. In so doing, they leave a warmer, drier, more open and less complex microhabitat than is found in native perennial habitats. This change may pose challenges for arthropods sensitive to desiccation but may benefit those that thrive in the greater warmth. The research of this dissertation investigates these differences to better understand how arthropods and spiders respond to non-native annual grasses.

Understanding what happens to an ecosystem when species invade is critical to future monitoring and restoration of that system. The first chapter of this dissertation delves into description of the functional groups of arthropods and arthropod biodiversity in the grassland dominated by native perennial and non-native annual grasses. I describe differences in the populations of arthropod predators, sap-feeders, pollinators, and scavengers as observed, captured through pitfall traps and sweep-net surveys in the two habitat types. This chapter is an initial step in understanding these various arthropod elements of California’s grassland.

The many facets of a changing ecosystem require vigilance and rigorous study of the many "cogs and wheels" that work together. In the second chapter, I describe how the proximity to the woodland border affects wandering spiders' ability to forage into the grassland, particularly juvenile Lycosidae spiders. I also describe how this border, in relation to native and non-native grasses, affects spiders' potential prey populations. Spiders can help free ecosystems from an overburden of insects and have been shown to positively affect biodiversity of ecosystems, particularly grasslands, through their feeding behavior. They can scare their prey into eating different plants, cause herbivores to suppress the abundance of competitively dominant plants, facilitate change in the soil nutrient content, and, as a diverse group of predators, they form a source of biological control (Hawlena et al 2012, Birkhofer et al 2008, Schmitz 1998, Wise 1993). This chapter is a step in understanding how wandering spiders roam through the altered grassland in relation to potential prey.

The final chapter describes an experimental manipulation used to understand the potential effects of the dominant grassland spider's (*Schizocosa mccooki*) presence (or absence) on herbivory in native, non-native, and newly restored grassland habitats. I choose to study how the grassland environment effects spiders' ability to alter prey feeding behavior, as evidenced through herbivore damage to plants. This chapter is a step in understanding how invertebrate feeding behavior and interactions with predators may be changed in newly restored habitat. The most critical message from this chapter is that recent soil disturbance can increase the heat load within a microhabitat, alter potential interactions between predator and prey, and leave newly restored plants vulnerable to greater herbivory.

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Chapter 1

Arthropod assemblages in native perennial and non-native annual grass assemblages.

Kirsten Hill

Abstract

In California's grasslands, during the last 250 years, native perennial bunch grasses and forbs have been displaced by invasive annual grasses and forbs, dramatically altering the habitat and food availability for grassland invertebrates. I hypothesized that when compared to non-native annual grass assemblages, native perennial grass assemblages would sustain an greater abundance of sap-feeding insects, predatory arthropods, flower-feeding insects, and juvenile arthropods. I hypothesized that non-native annual grass senescence would encourage populations of scavenging arthropods and that arthropod diversity would be link with native plant diversity rather than overall plant diversity. I analyzed arthropod populations using observations and pitfall traps in transects that extended from the forest meadow boundary to the meadow interior (30m) and in sweep-net surveys of centrally located grassland patches dominated by either native or non-native grasses. Sap-feeding insects, predatory arthropods, and flower-feeding insect abundances were higher in plant assemblages dominated by native grasses. Flower-feeding insect abundance was largely dictated by Tumbling Flower beetles (*Mordellidae*), wasps (*Vespoideae*), and moths (Heterocera) whereas bees dispersed easily throughout the grassland. Mites were the only scavenging arthropod that increased with non-native annual grass cover; there was no effect of native plant cover on other scavenging species. These results suggest that native perennial grasses support the bulk of invertebrate activity during the driest months of the year and suggest that grassland habitat shrinks with increasing non-native annual grass cover.

Introduction

California's grasslands, prior to European settlement, were dominated by perennial grasses, but are now characterized by non-native annual grasses and alien forbs; recent estimates have placed the coverage of non-native plants at over 90% of the grasslands within the state. With this sea-change, the composition of invertebrates has also likely been reshaped. In fact, a recent review has confirmed that invasive plants negatively impact arthropod diversity (Spafford et al 2013). Arthropods rely on plants for food, shelter, and as a wellspring for their young. Interactions between arthropods and between arthropods and plants have been shown to promote plant diversity and their abundance affects higher trophic levels (Spiller and Schoener 1988, Schmitz 2008, Rogers et al 2012). Few data exist on the characteristics of invertebrate assemblages within the native and altered grasslands in California, and more information would aid in our understanding of these grassland food webs (see Porter et al 1996, 1997, Wolkovich et al 2009). Previous experimental studies of soil disturbance (Kotanen 1997) and rainfall timing in northern California's grasslands unveiled roles for disturbance and climate change in increasing non-native annual plant abundance, and in the case of climate change, also lowering arthropod species richness ((Suttle et al. 2007). Baseline data characterizing arthropod assemblages in native and non-native grassland within California will be useful to land managers and others seeking to understand the invaded grassland and develop restoration guidelines.

To better understand how arthropod populations have been affected by non-native annual grasses, the goal of this study was to describe the abundance of different functional groups of arthropods, and the diversity of arthropods in relation to areas of the grassland dominated by either native perennial or non-native annual grasses. Recent study of invaded habitats has revealed that arthropod diversity is strongly and negatively impacted by plant invasions, but information about these impacts is useful for assessing the overall impact and resilience of a given ecosystem (Spaffod et al 2013). This study was conducted during the hottest and driest period of the year when differences in the environment and available food is most sharply contrasted between patches of living native perennial and senescent non-native annual grasses. Many grassland arthropod populations reach peak abundance during this summer drought and living perennial grasses and forbs (mostly native plants within California grasslands) continue to face feeding pressure through the summer with unknown consequences (Joern 1989). I studied the effects of grass assemblage types on arthropod populations in a reserve in northern California within series of meadows, some of which support thriving stands of native perennials grasses; others are primarily dominated by non-native annual grasses. These meadows occur on elevated river terraces as isolated habitat islands within a forest mosaic. As such, they provide natural replicate habitats for study of grassland invertebrates.

Grassland characteristics

Functional arthropod groups. Non-native annual assemblages wither before the peak of summer drought and leave the soil and surroundings exposed to higher temperatures with scarce living shade, and few food resources. However, as non-native annuals senesce, they leave behind abundant seeds, dry plant matter, and other detritus. As a result, I predicted that scavenging arthropods would be more abundant here than in native perennial patches of grassland.

Native perennial grasses and other late blooming grassland plants (e.g. yampah (*Perideridia sp.)*, tarweed (*Hemizonia congesta*), vinegar weed (*Trichostema lanceolatum*), and yarrow (*Achillea millefolium*)) provide sap, pollen and nectar, to arthropods during the dry season. I predicted that sap and pollen feeders would be more abundant in stands of these late blooming forbs and living grasses than in senescing patches of non-native annuals.

I also expected to find that arthropod predators would be more abundant in patches of native perennial plants for three reasons. First, arthropod predators would track herbivorous prey in patches of native plants. Second, the structure of the native grasses would provide arthropods with shade and structure, creating refugia for arthropod predators sensitive to desiccation. Moist microclimates would be particularly important for juvenile arthropods sensitive to desiccation as they undergo molting (Hadley, 1994). Third, perennial assemblage structure would also provide refuges for small predatory arthropods (e.g., spiders) from larger predators (e.g., vertebrates).

Diversity. Many studies have shown that arthropod diversity increases with plant diversity (Castagneyrol and Jactel, 2012). Within this system, however, I predicted that arthropod diversity would not correlate with overall plant diversity but rather, native plant diversity. Most of the grasslands non-native plants senesce by mid-summer when arthropod populations reach peak activity. Furthermore, many types of herbivorous arthropods prefer native plants when given a choice between a known native and an unknown congener (Spafford et al 2013). I therefore expected that most herbivores and their potential prey would be found in native dominated areas of the grassland, and that their diversity would reflect the native plant diversity where they were collected.

Summarizing, I hypothesized that: 1) assemblages dominated by native perennial grasses and forbs would support more arthropod predators, sap-feeding insects, pollen-feeders, and juvenile arthropods (i.e. subject to molting or pupation) than non-native annual assemblages, 2) non-native assemblages would support more scavenging and detritivore species, such as mites, ants, and some beetles during the late summer season due to influx of seeds, dead insects, and decaying matter in senescing grassland patches, and 3) native dominated assemblages and those assemblages with greater native plant diversity (but not total plant diversity) would support a greater diversity (H') and richness of arthropod species than those areas of the meadows with less native plant diversity due to the fact that non-native plants, and those areas of the grassland that are less productive (e.g., senescent) tend to experience reduced herbivory and little if any attack from specialist herbivores (Spafford et al 2013).

Methods

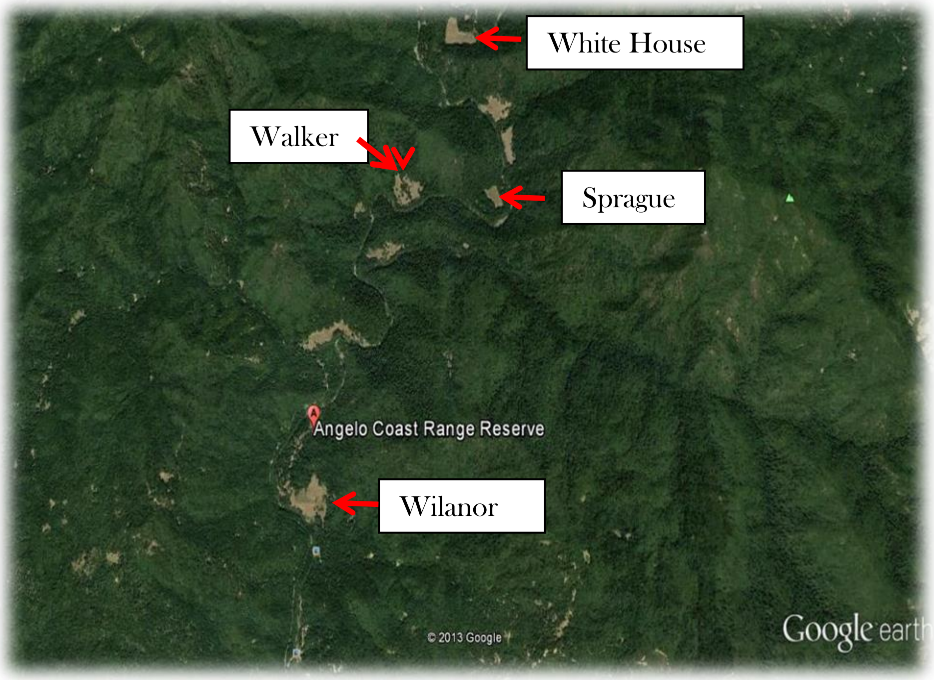
Study System

I compared the abundance and diversity of arthropods in native and non-native grass assemblages in three meadows of the Angelo Coast Range Reserve of Mendocino County California. This 3200 hectare reserve protects 6 km of the South Fork Eel River (39° 44' N, 123° 39'W), and is primarily forested with mature mixed Douglas fir-tanoak and Coastal Redwood. The climate has Mediterranean-like cool wet winters and long, hot, dry summers. Regional native meadow perennial grasses include *Danthonia californica, Elymus glaucus, Elymus multisetus, Festuca idahoensis, Festuca californica, and Bromus carinatus*. Dominant invasive annual grass species are *Bromus hordecious, Bromus diandrus, Bromus tectorum,* and *Avena barbata.* Some non-native plants that may also provide late season food include Star thistle (*Centaurea solstitialis*), and Common Plantain (*Plantago lanceolata*). The meadows in this reserve occur on elevated strath terraces near but well above the South Fork Eel River. These terraces were river floodplain that became abandoned as the river incised (Seidl and Dietrich 1992). Consequently, the meadows have a similar (flat) slopes and elevations with a thin soil veneer over the bedrock and alluvium of the former channel bed.

Grassland vegetation

Meadow boundary to interior transects In June 2010, I measured plant species cover along 14 transects (7 non-native and 7 native dominated) that extended 30 m from forest boundaries to meadow interiors. There were four to six transects in each of three meadows (Sprague, White House, and Wilanor Figure 1). Vegetation dominance (native, non-native) and percent cover by plant species were measured at 5-m intervals with standard point frame methods (Sutherland, 2004).

Figure 1: Meadows of the Angelo Coast Range Reserve



Percent cover (of Plant Sp. A) was estimated as the number of hits of Sp. A divided by the total number of points hit per plot x 100.

Meadow patches I also examined arthropod assemblages within native and non-native dominated grassland patches (range =158-2112 m^2 ,average size = 972 m^2) away from the woodland boundary ($\geq$ 10 m from woodland boundary) within three meadows. In June 2011, I measured plant species cover in 12 native and 12 non-native meadow patches; eight patches each in three meadows (Walker, Wilanor, and White House). The patches ranged in size (158 – 5346 m^2). I measured vegetation within the patches using bisecting transects and point frame counts at intervals of 5m (as described above). In total area, native patches encompassed 9157m^2 and non-native patches encompassed 13,100 m^2. The proportion of native plants found in each patch type was significantly different (non-native mean=33%, native mean=74%; t = -8.8, F = 2.6, df=22, $p<0.001$).

Arthropod assemblages

Meadow boundary to interior transects Two methods were used to characterize arthropod assemblages along transects. First, seven pitfall traps were placed along each 30-m transect at 5m intervals to capture spiders and other ground dwelling arthropods (98 total). As live traps, pitfall traps were left open for a 24 hour period. Small Douglas fir cones were placed in the traps to reduce predation. Second, I visually counted arthropods in each transect, every 5 meters, 2 minute per 1m^2 (daytime "scan samples" *sensu* Altmann 1974). Observations and trappings were conducted weekly (an average of eight observations and five trappings per transect) between June and September 2010. Arthropods were identified to species level, where possible, or grouped according to lowest recognizable taxonomic unit.

Meadow patches From June through August, 2011, arthropod assemblages were surveyed monthly in the twenty-four meadow patches using ten minute interval sweep-net sampling. After collection, samples were immediately taken to the lab for sorting to species level where possible. Samples not sorted immediately were frozen for future identification. All collections were preserved in 70% ethanol.

Data Analysis

ANCOVA for repeated measures were used to analyze the abundance of functional group of arthropods across transects for observations and pitfall traps. ANCOVA was used to analyze the average abundance of functional and taxonomic groups in patches with varying degrees of native plant cover (JMP® 2007). Abundance data was transformed to meet the assumptions of normality. Arthropod diversity was analyzed using the Shannon Diversity Index (H') and compared between transects and between patches, in relation to native plant cover and native plant diversity using regression analyses (JMP® 2007).

Functional groups were defined in the following manner. Predators included all arthropods known to prey upon other animals (arthropods or otherwise) in their primary feeding habits, these typically include spiders, Carabid beetles, Assassin bugs (*Reduviidae*) but also wasps that collect spiders and other insects to feed their young in their nests. Sap-feeding insects are those insects that pierce leaves or stems with their sharp, needle-like proboscis, feeding on the plant's fluids by sucking it out of the plant. Pollen and nectar feeding insects were defined as those insect species that primarily eat pollen or drink nectar from flowers for sustenance; these typically include bees, butterflies, moths, wasps and some beetles. Arthropods most vulnerable to stress or death from desiccation included hemimetabolous juvenile insects and juvenile spiders that need undergo molting; these species were labelled as vulnerables. Scavenging or detritivorous arthropods included those species known to feed on dead or decaying plant or animal matter and can include millipedes, mites, some species of beetles, ants, collembola and earthworms, among other species.

Results

Grassland vegetation

Meadow boundary to interior transects The proportion of native plants was significantly different between non-native and native designated transects (non-native mean=32%, native mean=79%; t=-9.9, df=10.3, p<0.0001).

Plants primarily found in non-native transects were the non-native grasses Aira *carophylla* (25%), *Vulpia myuros* (13%), *Bromus hordeaceaus* (8%), *Cynosurus echinatus* (2%), *Bromus diandrus* (1%) and the native grass *Danthonia californica* (24%). Common forb species in non-native transects included native *Hemizonia congesta* (4%) and *Lotus micranthus* (2%), naturalized *Galium aparine* (1%), and non-native *Plantago lanceolata* (5%) and *Hypocherus species* (6%).

Native transects were characterized by native grasses *Danthonia californica* (22%), and *Elymus glaucus* (17%), and various sedge species (13%). Common forb species found within native transects included native *Hemizonia congesta* (10%), *Lupinus formosus* (4%), *Vicia americana* (2%), and the naturalized *Galium aparine* (6%) (see Appendix 1; Table 1 for further details).

Meadow patches As in the transects described above, non-native meadow patches were composed primarily of the non-native grasses *Aira carophylla (*19%), *Bromus hordeaceus (11%)* and *Vulpia myuros (5%)* and the native grass *Danthonia californica (26%)* and sedges (14%). Forbs found in these patches included the non-native *Plantago lanceolata (*2%) and the native species *Trichostema lanceolatum* (4%) and *Hemizonia congesta* (2%) and the naturalized *Galium aparine* (3%).

Native patches were composed primarily of *Danthonia californica* (44%), sedges (14%), and *Elymus glaucus* (10%). Native forbs found in native patches were *Perideridia bolanderi* (2%), *Hemizonia congesta* (1%), and *Achillia millefolium* (1%). The non-native forbs *Plantago lanceolata, Galium aparine, Cirsium vulgare* and *Trifolium campestre* each comprised ≤ 1% of cover within these patches (Appendix 1; Table 2).

H 1: The abundance of predators, sap-feeders, pollen feeders, and vulnerable arthropods in relation to grass dominance type

Observations of functional groups in transects

I observed 2024 arthropods in 49 insect families in transects between June and September 2010 (species listed in Appendix 1; Figure 1). Observed sap-feeding insects increased with native plant cover (Figure 2). There was no effect of native plant cover on the observed number of pollen-nectar feeders (pollen and nectar feeders included: *Megachile, Osmia, Andrenid, A*pis and *Bombus* bee species; *Braconid, Halictid, Xylocopinae* and *Tenthrenidae* wasp species; *Meloidae* and *Mordellidae* beetles, and adult Lepidoptera), vulnerable life-stages (i.e., eggs and Lepidoptera larvae, *Tettigonidae, Caelifera* and *Grillidae* nymphs, *Araneae* juveniles).

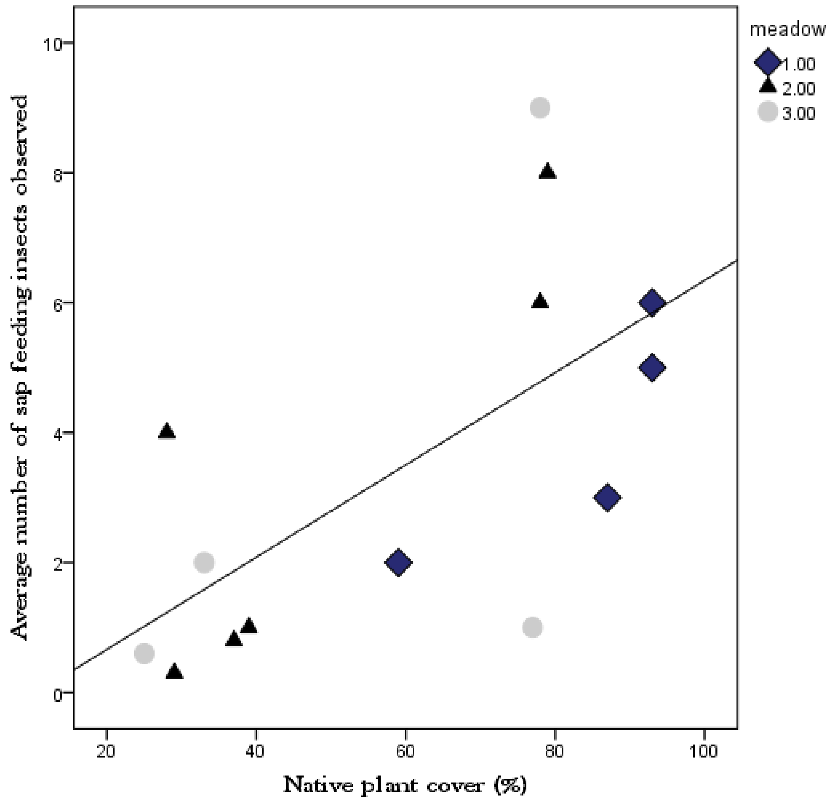


Figure 2: The average number of sap-feeding insects observed in relation to native plant cover (n = 410, R2 =0.56, F(1,13)=12.75, p < 0.01).

The abundance of predatory insects (*Melyridae* and *Coccinellida*e beetles, *Asildae* and *Therevidae* flies, *Reduviidae* bugs and *Sphecidae* wasps) was also not related to native plant cover (Fig. 5) (Species listed in Appendix 1; Figure 1). However, the number of spiders observed was positively associated with native plant cover (Fig. 3). Because spiders made up 70% of all observed predators, total arthropod predator numbers were strongly correlated with native plant cover (Fig. 4).

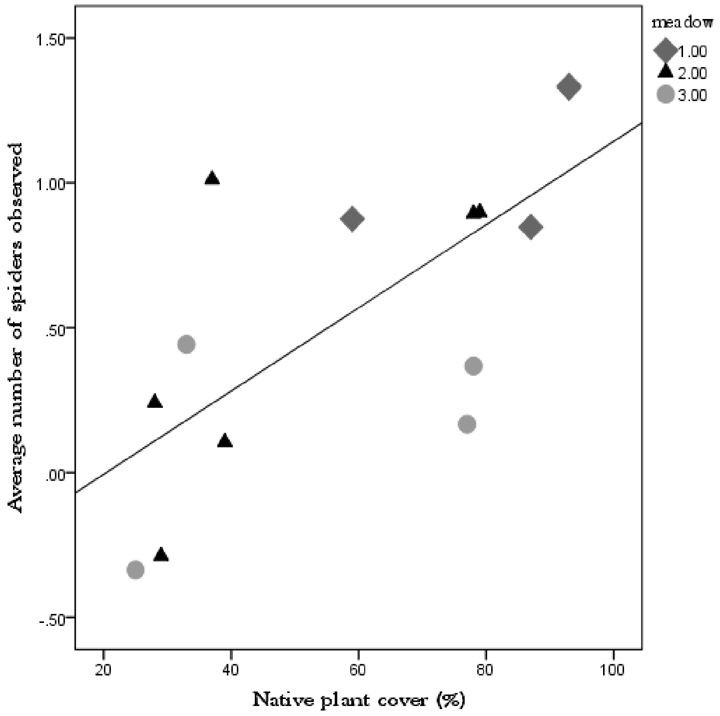


Figure 3: The average number of spiders observed in relation to native plant cover. (R^2 =0.66, F(1,13) = 5.38, $p < 0.05$)

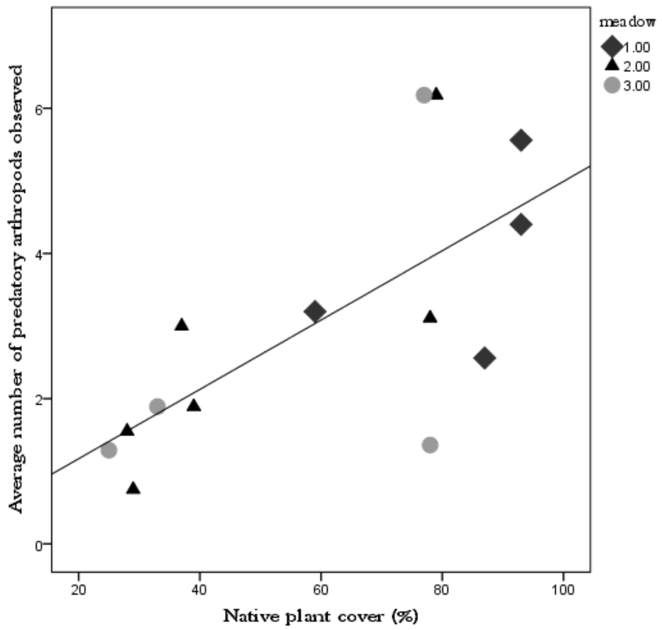


Figure 4: The number of arthropod predators observed in relation to native plant cover (R^2 =0.47 F(1,13)=7.69, p= 0.02).

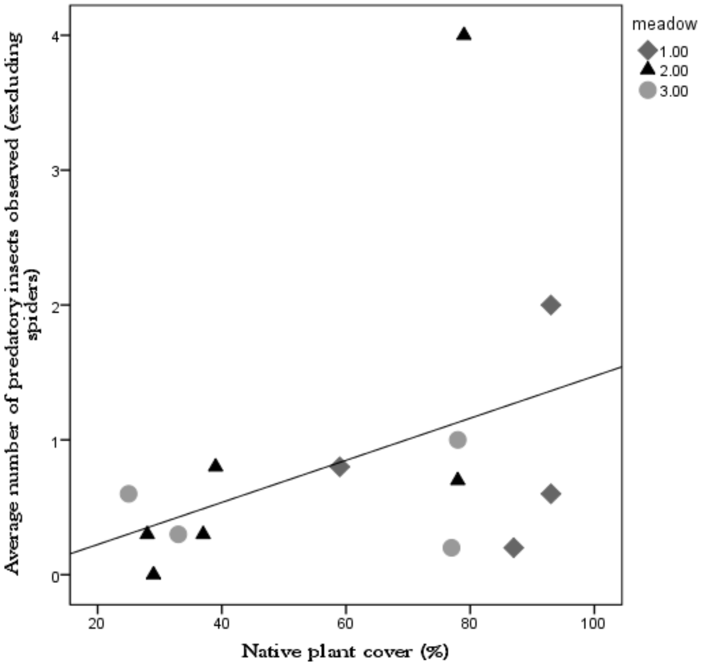


Figure 5: The relationships between arthropod predators (*sans* spiders) observed in relation to native plant cover. (R^2 =0.28, F(1.13) = 3.44, p = 0.09)

Observations of arthropod family and species in transects

Among sap-feeding insects, Tarnished plant bugs (*Lygus hesperus),* Shield-back bugs (Heteroptera *Scutelleridae),* and leafhoppers (Hemiptera *Cicadellidae*) increased with native plant cover (Fig. 6). Tarnished plant bugs were frequently observed on Tarweed (*Hemizonia congesta).* Shield-back bugs were observed clinging to the stems of perennial grass culms, usually on the peduncle. There was no effect of native plant cover on other major family groups of arthropods found in functional groups, including ants (Hymenoptera *Formicidae*), ladybugs (Coleoptera *Coccinellidae*) or grasshopper nymphs (Orthoptera *Caelifera*).

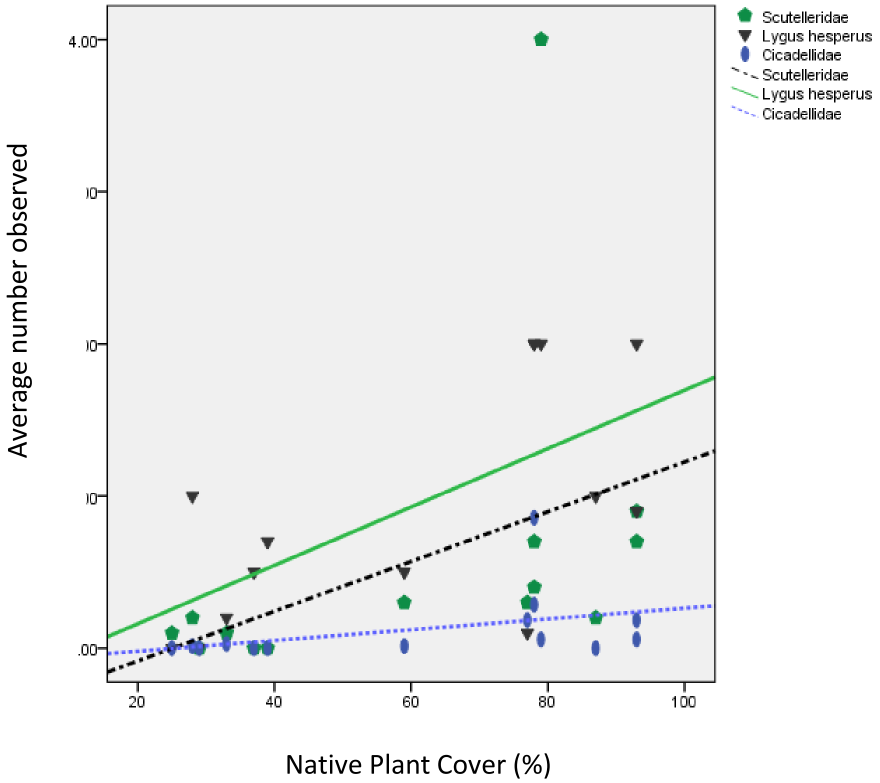


Figure 6: Observed Tarnished plant bug (F(3,13) = 9.6, p=0.01), Shield-back bugs (F (3,13) = 4.9, p=0.05), and Leafhoppers (F(3,13)=6.75, p = 0.03) in relation to native plant cover.

Functional groups captured in pitfall traps

I captured 833 arthropods in pitfall traps between June and September 2010. The average number of predators (n=296) that were captured in pitfall traps increased with native plant cover (Assassin bugs, Big-eyed bugs (Geocoridae), Carabid beetles, Harvestmen (Opiliones), Sphecid wasps, spiders, and Soft-winged flower beetles (Melyridae))(Fig.7). Juvenile spiders comprised the largest proportion of predators (49%) (Appendix 1; Table 3).

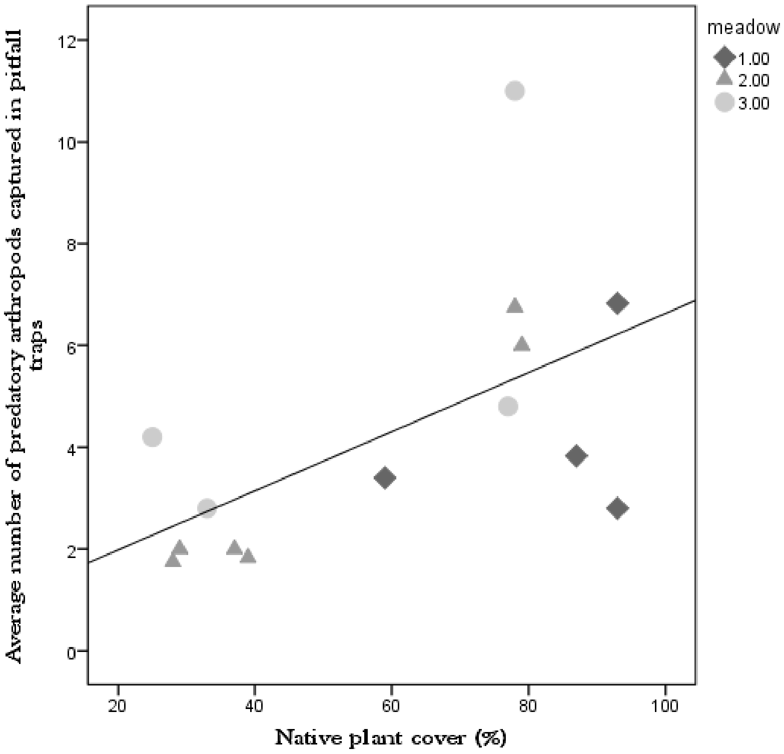


Figure 7: Arthropod predators captured in pitfall traps increased with native plant cover, (R^2=0.62, F(1.13) = 9.97, p = 0.01)

The average number of juvenile arthropods (n = 154) (which included caterpillars, spiderlings, and cricket nymphs) captured in pitfall traps increased with native plant cover (Fig. 8). Juvenile spiders comprised the bulk of these arthropods captured (96%). There was no effect of native plant cover on sap or pollen-feeding insects captured in pitfall traps as very few were captured.

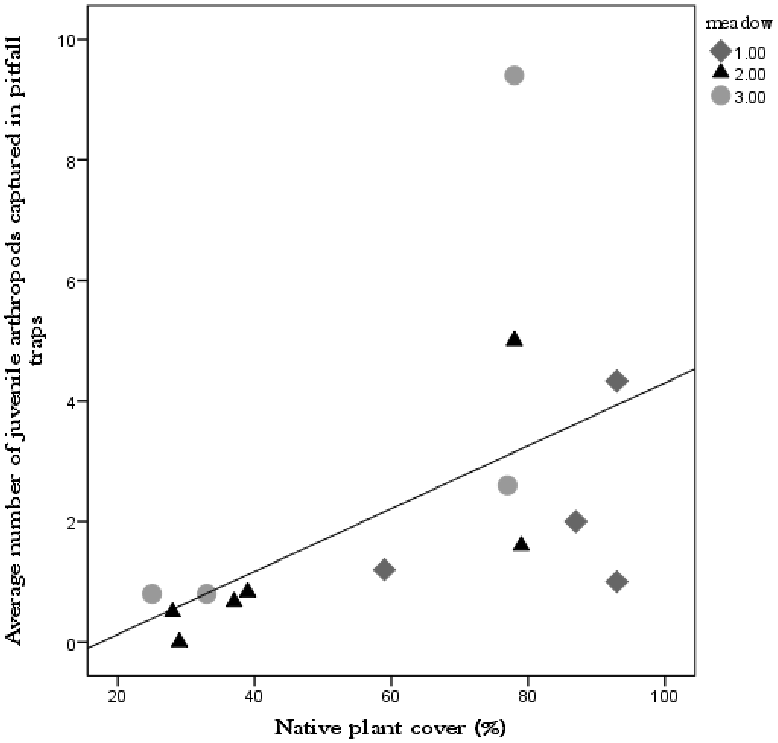


Figure 8: Juvenile arthropods captured in pitfall traps increased with native plant cover, (R^2 = 0.54, F(1,13)=9.16, p = 0.01).

Functional groups captured in sweep-net surveys of meadow patches

In total, I captured 27,675 arthropods in sweep-net surveys (Appendix 1; Figure 3). Predator abundance, excluding spiders, (n=402) but including *Carabidae, Coccinellidae, Melyridae* beetles; *Geocoridae, Reduviidae* bugs; *Sciomyzidae* (43%) and *Asilidae* flies; *Neuroptera, Raphidioptera, Mantodea* and *Pompilid* wasps increased with native plant cover (Fig. 9). Spider abundance also increased with native plant cover (Fig. 12). Sap-feeders (Hemipteran insects such as *Fulgoroidea, Lygus, Miridae, Membracidae, Nysius* and *Pentatomidae* increased with native plant cover (Fig. 10). Different from observations described earlier, pollen/nectar feeding insects caught in sweep-net surveys, (n = 623); largely *Vespoidea* (wasps) (35%) and *Mordellidae* beetles (30%) but including all *Anthophila,* and adult *Lepidoptera*) increased with native plant cover (Fig. 11). There was no effect of native plant cover on numbers of arthropods in vulnerable stages (n=6653) including, as a group, caterpillars, juvenile *Lygus* sp. bugs (57%) and juvenile spiders (42%) collected in sweep nets.

Figure 9: Predators

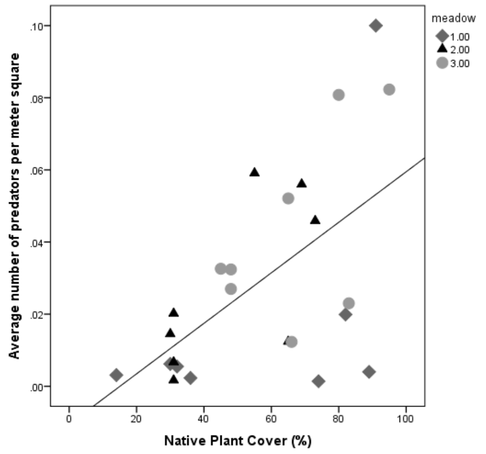


Figure 10: Sap-feeders

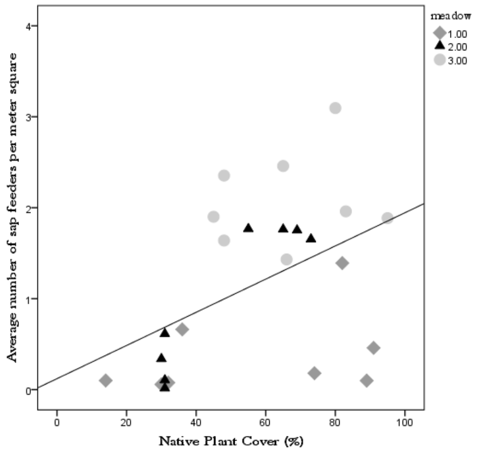


Figure 11: Flower-feeders

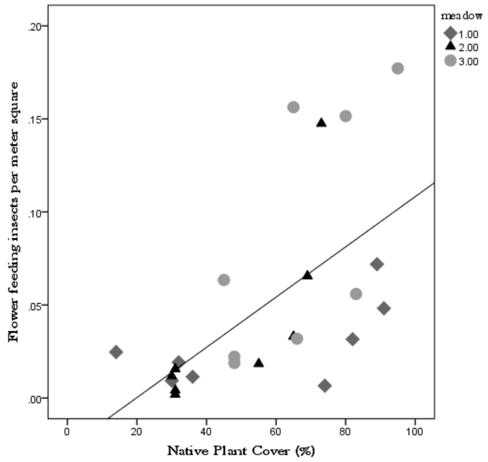
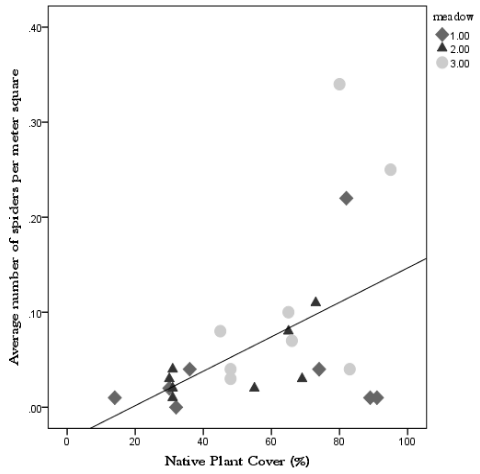


Figure 12: Spiders



Figures 9 - 12: Sweep-net surveys of functional group abundances. Predators, excluding spiders, increased with increasing native plant cover (n =402, R^2 = 0.49, F(1,23) = 7.10, p = 0.01). Sap-feeding insects increased with increasing native plant cover (n= 15,829, R^2 = 0.42, F(1,23)=6.54, p = 0.02). Pollen/nectar feeders increased with increasing native plant cover (n =623 R^2 = 0.52, F(1,23)=12.5, p = 0.002). Spider abundance increased with increasing native plant cover (n =3673, R^2 = 0.44, F(1,23)=5.84, p = 0.02).

Arthropod families and species captured in sweep-net surveys

Within non-native patches, one-third (33%) of the arthropods captured were Hemipterans (*Lygus* sp.). Grasshoppers were the second most abundant (16%), followed by leafhoppers (9%). Native patches harbored greater numbers of leafhoppers [Cicadellidae], which made up the largest numerical portion of all insects in native patches (45%). The second largest group captured was spiders (mostly juvenile spiders) (14%). Juvenile spider abundance increased with native plant cover (Fig. 13). Katydids (8.4%) were also more abundant in native plant patches (see Appendix 1; Table 5 for further details).

Few individuals of most individual predator species were captured, precluding statistical testing at this population scale. The exception was *Sciomyzidae* flies, a predator during its larval stage that feeds on gastropods, adult food is unknown but eggs are layed on snails or slugs. These flies were most abundant in June (67% were captured in June) and their abundance increased with native plant cover (Fig. 16).

Among sap-feeding insects, leafhoppers (*Cicadellidae*) abundance increased with native plant cover (Fig. 14). Scutelleridae also increased with native plant cover (Fig. 15). Juvenile Hemipterans (likely *Lygus hespersus*) did not increase with native plant cover, but showed a trend towards increasing with non-native plant cover (F(1,23) = 3.05, p = 0.09).

Within the pollen/nectar feedings insects, bees were fairly evenly distributed across patch types. Bees were frequently observed to be visiting late blooming Vinegar weed (*Trichostema lanceolatum)* and California Poppy (*Eschoscholizia californica)* found in areas where non-native annual grasses also thrive. Beetles (*Mordellidae)* and wasps (*Vespoideae*) were observed in native dominated patches where Yampah (*Perideridia sp)* blooms in mid to late summer.

Figure 13: Juvenile spiders (*Araneae)*

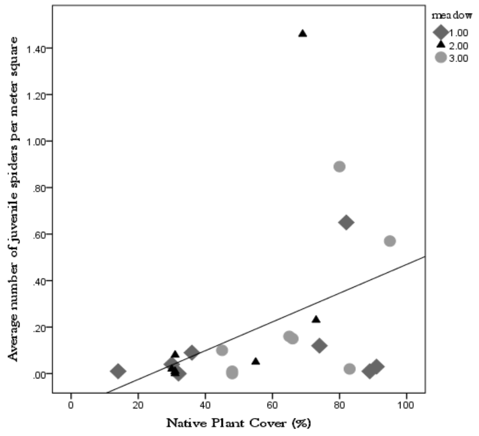


Figure 14:Leafhoppers (*Cicadellidae*)

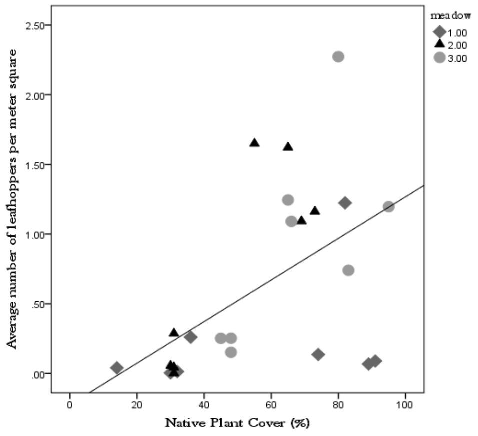


Figure 15: Shield-bugs (*Scutelleridae*)

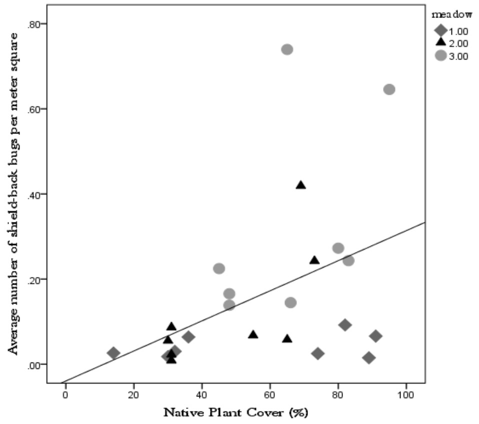
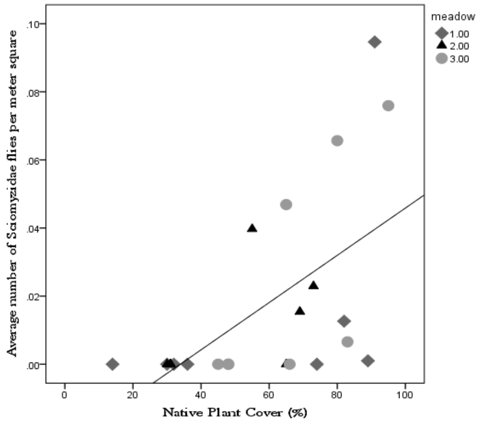


Figure 16: Marsh Flies (*Sciomyzidae*)



Figures 13 -16: Arthropod species groups captured in sweep-net surveys. Juvenile spiders increased with increasing native plant cover (n = 2815, R^2= 0.26, F (1,20) =4.7, p = 0.04). Leafhoppers increased with native plant cover (n =9034, R^2 = 0.46, F(1,23) = 12.25, p=0.002). Shield-back bugs increased with native plant cover (n =1781, R^2 = 0.61, F(1,23=5.4, p = 0.03). Marsh flies increased with increasing native plant cover (n =174, R^2 = 0.36, F(1,23)=9.54, p = 0.006).

H.2: Scavenging arthropods

Observations of scavenging arthropods in transects There was no effect of composition of plant cover on the observed number of scavenging arthropods (mites, ants, sow-bugs (Isopoda) or Dermestid beetles (Appendix 1).

Scavenging arthropods captured in pitfall traps There was no effect of native plant cover on the total abundance of scavenging arthropods captured in pitfall traps (n =536, $R^2 = 0.39$, F(1,13) = 2.17, p = 0.17); this included ants, mites, millepedes, Tenebrionid beetles, Sow-bugs (Isopoda) and jumping bristletails (Microcoryphia).

Scavenging arthropods family and species captured in pitfall traps

Different from the bulk of scavenging species, Mites (Acari) increased with non-native annual plant cover (Fig.17). There was no effect of grass assemblage on ants or isopods captured in pitfall traps.

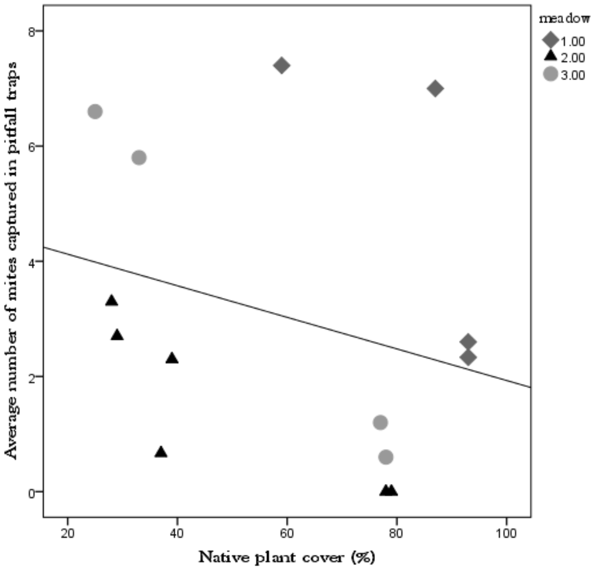


Figure 17: Mites (Acari) captured in in pitfall traps, decreased with increasing native plant cover (n = 214, $R^2 = 0.80$, F(1,13)=23.5, p <0.001)

Scavenging arthopods captured in sweep-net surveys Very few scavenging arthropods were captured in sweep-net surveys, and other than 7 mites, all were ants (n=783). Ants were not affected by native plant cover (F(1,23)=1.09, p=0.31).

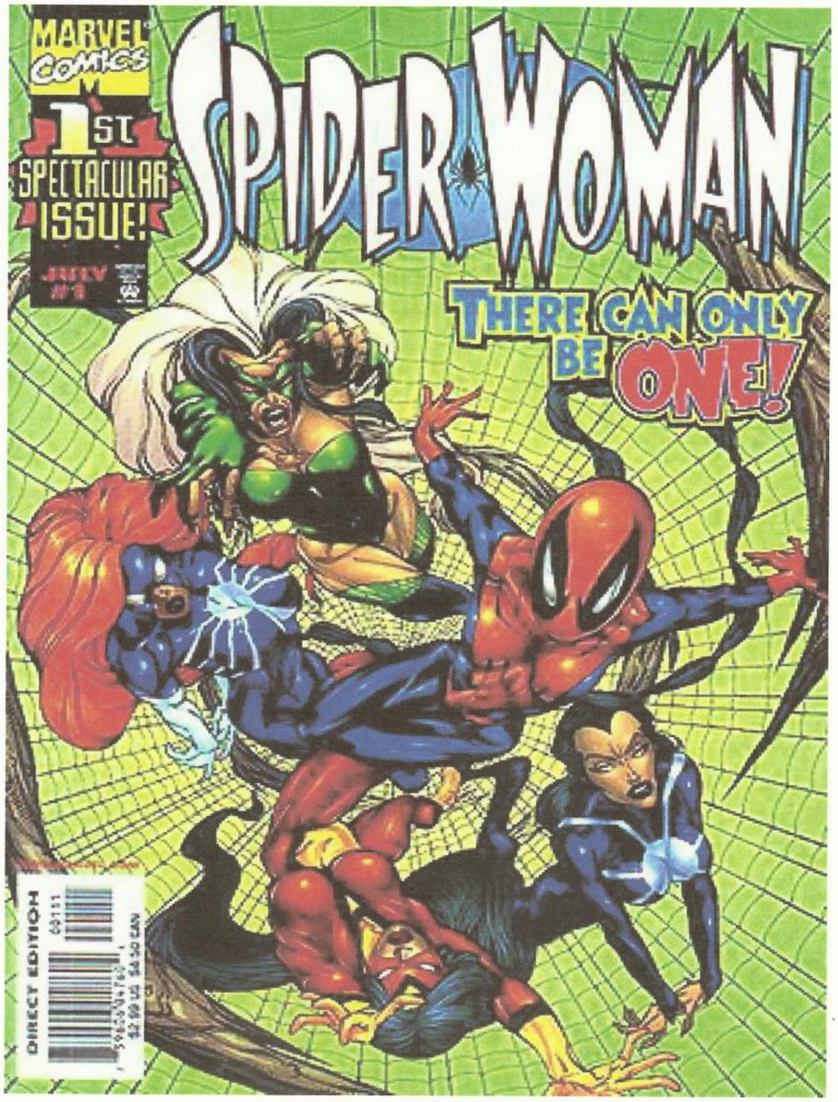


Figure 18: The author is congratulated by Spider Woman for the completion of her dissertation uncovering the role of native grasses in protecting grassland spider populations.

Table 1: Results of ANCOVA (*F* values) of the effect of native plant cover (NPC) on functional and taxonomic groups of species in grasslands of the Angelo Coast Range Reserve.

Functional group	df	Response to NPC	Observations	df	Pitfall Trapping	df	Sweep-net Survey
Predators	13	+	7.69*	13	9.97**	23	7.10**
Spiders (*Araneae*)	13	+	5.38*	13	5.63*	23	5.84*
Marsh Flies (*Sciomyzidae*)	13	+	na	13	na	23	9.54**
Vulnerable arthropods	13	+	0.081	13	9.16**	23	0.052
Spiderlings	13	+	2.70	13	2.31	23	4.70*
Sap-feeders	13	+	12.75**	13	na	23	6.54*
Cicadellidae	13	+	6.75*	13	na	23	12.25**
Scutelleridae	13	+	4.9*	13	na	23	5.4*
Lygus hesperus	13	˜/+	9.6**	13	na	23	.005
Flower-feeders	13	˜/+	0.012	13	na	23	12.50**
Scavengers	13	˜	na	13	2.17	23	na
Mites (Acari)	13	---	na	13	23.47**	23	na

Notes: na = small samples sizes precluding statistical analysis.

Response to native plant cover: (*+*) = positive, increased with increasing native cover; (--) = negative, increased with non-native cover; (˜) = ambiguous, no clear directional response. $^{*}P \leq 0.05$: $^{**}P \leq 0.01$.

H 3: Native dominated assemblages and those areas of the grassland with greater native plant diversity support a greater diversity (H') and richness of arthropod species than those areas of the meadows with less native plant diversity and native plant cover.

Diversity (evenness and richness) of arthropods observed in transects

There was no effect of native plant cover on observed arthropod richness. There was a trend toward an increase in observed arthropod evenness with increased native plant cover (H') but no effect of native plant diversity on the evenness of arthropods observed (Fig. 19).

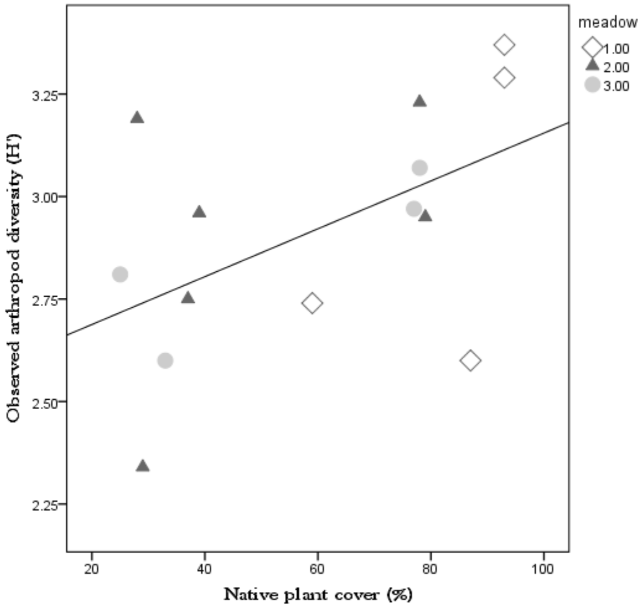


Figure 19: Observed arthropod diversity (H') in relation to native plant cover (F(1,13) = 3.87, p = 0.08)

Diversity and evenness of arthropods captured in pitfall traps

There was no effect of native plant cover or native plant diversity on the richness or evenness of arthropods captured in pitfall traps.

Diversity (evenness and richness) of arthropods captured in sweep-net surveys

Sweep-net surveys revealed that arthropod diversity (H’) *decreased* with increasing native plant cover (Fig. 20). Native grasses such as *Danthonia californica* and *Elymus glaucus* predominated patches with greater native plant coverage. There was a trend toward increased arthropod richness with increasing native plant cover (Fig. 21) but richness was also affected by meadow ($F(1,23) = 6.7$, $p < 0.01$). The White-house meadow had the lowest average richness (33), followed by Wilanor (36) and Walker (45). This trend was different for species evenness; White-house (2.26), Walker (2.20), and Wilanor (2.03).

Arthopod diversity *increased* with increasing native plant diversity (evenness = H’) (Fig. 22). Those areas that were not as densely inhabited by native grasses, as described above, were sometimes characterized by a greater diversity of native forbs, including California poppy, Tarweed, Bird’s foot trefoil, Cup clover, various Lupine species, Vinegar weed, Yarrow, and Wild strawberry, intermingled with non-native grasses (Appendix 1; Table 2). Measures of overall plant diversity (H’) did not siginficantly affect arthropod diversity ($p = 0.15$), rather arthropod diversity was effected more specifically by native plant diversity.

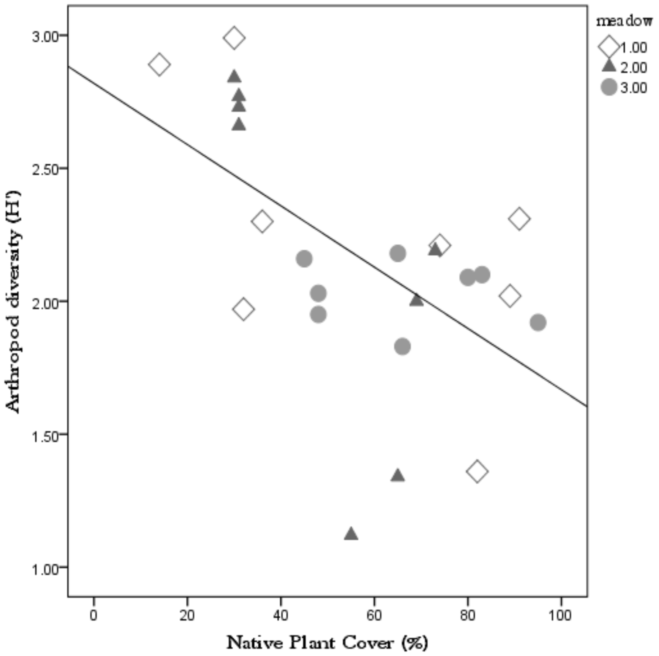


Figure 20: Sweep-net results of arthropod diversity (H') in relation to native plant cover, (F(1,23) = 8.97,p < 0.01)

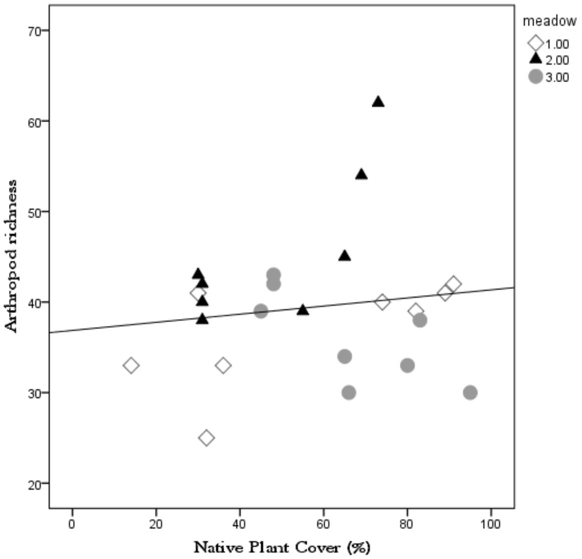


Figure 21: Sweep-net survey arthropod richness in relation to native plant cover (F(1,23) = 3.26, p = 0.08)

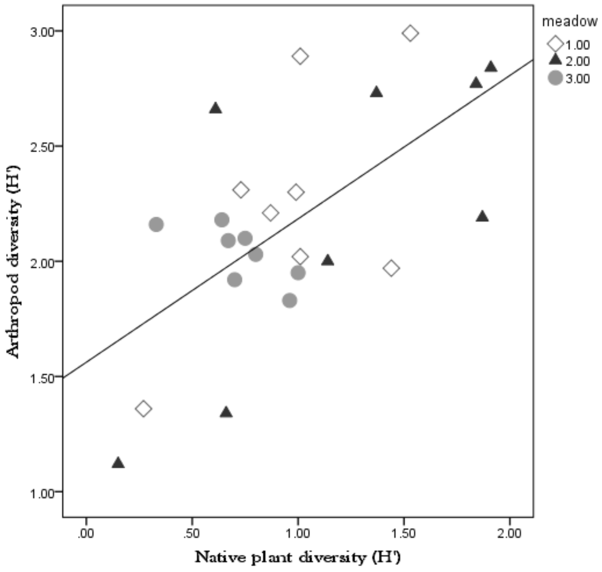


Figure 22: Sweep-net survey, arthopod diversity (H') in relation to native plant diversity ($R^2 = 0.60$, $\beta = 0.71$, $p = 0.002$)

Discussion

As predicted, the resources (food, and shelter) of living perennial grasses and other forbs, native dominated assemblages of the grassland did support a greater abundance of predators, sap-feeding insects, pollen and nectar feeders (particularly some moths, beetles, and wasps). Predator guilds were dominated by spiders, which were found predominantly in native plant dominated areas of grasslands. Sweep-net surveys of grassland patches proved most effective in capturing all predators, although observations and pitfall trapping also proved effective in capturing spiders. Predatory flies captured in sweep-net surveys, and juvenile spiders observed, captured in pitfall traps, and captured in sweep-net surveys, had the greatest occurrence of any of the predators found within the grassland. Different from other predators, assassin beetles (*Reduviidae*) occurred at higher frequencies in non-native dominated areas of the grassland than other predators (Appendix 1; Figure 2). Frequently, native dominated areas of the grassland, where more predators occurred, were dominated primarily the native grasses *Danthonia californica* and *Elymus glaucus.* These grasses provide shade and habitat structure and likely protection from desiccation; this may explain why so many juvenile spiders were found in these areas. These areas of the grassland are also a source of abundant prey, particularly leafhoppers, which may be important prey for juvenile spiders.

In general, vulnerable juvenile arthropods, captured in sweep-net surveys and observed, did not show a clear response to native plant cover. The strong exception to this was for juvenile (vulnerable) arthropods captured in pitfall traps, the bulk of these were juvenile spiders that were found in stands of native grasses. As described above, this habitat likely provides protection from desiccation and predators, and abundant small prey.

Sap-feeding insects were generally more abundant in native dominated areas of the grassland. I did find that native assemblages did not necessarily support one of the most abundant sap-feeders, the Tarnished plant bug (*Lygus hesperus),* which I observed frequently on Tarweed (*Hemizonia congesta*) in drier areas of the grassland that supported non-native grasses. However, this evidence, together, suggests that sap-feeding insects continue to rely primarily on native plants for sustenance through the dry season. Sap-feeding insect abundance was captured effectively through observations and sweep-net surveys of the grassland.

With the exception of bees, which appeared to disperse easily throughout the grassland to collect available pollen/nectar sources from the forbs found in drier areas of the grassland, (such as the late blooming Vinegar weed, California poppy, and Tarweed) other flower-feeding insects including Lepidoptera (moths), wasps, and *Mordellidae* beetles, were more abundant in native dominated areas of the grassland. Within native grass stands, Yampah and Birds foot trefoil (*Lotus purshianus*) and patches of Summer Lupine (*Lupine formosus)* occurred with greater frequency than elsewhere in the grassland. Sweep-net surveys of the grassland effectively captured the difference in abundance among the pollen and nectar feeding species in the two grassland patch types. Observations of pollen and nectar feeding insects revealed no difference between the assemblages. This evidence suggests that their abundance may be specific to particular species of flowering plants that were not evenly dispersed through the grassland but more clumped, such as the Yampah. Many moths were found among dense stands of sedges; these moist areas of the grassland may support larval growth and adults from predation.

My hypothesis that scavenging arthropods would increase with non-native plant cover was not supported, with the exception of mites. All scavenging arthropods were most effectively captured through pitfall traps. Some scavenging species captured more frequently in native dominated areas of the grassland included sow-bugs and millipedes, which are likely less tolerant of desiccation. This intolerance may have reflected in the overall low abundance of scavengers found in non-native dominated areas of the grassland. Scavenging arthropods were rarely observed or caught in sweep-net surveys.

Arthropod diversity, which included native and non-native arthropods, was not necessarily supported by increasing native plant cover. Previous studies have shown arthropod diversity increases with increasing plant diversity. In this study system, however, native plant diversity did not equate with native plant diversity, as some areas of the grassland with high native plant cover were characterized by mono-specific stands of native perennial grasses, mostly *Danthonia californica* but also *Elymus glaucus*. While these stands are important habitats for pollinators, predators, juvenile arthropods, and sap-feeding insects; they did not support as many native forbs as other grassland patches, likely reducing local diversity of arthropods. There was a trend toward increased arthropod diversity observed in transects with increasing native plant cover ($p = 0.08$). Pitfall trapping and sweep-net surveys did not confirm this trend.

There was a relationship between native plant diversity and arthropod (both native and non-native arthropod) diversity (H') for those arthropods caught in sweep-net surveys. Arthropod diversity increased with native plant diversity but not overall plant diversity. Between June and July, non-native annual plants senesce, leaving native perennial grasses and late-blooming and long-lived native plants for food. Previous research has found that native arthropods prefer native over introduced host species (see Spafford et al. 2013 for review). The results from findings of this study suggest that 250 years after initial invasion by non-native annual grasses, most herbivorous arthropods, (including non-native arthropods), are relying on remnant native plants that survive in a dwindling habitat range.

Of the three methods utilized to understand arthropod assemblages in the grassland, sweep-net surveys were the most thorough in capturing the abundance and diversity of arthropods residing in the grassland canopy. Pitfall trapping was the most useful method for capturing ground-dwelling arthropod activity that was not evidenced through sweep-net surveys. Observations were helpful for capturing the activity of some invertebrates and getting a sense of invertebrate diversity but as a single method this did not prove to be most powerful for capturing the activity of canopy or ground dwelling arthropods. The three methods worked well together to confirm or counter findings from the other methods used and together made a good combination for a more complete understanding of arthropod activity within the grassland.

These results highlight the importance of patchiness and scale in the grassland landscape. Many of the open drier areas of the meadows supported a variety of forb species that were not abundant within dense stands of native perennial grasses. Mosaics with some areas dominated by native perennial grasses and some by native forbs supported more grassland arthropods of diverse functional groups. Comparisons with California's other grasslands are needed, but these results suggest that where non-native annual grasses dominate, critical drought-refugia and habitat for native arthropod predators, pollinators, and juvenile arthropods is also disappearing, with unknown effects for higher trophic levels that depend on grassland arthropods for survival. Statewide surveys of arthropod populations in California's grasslands would be helpful in generating a fuller understanding of how their populations respond to native and non-native plant cover. More investigation of landscape scale habitat mosaics could also reveal how bird, lizard, and other mammalian predators have been affected by shifts in grassland arthropod populations.

Chapter 2

Characteristics of wandering spiders and their potential prey in meadows with native and non-native grasses.

Kirsten Hill

Abstract

Wandering spiders are good indicators of microhabitat change; each species has different temperature and humidity requirements and responds differently to litter, vegetation and other habitat characteristics. In California's grasslands, during the last 250 years, native perennial bunch grasses and forbs have been displaced by invasive annual grasses and forbs, dramatically altering the habitat and food availability for grassland invertebrates. I hypothesized native perennial grass tussocks and assemblages would sustain more vertical structure and cooler microhabitats during mid and late summer; therefore supporting more prey, particularly leafhoppers, and provide cover for spiders (particularly small spiders that may be escaping larger predators), allowing them to forage further from the forest-meadow boundary. I analyzed spider populations using pitfall traps in transects that extended from the forest meadow boundary to the meadow interior (30m) and in sweep-net surveys of centrally located grassland patches dominated by either native or non-native grasses. Spider abundance was higher in plant assemblages dominated by native grasses and higher in interior portions of the meadow in native than in non-native transects. Leafhopper abundance and native plant diversity were the best predictors of hatchling and juvenile spider abundance in meadow patches. Spiderling abundance was greatest in areas of the grassland with greater native plant coverage and lower native plant diversity. These areas of the grassland supported solid stands of native perennial grasses. These results suggest that native perennial grasses act as incubators for fledgling spiders and as such support the grassland predator community that can facilitate trophic interactions and native plant diversity.

Introduction

Nonnative plants are altering the structure and function of terrestrial ecosystems worldwide, with impacts on native plants, including their associations and interactions with arthropods. In California's grasslands, during the last 250 years, native perennial bunch grasses and forbs have been displaced by invasive annual grasses and forbs. Some of the non-natives and invasive plants were originally brought by Europeans for domestic animal fodder but many accidental seed introductions have since taken hold. The resulting invasion has dramatically altered the habitat by reducing native plant cover to less than 10 percent of the former range and changed the face of food availability for grassland invertebrates. The consequences of this invasion have been documented for soil microbial systems, rates of nutrient cycling, hydrological regimes, and bird and mammal populations (Stromberg et al. 2007). The impacts of this invasion on arthropod populations in California's grassland have been less studied, and may be complicated by context-dependencies. Recent studies have shown that the effects of plant invasions on invertebrates and their ecological interactions can change, sometimes qualitatively, from site to site (Fork 2010, Litt and Steidl 2010, Pearson 2009, Rzanny and Voigt 2012, Tang et al 2012) pointing to the need for further study. Here, we investigate effects of the transition from perennial to annual grass on wandering spiders (Gnaphosidae, Lycosidae, Oxyopidae, Thomisidae and others) and their prey.

As predators, spiders can affect community structure and function through trophic cascades (Schmitz 1998, Danner and Joern 2003). Wandering spiders are also good indicators of microhabitat change; each species has different temperature and humidity requirements and responds differently to litter, vegetation and other habitat characteristics (Wise, 1993). Wandering spiders and particularly juvenile or small wandering spiders are often more sensitive to desiccation than web building spiders as these web building spiders usually have a shelter for hotter portions of the day (Foelix 2010). Juvenile wandering spiders are abundant in habitats with greater refugia from predators (e.g. protection from conspecific spider cannibalism) and more small prey (DeVito and Formanowicz 2003, Foelix 2010, Schmidt and Rypstra 2010, Rodrigues and Mendonca 2012). Many wandering spiders that hunt in grasslands may reside in the shaded boundary or woodland and grassland edges, moving into more exposed areas for limited periods to forage (Suttle 2005). California's native perennial grass assemblages are likely to offer spiders more cover and favorable microclimates than senescent annual grasses that wither and flatten during the hottest and driest summer months.

In addition to providing refuge from other predators and shade from the hot sun, perennial grasses can sustain small prey that feed off the living plant tissue (Finke and Denno 2006, Malumbres Olarte et al 2013). For example, sap-feeding leafhoppers [Cicadellidae] (Wise 1993, Lewis and Denno 2009, Virant-Doberlet et al 2011, Barrion et al. 2012, Bartos and Szczepko 2012) are important components of grassland spider diets, and may be critical prey for juvenile spiders incapable of attacking larger arthropods. Adult leafhoppers abound in the early summer in California's native grasslands, and some species of hatchlings emerge in the late summer season to overwinter as adults (K.Hill pers. observation, Nault et al, 1985). Adult wolf spiders may prey on the abundant juvenile grasshoppers and katydids (3-11mm in length) but may also catch adult orthopterans. Hungry spiders would be predicted to track leafhoppers, orthopterans, and other prey across the invaded grassland.

I hypothesized that relative to withered annual grasses, native perennial grass tussocks and assemblages would:

(H1) sustain more vertical structure and cooler microhabitats during mid and late summer;

(H2) support more prey, particularly leafhoppers, throughout the late summer.

(H3) provide cover for spiders (particularly small spiders), allowing them to forage further from shaded meadow boundaries into meadow interiors than they could in grass assemblages dominated by annual grasses.

As a result of all of these effects, I predicted that where perennial grasses dominated, meadows would support a more abundant and diverse spider guild than nonnative annual grass assemblages; and that indirect protective effects of spiders on plants might be more apparent.

Methods

Study System

I studied wandering spiders and their potential prey in meadows of the Angelo Coast Range Reserve (39° 44' N, 123° 39'W) of Mendocino County California. This 3200 hectare reserve protects 6 km of the South Fork Eel River, and is primarily mature forest of mixed Douglas fir (*Pseudotsuga menziesii*)-Tanoak(*Notholithocarpus densiflorus*) and Coastal Redwood (*Sequoia sempervirens*). The climate has Mediterranean-like cool wet winters and long, hot, dry summers. The meadows in this reserve are perched on high strath terraces that flank the South Fork Eel River (39° 44' N, 123° 39'W). These terrace meadows have a similar flat slope and elevations with thin soils that were originally cut into bedrock as floodplains along the S. Fk. Eel River, but later became abandoned strath terrace surfaces as the river incised (Seidl and Dietrich 1992). Regional native meadow perennial grasses include *Danthonia californica, Elymus glaucus, Elymus multisetus, Festuca idahoensis, Festuca californica, and Bromus carinatus*. Dominant invasive annual grass species are *Bromus hordecious, Bromus diandrus, Bromus tectorum,* and *Avena barbata*.

I compared the abundance and diversity of wandering spiders and the abundance of potential prey (leafhoppers, plant-bugs, grasshoppers and katydids) in native and non-native grass assemblages on a weekly basis between June and August, within transects extending from forest boundaries to meadow interiors in the three meadows. I also examined wandering spider assemblages within native and non-native dominated grassland patches (average size of 972 m^2) with monthly sweep-net surveys located away from the woodland boundary ($\geq$ 10 m from woodland boundary) within each of the three meadows.

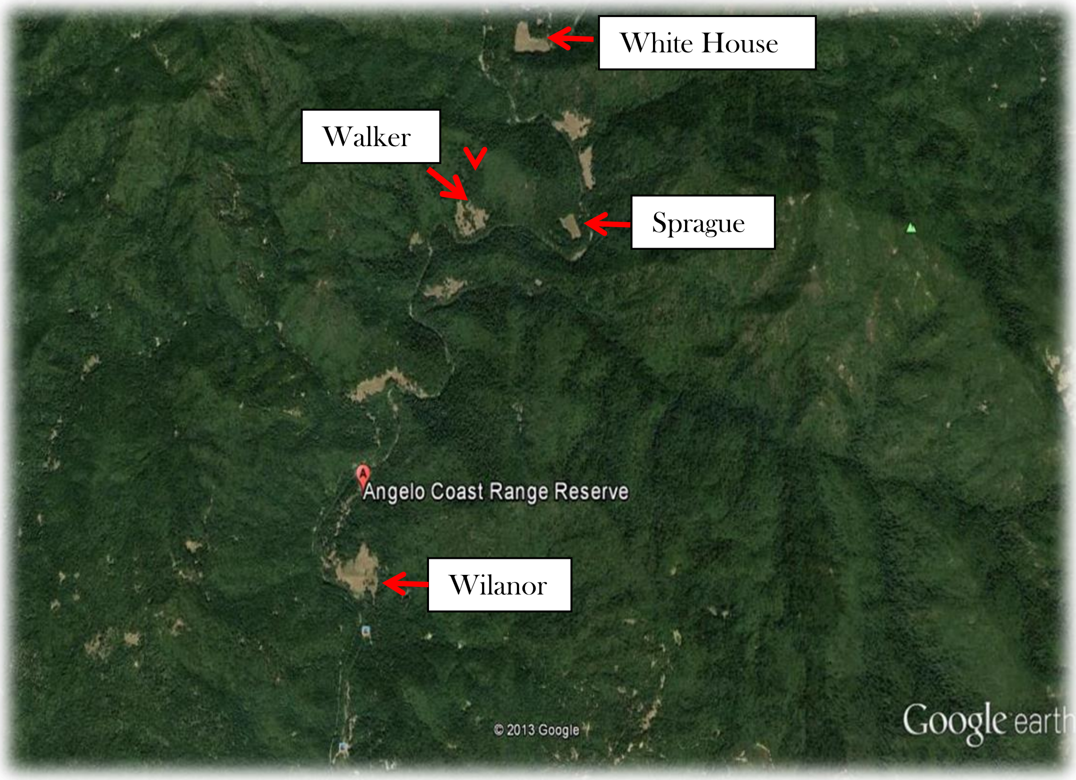
Potential spider prey

Angelo Coast Range Reserve's grasslands are home to the Devastating grasshopper (*Melanoplus devastator*) and several other less dominant grasshoppers such as *Camnula pellucida, Melanoplus sanguinipes,* and *Opeia obscura.* The meadows are also home to the non-native katydid (*Tessellana tessellata),* a native to Europe and northern Africa. It was first described in California in 1955 (Biyoekolojisi S. P. C. O. T. 2006). I observed in the field and in experiment that both grasshoppers and katydids are potential prey for large wandering spiders (e.g., the dominant wolf spider, *Schizocosa mccooki*). Sap-feeding plant bugs of which, other than leafhoppers, the most abundant in this grassland system is the Tarnished Plant Bug (*Lygus hesperus)* and may be viable prey for Lynx (Oxyopidae) and other spiders such as Thomisidae and Lycosidae (Young and Lockley 1986). Many species of leafhoppers are abundant throughout the summer in the meadows and are accessible to a variety of spider species.

Grassland vegetation

Meadow boundary to interior transects. In June 2010, I measured plant species cover in forest to meadow interior transects in seven 30-meter non-native and seven native dominated transects in three meadows (4 transects in each of two meadows (Sprague and Wilanor) and 6 transects in the White House meadow) Figure 1. Vegetation was measured at 5m intervals with standard point frame methods. The point frame is a wooden standing frame that holds 10 vertically aligned pins, 10 centimeters apart. For each pin, the vegetation was recorded at three heights (0, 10, and 20cm from the ground surface) for each of the ten pins. Within each 5m interval, the frame was turned perpendicular to the original position for a second recording. Each height recording for each pin was considered a hit for a given plant species (Sutherland 2006).

Figure 1: Meadows of the Angelo Coast Range Reserve



Native plant cover was estimated as:

*Cover of Spp A (# hits of Spp A/ total # of points per plot) * 100.* (eq. 1)

The percent cover of vegetation was analyzed by plant species and by native or non-native type. Transects designated as native had over twice the proportion of native plant cover (mean = 79%, std. dev. = 11%) as transects designated as non-native (native cover mean=32%, std. dev = 5%, t=-9.4, df=12, p<0.0001).

Meadow patches In June 2011, I measured plant species cover in twenty-four meadow patches, 4 native and 4 non-native patches in each of the three meadows (Walker, Wilanor, and White House). These patches ranged in size from 158 – 5346 m^2. Total patch area for native and non-native dominated stands were 9157m^2 and 13,100 m^2, respectively using bisecting transects and point frame counts across each patch at intervals of 5m (as described above). The average percent cover by native plants in designated native plots was mean = 74%, std. dev. = 13%; in non-native plots the mean = 33%, std. dev. = 9%, (t = -8.8, df=22, p<0.001).

Spider assemblages

Meadow boundary to interior transects Two methods were used to characterize spider assemblages along transects. First, to characterize ground dwelling arthropods, 7 pitfall traps were set at 5m intervals in each of the 14 transects (7 native dominated, 7 non-native dominated) for a total of 98 pitfall traps. Small Douglas-fir cones were placed in the traps to reduce spider cannibalism and predatory behavior. Pitfall traps were left open for a 24 hour period. Arthropods captured were recorded and immediately released back to the field. Second, I visually counted arthropods seen over 2 minute observation periods within each of a sequence of $1m^2$ quadrats spaced every 5 meters along each transect. (Altmann 1974). Observations and trappings were staggered between 8:00 and 16:00 h among the three meadows in order to observe activity throughout the day in each meadow. On average, 8 observations and 5 trappings were recorded per transect between June and September 2010. Annual grass senescence begins in June is thoroughly desiccated by August. Arthropods were identified to species level, where possible, or grouped according to lowest recognizable taxonomic unit.

Meadow patches From June through August, 2011, arthropod assemblages were surveyed monthly in the twenty-four meadow patches using 10-minute interval sweep-net sampling. After collection, samples were immediately taken to the lab for sorting to species level where possible. Samples not sorted immediately were frozen for future identification. All collections were preserved in 70% ethanol.

Abiotic conditions In 2010, I conducted a microhabitat ($\leq 1m^2$) study of grassland temperatures in native and non-native dominated areas of the grassland. Across habitat types, I monitored grassland temperatures at seven heights, from the 0cm to 42cm above ground surface (at 7cm intervals), using an O.W.L (On-site Weather Logger) system (by EME Systems, T.Allen, Berkeley, CA). The "Spider 49" System houses seven sets of seven probes. Each set of seven probes was attached to a metal flag pole and temperatures were recorded within 4 native and 3 non-native dominated habitats between July 4 and 16th and within 3 native and 4 non-native dominated habitats between July 16th and August 4th. Non-native probes were on average, 9 meters from the meadow-woodland boundary and native probes averaged 10 meters from the meadow-woodland boundary. Native microhabitats were dominated by mixtures of *Elymus glaucus, Danthonia californica*, *Bromus carinatus*, and minor amounts (<10%) of *Verbena lasiostachys.* Non-native microhabitats were dominated by mixtures of *Bromus hordeaceus, Aira carophylla* and *Hypocherus glabra.* In 2011, Maxim's ibutton® devices were used to monitor the temperature in central portions of meadow patches.

Data Analysis

Spider diversity was analyzed using the Shannon Diversity Index (H') and compared between transects and between patches using a one-way ANOVA. ANCOVA for repeated measures were used to analyze average spider abundance across transect and patch types. Average abundance at each of the seven distances (0-30m) from grassland boundary was the dependent variable, meadow was the fixed factor and native plant cover per transect was a covariate (JMP 2007). Regression analyses were used to compare average abundance of spiders per transect in relation to native plant cover and field, spider abundance was the dependent variable and field and native plant cover were independent variables (IBM® SPSS® Statistics version 20 2012).

For meadow patch sweep-net samples, average spider and leafhopper abundances (per m^2) per visit were compared across months using ANCOVA for repeated measures (IBM® SPSS® Statistics version 20 2012), meadow was a fixed factor and native plant cover was a covariate. Average monthly spider abundance was analyzed in relation to leafhopper abundance and the other potential prey, including grasshoppers, katydids, and plant bugs using step-wise regression analyses; meadow, percent native vegetation, and the chosen prey species were independent factors (IBM® SPSS® Statistics version 20 2012). Spider abundance from meadow patches was log transformed to meet the requirements of a normal distribution.

Microhabitat temperatures between habitat types collected from the O.W.L. system were compared across microhabitats and distance from the ground surface using t-tests. Temperatures were averaged across each set of probes within a given microhabitat and compared across native and non-native habitat types using t-tests.

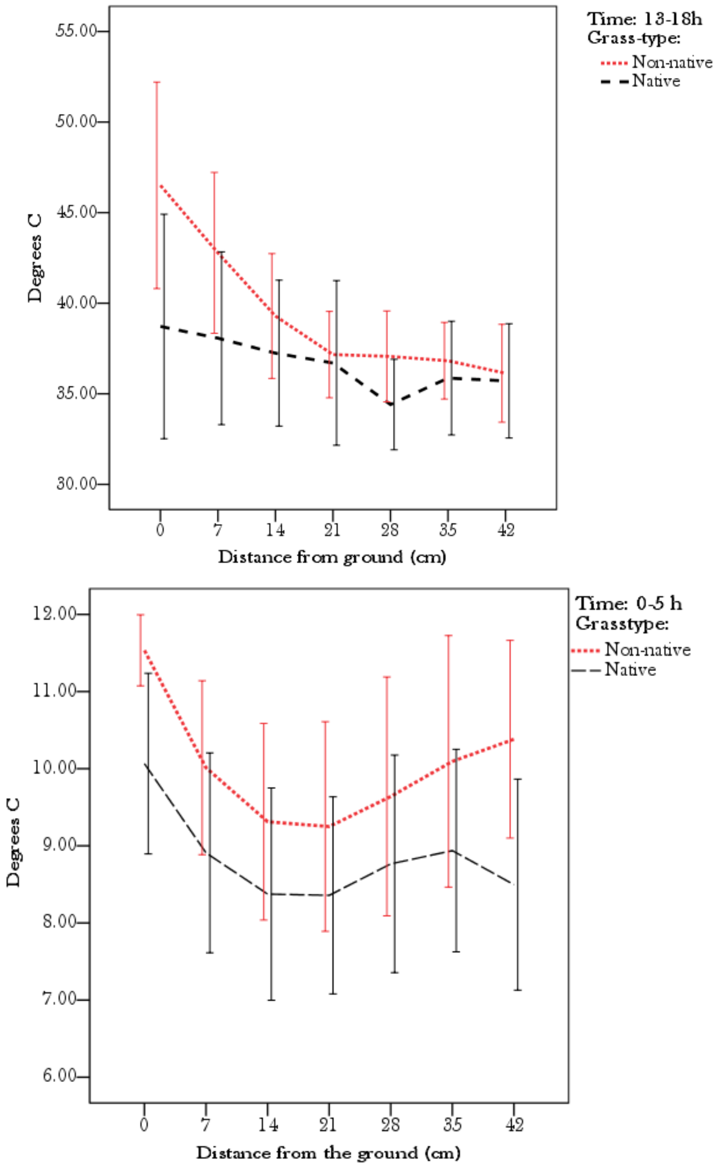
Results

Native and non-native grass assemblage temperatures

Microhabitat temperatures, as monitored by the O.W.L logger, were significantly cooler in native microhabitats than non-native annual microhabitats during the hottest portion of the day ($t=2.1$, df = 93, $p<0.05$) and coolest portion of the night ($t = 3.4$, df= 91, $p < 0.05$) between July 4th and August 4th, 2010 (Table 1). This difference was greatest closest to the ground surface (Fig.s 2-3) during the hottest portion of the day.

Table 1: Temperatures (C°) in native and non-native microhabitats, July 4th - August 4th, 2010.

13-18 hrs	Non-native			Native		
Distance from ground (cm)	N	Mean	S.D.	N	Mean	S.D.
0	7	46.50	7.54	7	38.72	8.20
7	7	42.78	5.88	7	38.07	6.31
14	7	39.29	4.56	7	37.24	5.33
21	7	37.16	3.16	7	36.70	6.01
28	6	37.06	3.07	6	34.41	3.06
35	7	36.82	2.80	7	35.87	4.15
42	6	36.13	3.30	7	35.71	4.17
0-5 hrs						
Distance from ground (cm)	N	Mean	S.D.	N	Mean	S.D.
0	7	11.54	0.61	7	10.07	1.55
7	7	10.01	1.49	7	8.91	1.72
14	7	9.31	1.69	7	8.37	1.82
21	7	9.25	1.80	7	8.36	1.69
28	6	9.64	1.90	6	8.77	1.73
35	6	10.09	2.00	6	8.94	1.61
42	6	10.38	1.57	7	8.50	1.81



Figures 2 and 3: Grassland microhabitat temperatures (°C) by distance (cm) from ground surface. Temperatures depicted here are means +/- 2 SE.

Spider abundance

Transect Observations: Observed spider abundance increased with native plant cover and decreased with distance from the forest-meadow boundary; the interaction between distance and native vegetation was marginally significant (Fig. 4). However, there was a significant effect of native plant cover on average number of spiders observed per transect (Fig. 5). There was no effect of field on the number of spiders observed.

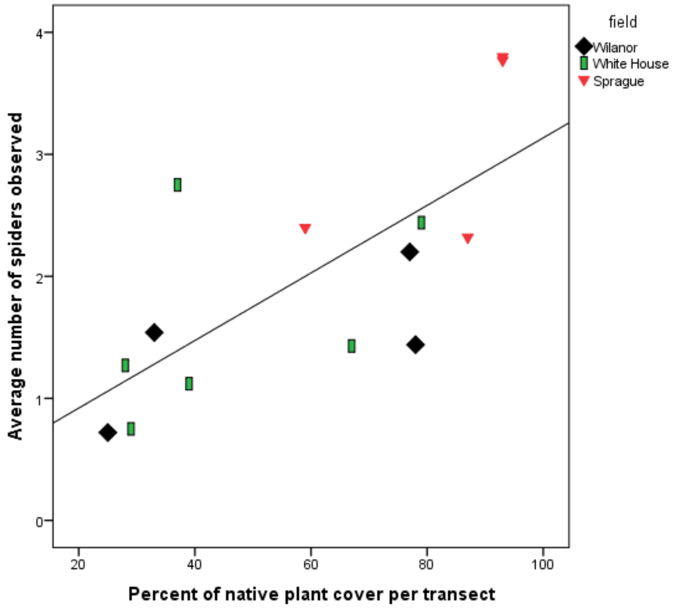


Figure 4: The average number of spiders observed per transect in relation to native plant cover (β = 0.56, t(13) =2.77, p = 0.018).

For the purpose of figures below, those transects with ≥ 60% native plant cover were grouped together as native transects and those with < 40% native plant cover were grouped together as non-native transects.

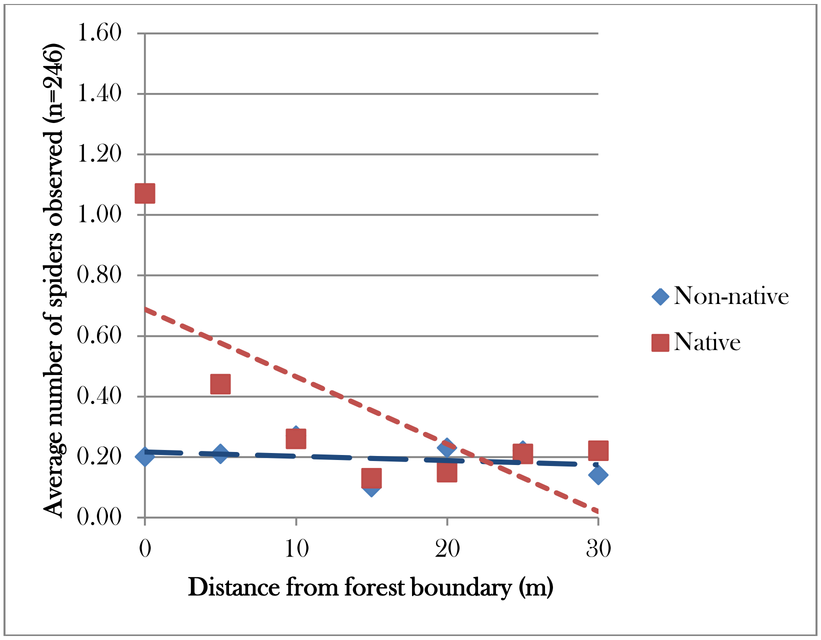


Figure 5: Average number of spiders observed per visit in relation to distance and grass type (F (1,10) = 2.3, p =0.057).

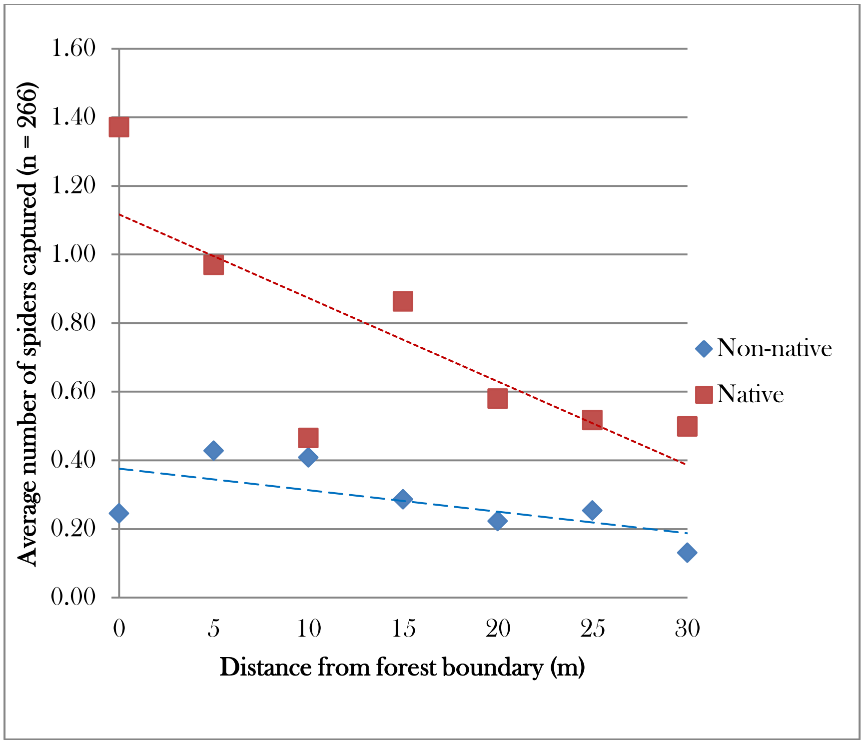


Figure 6: Spiders captured in pitfall traps in relation to distance from meadow boundary and grass type (F (1, 10) = 1.5, p<0.01).

Table 2 : Average Spider Abundance ($1m^2$) by Transect Type and Distance from Woodland

	Distance (m)						
Observed	**0**	**5**	**10**	**15**	**20**	**25**	**30**
Non-native (<50%)	0.20	0.21	0.27	0.10	0.23	0.22	0.14
Native (>50%)	1.07	0.44	0.26	0.13	0.15	0.21	0.22
Captured in pitfall traps	**0**	**5**	**10**	**15**	**20**	**25**	**30**
Non-native (<50%)	0.24	0.43	0.41	0.29	0.22	0.25	0.13
Native (>50%)	1.37	0.97	0.46	0.86	0.58	0.52	0.50

Transect pitfall traps: The average number of spiders captured in each pitfall trap also increased with native plant cover and decreased with increasing distance from the shaded meadow boundary (Fig. 6). Most of the spiders in pitfall traps (62%) were juveniles. The total number of spiders captured in each transect was significantly affected by the percent native plant cover and by meadow (Fig. 7).

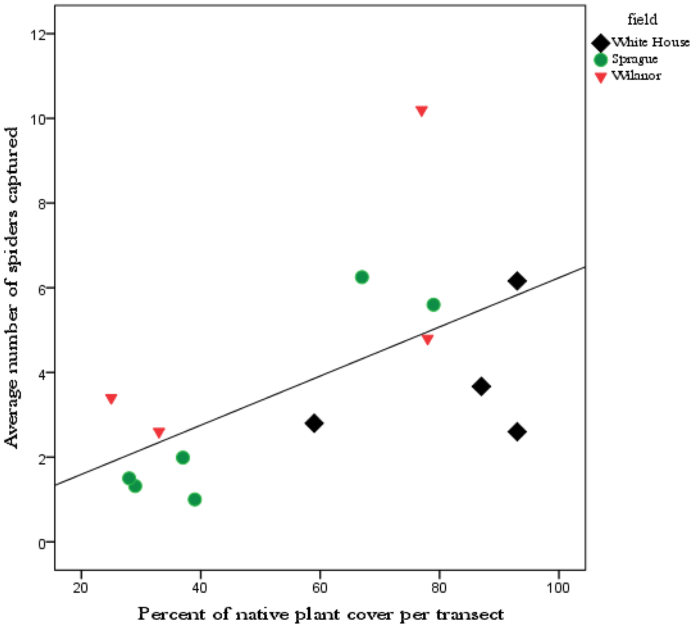


Figure 7: Spider abundance in pitfall traps in relation to native plant cover (β = 0.87, t(13) =4.42, $p < 0.01$) and meadow (β = 0.61, t(13) =3.1, p =0.01).

Meadow patches: In 2011, 2907 spiders were captured between June and August with sweep-net surveys. Spider abundance was influenced by time and native plant cover (Fig. 8). Most spiders captured were juveniles (71%). Juvenile spider abundance increased in August in patches that contained the higher proportions of native plant cover.

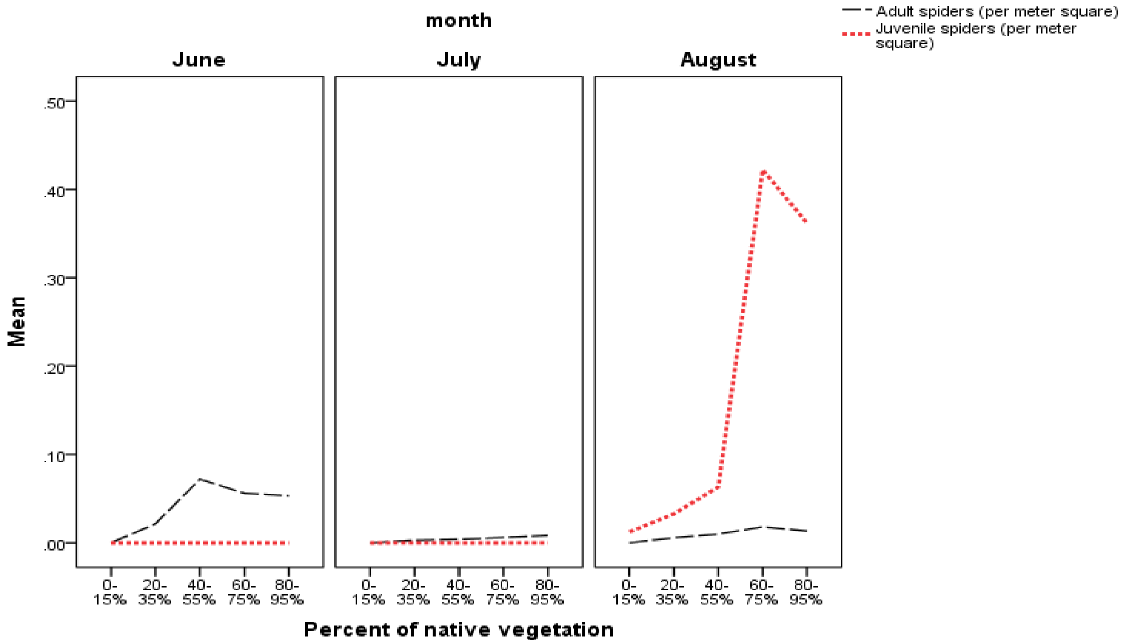


Figure 8: Sweep net samples of spider abundance (per m^2) in relation to native plant cover. Spider abundance was influence by time (June = 613, July = 77, August = 2217) (F (2,19) = 3.6, $p < 0.05$), and by native plant cover (F (1,20) = 5.25, $p < 0.05$).

Spider diversity

Transect observations: Nine families and nine species of spiders were observed in transects (Appendix 2, Table 1). Observed spider evenness (H') increased with native plant cover (Fig. 9). Observed spider richness also increased with native plant cover (Fig. 10). Juvenile Lycosidae (Wolf) and Oxyopidae (Lynx) spider abundance was higher in native assemblages. Ground dwelling spiders (e.g., Lycosidae) may seek to avoid desiccation more than canopy dwelling Oxyopidae, Thomisidae (Crab), and web building spiders (Volllmer and MacMahon 1974). Web building and canopy spiders may avoid desiccation with shaded retreats associated with their webs or shelters (Foelix 2010). Rarer species were generally observed more frequently in native assemblages (Appendix 2).

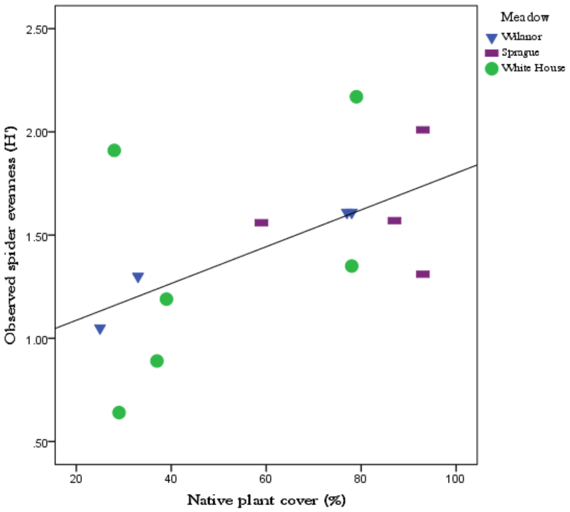


Figure 9: Observed diversity (H') of spider species in transects, relative to native plant cover (F (1, 13) = 4.8, p =0.05)

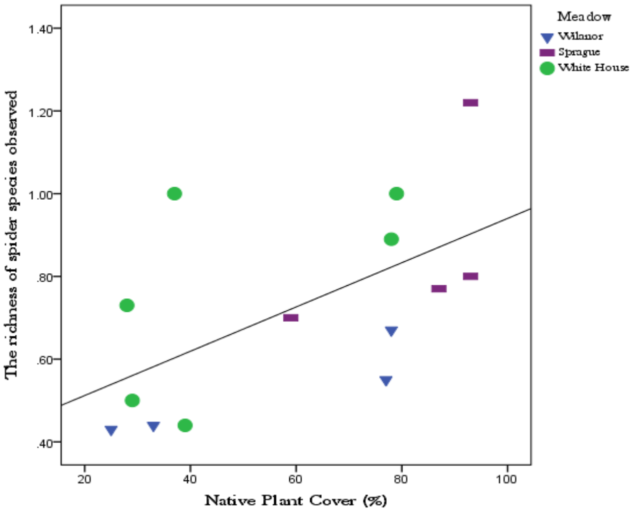


Figure 10: Observed richness of spider species in transects, relative to native plant cover (F (1,13) = 5.16, p = 0.05)

Transect pitfall traps and meadow patch samples: There was no effect of native vegetation on the diversity of spiders captured in pitfall traps (Appendix 2, Table 2). There was also no effect of native vegetation on spider species diversity captured in sweep-net samples in meadow patches (Appendix 2, Table 3). Most spiders captured in sweep-net surveys were likely Oxyopidae and Thomisidae spiderlings but as juveniles, they were impossible to identify to the species level.

Prey availability

Transect observations: Leafhopper observed abundances increased with native plant cover and was greatest at 5 meters distance from the forest boundary (Fig. 11).

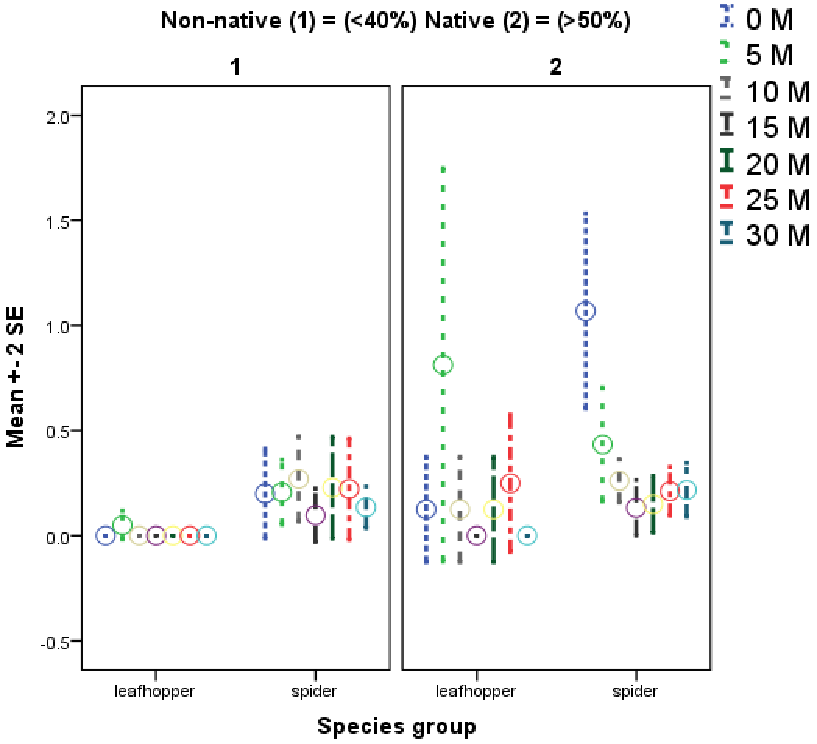


Figure 11: Leafhoppers (n =169) and spiders in relation to grass assemblage (F(1,10) = 6.7, $p < 0.05$) and the forest boundary (5m distance: F (2,20)= 3.4, p = 0.05).

Orthopteran abundance increased toward the meadow interior in all three meadows (Fig. 12). There was no effect of native vegetation on the total number of Orthopterans observed. Within the smallest meadow, Sprague, I observed the greatest abundance of Orthoptera.

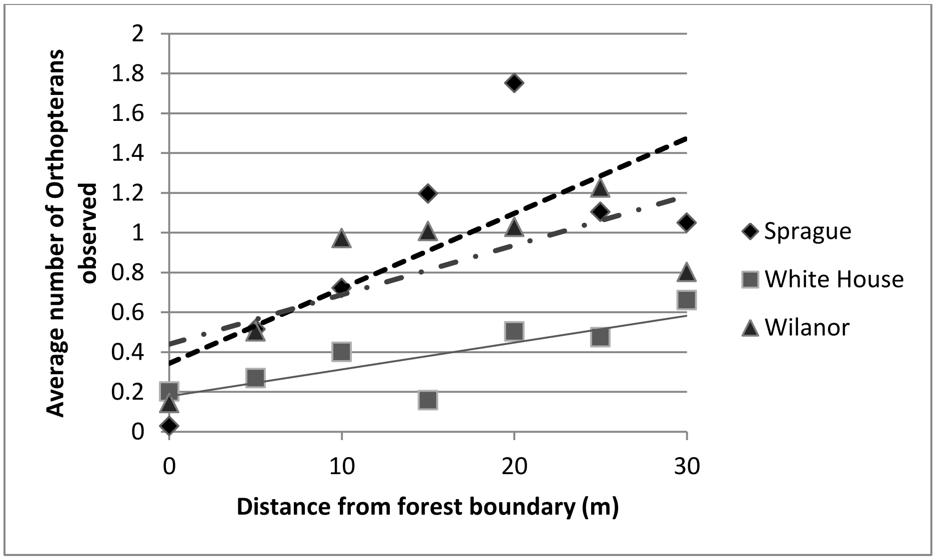


Figure 12: Orthopterans (grasshoppers = 406; katydids = 135) observed by distance from the forest.

I also observed 97 plant (*Lygus sp.)* bugs, the third most abundant potential prey group for spiders. Plant bugs observed abundance was not affected by native vegetation or distance from the forest boundary (Figure 13). Overall, stepwise regression analysis revealed no effect of observed plant bug abundance on observed spider abundance.

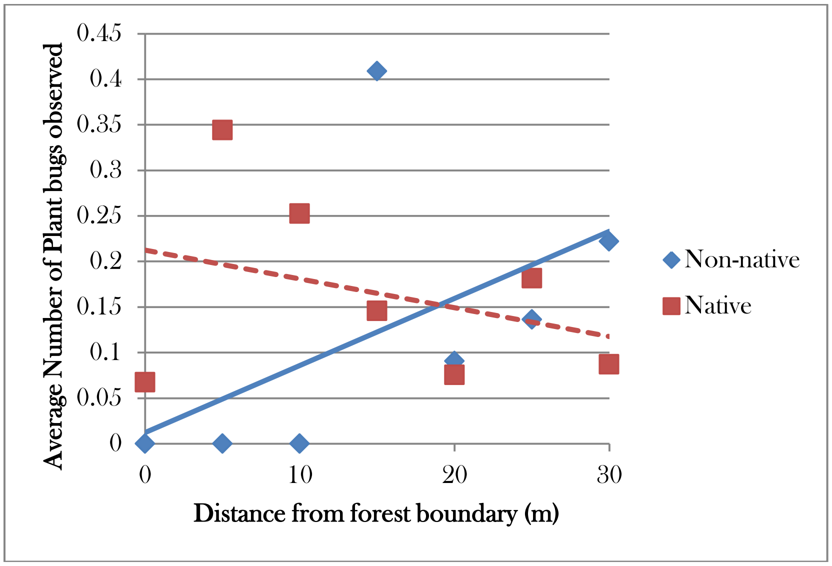


Figure 13: Plant bugs observed by distance from the forest and transect type.

Sweep-net surveys in meadow patches: The most abundant potential prey groups captured in sweep-net samples in 2011 included leafhoppers (n=9034), plant bugs (*Lygus sp*)(n=3757), katydids (*Tessellana tessellata)* (n=2230), and a variety of grasshoppers (n=2178). Stepwise regression analysis revealed that leafhopper abundance and native plant diversity were the greatest predictors of spider abundance, with native plant cover and overall plant diversity (native and non-native plants) having small effects. As stated earlier, spider diversity was greatest in areas of high native plant cover, low native plant diversity, and high leafhopper abundance. These areas had higher proportions of native perennial grass such as *Danthonia californica* and *Elymus glaucus* (Fig.14).

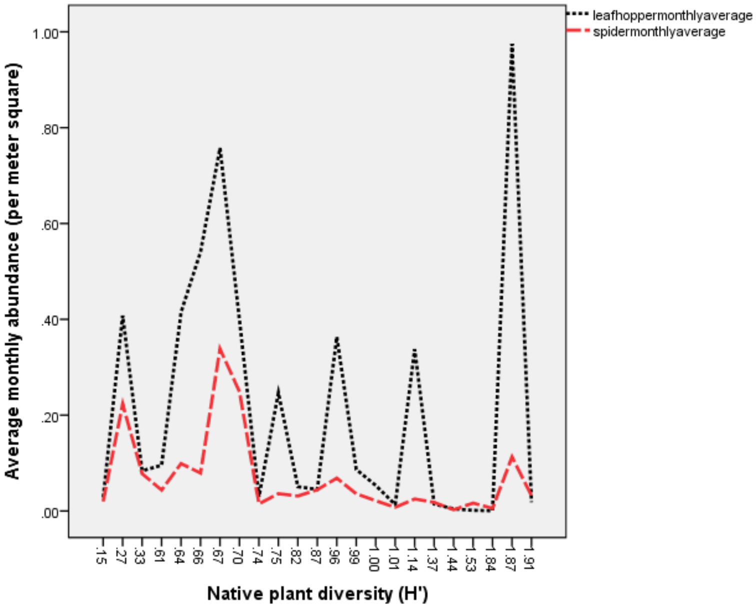


Figure 14: Spider and leafhopper abundance in relation to native plant diversity (R^2 = 0.68, F(1,22) = 21.97, p < 0.0001).

The increased abundance of juvenile spiders that were collected in August, relative to July, coincided with a slight increase in capture of juvenile leafhoppers (July n =1026, August n= 2395). Overall, leafhopper abundance generally increased with native plant cover (Fig. 15). The effect of time and native plant cover on leafhopper abundance was marginally significant.

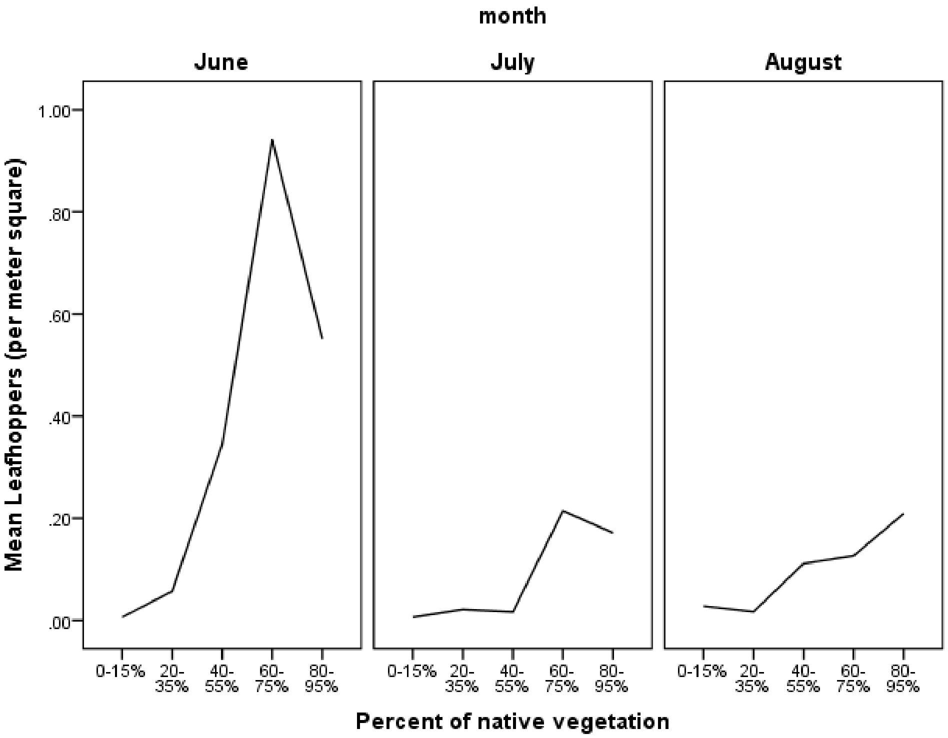
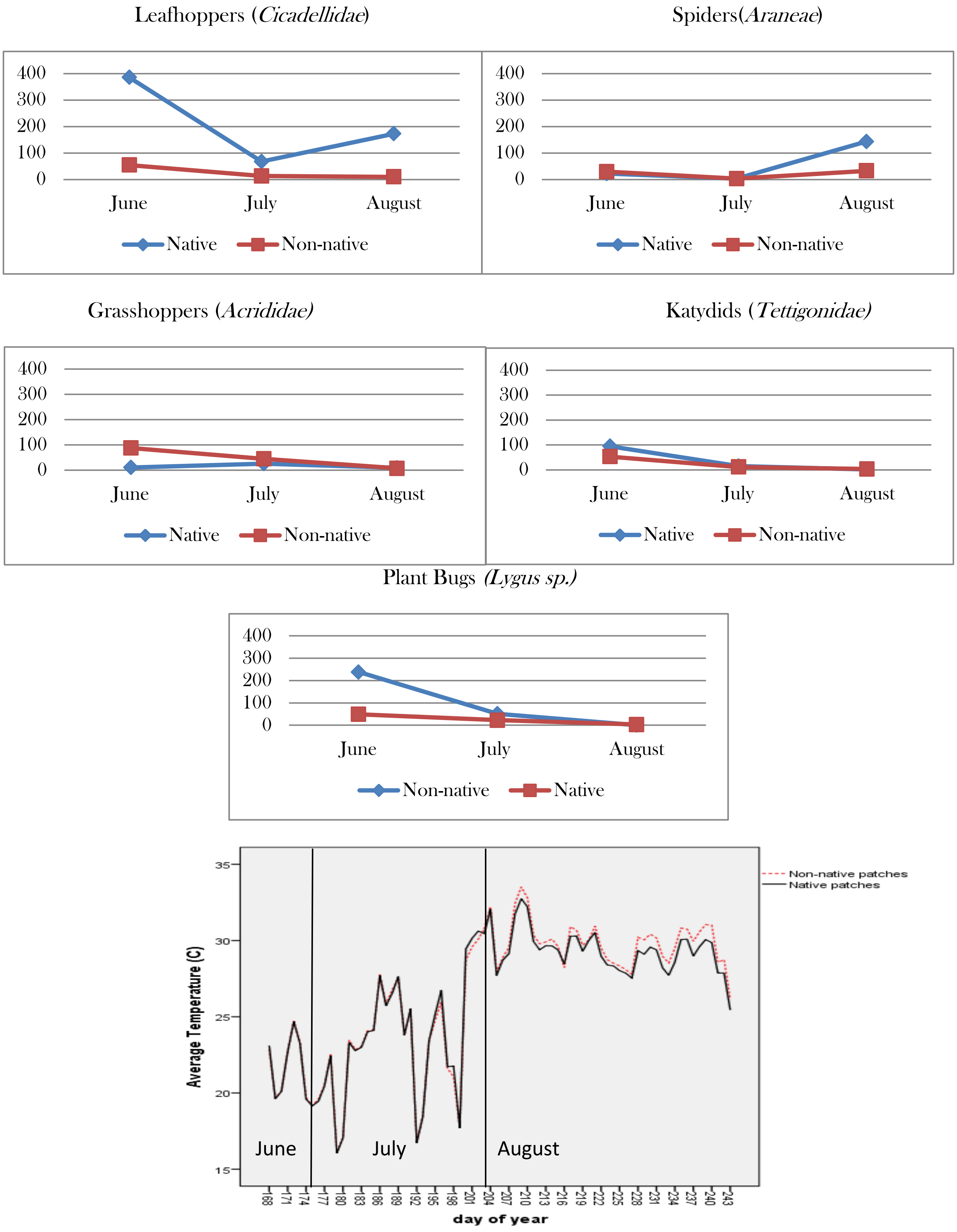


Figure 15: Leafhoppers captured (per m^2) monthly (F (2, 34) = 2.9, p = 0.07) through sweep net samples in meadow patches with variable amounts of native plant cover (F(1,20) = 8.7, p < 0.01).

The following figure (Fig. 16) depicts the monthly averages of spider, leafhopper, grasshopper, katydid and plant bug abundance in combination with average temperatures found in native and non-native dominated areas of the grassland. The temperatures depicted in the figure below were measured with devices that were 14 centimeters above the ground and underestimated the heat differences between native and annual stands, particularly near the earth surface. Juvenile spider and leafhopper abundance increased in August as seasonal temperatures rose.

Figure 16: Average abundance by patch type and month



Leafhoppers (*Cicadellidae*)

Spiders(*Araneae*)

Grasshoppers (*Acrididae)*

Katydids (*Tettigonidae)*

Plant Bugs *(Lygus sp.)*

Discussion

Grass Assemblage Abiotic Conditions

Microhabitat analysis of native and non-native plant assemblages in the grassland revealed that native assemblages were cooler during the hottest portion of the day and the coolest portion of the night. The differences between assemblages were most pronounced closest to the ground surface and during the hottest time of the year.

Spider abundance

Previous experiments have shown that wandering spiders frequently prefer cooler temperatures than other grassland invertebrates, such as grasshoppers (Law and Joern 2013, Joern 2006). The three different methods used to estimate abundances of adult and juvenile spiders and their potential prey were complementary. Observational data, collected an average of 8 times per transect over the course of the summer, documented spider taxa, larger invertebrates, and suggested differences in the abundance of juvenile spiders and leafhoppers between assemblages, a trend that was confirmed by sweep-net surveys and pitfall traps. Sweep netting and pitfall trapping revealed that spiders were more abundant in native plant assemblages than in non-native assemblages. Pitfall trapping was useful for capturing estimates of nighttime wandering spider activity-abundance-- many traps were empty until the morning after they had been set. These results indicate that wandering spiders were more active in the cooler native assemblages even during the coolest portion of the 24-h cycle (range = 2-30C°) Sweep-net surveys revealed that spiders were more evenly distributed throughout the grassland in the early and cool part of the season (i.e., June). Hatchling spiders, which are most abundant in late summer, the hottest season, were found more frequently in native than non-native grassland, and juvenile leafhoppers showed similar trends, suggesting that female egg-laying spiders choose sites where their future offspring will encounter more moist conditions, juvenile prey, or both. Ovipositing spiders in other studies have been found to favor sites with specific soil and atmospheric moisture, and specific habitat structure that will be beneficial to their offspring (DeVito and Formanowicz 2003, Hieber 1992, Suter, Doyle, and Shane 1987).

Spider diversity

More spider species were observed in native than non-native assemblages in transects, although pitfall and sweep net sampling did not detect this difference in spider diversity. Interestingly, sweep-net sample collections showed that spider abundance was greater in areas of low native plant diversity but high native plant cover. Areas of high native plant cover and low plant diversity supported solid stands of native perennial grasses. This suggests that the structure of perennial grass canopy aided juvenile spider survival during a vulnerable life stage. That diversity was not observed to be greater through sweep-net surveys, as it was through observational surveys may be due to the less disruptive nature of observations. Sweep-net surveys can send vibrations through the grassland canopy that may warn spiders to take shelter or flee. Sweep-nets can also easily crush fragile spider bodies leaving them unidentifiable. Sweep-net surveys were effective in capturing the abundance of small, difficult to see juvenile spiders but it was impossible to identify many spiders to the species level, therefore, the overall diversity of this sample remains unknown. It is not surprising that pitfall traps were limited in capturing the diversity of the spider species found within the grassland. Pitfall traps are excellent for capturing ground wandering activity-abundance but cannot adequately capture grassland canopy dwellers or activity. At least one other study has shown that grassland complexity contributes to spider diversity (Malumbres-Olarte et al 2013).

Prey Assemblage

Spider abundance increased in native assemblages with greater leafhopper abundance. Perennial plants provide food to invertebrate herbivores as non-native annual grasses wither during this the hottest and driest time of the year. Leafhopper abundance, unlike other potential abundant prey species, increased during the driest period in tandem with hatchling spiders. Juvenile spiders may be able to survive and grow through this season by eating hatchling leafhoppers but also other small species not accounted for here, such as collembola. The juvenile spiders captured in sweep-net surveys were likely Oxyopidae (Lynx spiders) and Thomisidae (Crab spiders) with a few other minor species. Overall, the variety of methods used to understand spider and prey activity within the grassland assemblages clarified their activity-abundance patterns in a way that no single method accomplished.

Conclusion

The more complex, cooler, living architecture of native grassland assemblages contributed to the greater abundance of spiders and higher indices of spider diversity observed during the summer. Native perennial grasses act as incubators for spiderlings that hatch during in the harsh dry summer and fall months, providing shelter from other predators and abundant food. This study shows how changes in California's grassland canopy have altered arthropod assemblages; as annual grasses have come to dominate grassland, spider prey and habitat, particularly for juvenile spiders, is greatly diminished in quality and quantity. Indirect consequences of reduced populations and diversity of spiders could devolve from the escape of certain heat tolerant folivores, like grasshoppers, with follow-on effects for plants and faunal diversity.

Chapter 3

Spiders in the grass: The effects of spiders, herbivores, and non-native annual grass on native plant damage.

Kirsten Hill

Abstract

Biological invasions are disrupting ecosystems worldwide. In California, native bunch grasses have been displaced by non-native annual grasses throughout their former range. Little is known about how interactions between grassland invertebrates have been affected by this displacement. I experimentally tested the hypothesis that warmer and senescent non-native annual summer grassland habitats weaken top-down control in comparison to cooler and more structured native perennial and newly restored habitats. In June 2012, wolf spiders (*Schizocosa mccooki*) were added or removed to 1m^2 plots in native, non-native, and restored habitats. After four weeks, I measured invertebrate chewing damage to native and non-native leaves by, 1) the proportion of leaves damaged per plot and, 2) the amount removed per leaf. Spider presence decreased the proportion of damaged native leaves across habitats ($p < 0.01$). Spiders had no effect on non-native leaf damage or the amount removed per leaf. Overall, habitat type affected spider impact ($p = 0.046$). Post-hoc comparisons revealed restored habitats had marginally more damaged native leaves than non-native habitats ($p=0.057$). Native plant damage was positively correlated with afternoon temperatures, highest in restored plots. One year after initial planting, restored plots in non-native habitats were warmer than undisturbed non-native habitats, likely due to soil disturbance. These findings suggest 1) native vegetation suffered a disproportionate frequency dependent damage when they were a smaller component of the assemblage, especially in newly restored habitats, and 2) spiders exerted a protective effect on native plants but more so in cooler habitats. These findings reveal the effects of plant assemblages on the impacts of predators that indirectly protect plants and imply that context-dependent movements, population dynamics, and interactions of invertebrates are relevant to grassland restoration.

Introduction

Biological invasions transform our ecosystems, alter species interactions, and change ecosystem functioning and resilience (White et al. 2006, Wolkovich et al. 2009). Since the arrival of European non-native annual grasses and forbs 250 years ago, California's native bunch grasses and forbs have been replaced by non-native annual grasses that now occupy more than 90 percent of the total grassland area (Stromberg et al. 2007). The documented consequences of this grassland invasion are extensive, ranging from shifting soil microbial systems, nutrient cycling, hydrologic dynamics, to impacts on populations of birds and small mammals (Stromberg et al. 2007). Indirect effects of non-native species on food web interactions are of concern (White et al. 2006). I was interested in understanding how these non-native grasses affect interactions between arthropods, in particular, spiders and their potential prey. Predators, such as spiders, can help to maintain biodiversity (Paine 1969, Estes et al. 2011). One long-term study has shown that invasion by European grasses can greatly diminish native plant and arthropod diversity in California grasslands (Suttle et al. 2007). I was interested in understanding how impacts of grasses on top predators (spiders) in food webs may help mediate these effects. Differences in the non-native annual and native perennial grasses may have differential effects on spiders and their prey.

Reduction of spider top down control may affect overall plant and arthropod abundance and biodiversity (Finke and Denno 2006, Sanders et al. 2008, Pearson 2009, Schmitz 2003, Snyder and Wise 2001, Spiller and Schoener 1994, Werner et al. 1993) net primary productivity (Huntly 1991), energy transfer, and nutrient cycling (Oksanen 1990, Power 1992). Although spider interactions with their prey have been studied in invaded salt marsh, (Petillon et al. 2006, Petillon et al. 2005), invaded Mediterranean scrub (Wolkovich et al. 2009), and with web spiders in Montana grasslands invaded by Spotted Knapweed (Pearson 2009), more needs to be known about how spiders are effected in non-native annual grasslands. As predators but also as prey to birds and mammals, spiders have been used as ecological indicators and can help us understand ecosystem state (Scott et al 2006). In California's grasslands in particular, I know less about how micro-environments and resource regimes within native perennial versus European annual grass assemblages affect predatory impacts of spiders. Greater understanding of these interactions could help us understand how arthropods are affected by grassland change and aid in future monitoring of native grasslands.

The change in plant species composition in California's grasslands has altered microclimates, habitat structure, and food sources for arthropods. Native bunchgrasses persist through the summer, providing a cooler, moister microclimate (Kotanen 1997, Green et al 1984). In contrast, non-native annual grasses senesce in June, and the near-ground microhabitat for arthropods subsequently dries and undergoes more extreme temperature fluctuation, including hotter daytime peaks. The resulting fluctuations in abiotic conditions and food sources can affect seasonal phenology, daily activity, and the strength and direction of species interaction paths, particularly complicating predator-prey interactions among arthropods (Schmitz 2008).

Grasshoppers thrive in hot dry environments, and can respond to higher temperatures by growing faster to a larger size; many species seek to raise their body temperature closer to that which induces maximal rate of development and increases efficiency of food use (Nufio et al. 2010, Joern et al 2006, Joern and Gaines 1990). Some evidence suggests that wolf spiders have lower temperature preferences than grasshoppers and should be increasingly limited in their diel activity and spatial distributions as annual grasses wither and moist microclimates disappear (Joern et al 2006). In our system, the dominant grassland wolf spider (*Schizocosa mccooki*) is active during the day in the spring (K.H. per observ), but is likely crepuscular and/or limited to cooler environments within the grassland as seasonal temperatures increase (Laws and Joern 2013, Li and Jackson 1996).

In other grassland systems, spiders have been shown to alter grasshopper behavior and sometimes limit grasshopper populations when conditions are favorably cool enough for spider activity (Law and Joern 2013). *Schizocosa spp.* spider presence has also been shown to have stronger effects on nymphal rather than adult Orthopterans, as smaller and wingless insects are easier to capture (Oedekoven and Joern, 1998). The dominant grasshopper in our system (*Melanoplus devastator*) emerges in late June. A non-native katydid (*Tessellana tessellata*), an import from Southern Europe, co-dominants the grassland with the devastating grasshopper but emerges as early as April and begins to reach adulthood in July (K.Hill pers. observation). Spiders may exert differential predation pressure on the two Orthopterans, as they coexist in different life stages and different microhabitats; any effect of spiders on plant damage may be apparent by in the microhabitats each Orthopteran dominantly occupies. Both herbivores may forage more heavily on palatable plants in hotter areas of the grassland (likely those areas dominated by senescent non-native grasses) either because of their physiological adaptations to hot dry habitats, or because they would be less inhibited by spider predation, or for both reasons (Danner and Joern 2003, Schmitz et al 1997, Schmitz 2003). As part of this study, I further investigated microhabitat use of these two Orthopterans through sweep-net surveys of the grassland.

I hypothesized 1) the microhabitat in senescent non-native grassland patches is hotter than living native grassland patches, 2) plant damage will be lower in the presence of spiders in cooler habitats 3) plant damage will be lower in the presence of spiders and nymphal rather than adult Orthoptera, 4) plants damage in restored habitats will be lower than in non-native habitats due the greater structure and shading provided for predators and 5) native plants found in hotter (non-native dominated) areas of the grassland will evidence greater herbivore damage than those found in cooler (native dominated) habitats; this may be due to either to habitat conditions or less fear from spider predation, or both. To better understand Orthopteran food preferences, I choose to study a variety of commonly abundant native and non-native forbs and grasses. Several are known food for the dominant grasshopper species (native foods are *Eschscholizia californica, Hemizonia congesta, Elymus glaucus* and the non-native is *Plantago lanceolata*) (Suttle 2005).

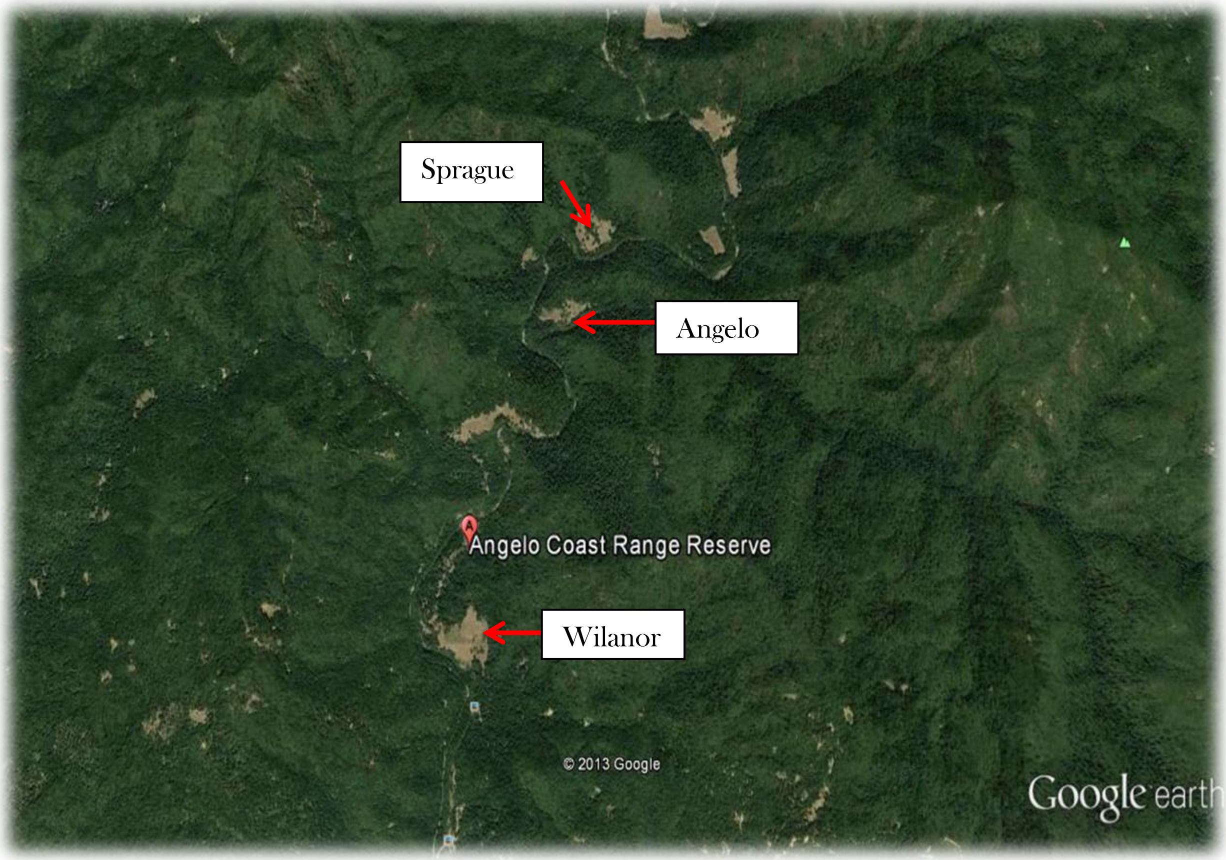
Methods and Results

Study System and Species

I compared the effects of large wolf spiders (*Schizocosa mccooki)* on foraging by the dominant orthopterans in native perennial versus European annual grass assemblages in meadows within the Angelo Coast Range Reserve of Mendocino County, California. This 3200 hectare reserve protects 6 km of the South Fork Eel River (39° 44' N, 123° 39'W) , and is primarily forested with mature mixed Douglas fir-tanoak (*Pseudotsuga menziesii and Notholithocarpus densiflorus*) and Coastal Redwood (*Sequoia sempervirens*). Within this forest matrix, nine isolated terrace meadows occur near but well above the river (Figure 1), within or adjacent to the Reserve. Under Mediterranean seasonality, the area has cool wet winters and long, hot, dry summers. Mean annual rainfall is 203 cm per year, most of which occurs in the winter.

Monitoring and field manipulations were conducted in three meadows: Sprague (18,444 m^2); Angelo (25,898 m^2); and Wilanor (72,578 m^2). These meadows have a similar slopes and elevations with soils that were originally formed as floodplains along the S. Fk. Eel River, and became abandoned as strath terrace surfaces as the river incised (Seidl and Dietrich 1993). Regional native meadow perennial grasses include *Danthonia californica, Elymus glaucus, Elymus multisetus, Festuca idahoensis, Festuca californica, and Bromus carinatus.* Dominant invasive annual grass species are *Bromus hordecious, Bromus diandrus, Bromus tectorum,* and *Avena barbata.* Abundant and highly palatable to orthopterans are the native forb species *Hemizonia congesta, Eschscholizia californica,* and *Trichostema lanceolatum* (Suttle, 2005). Common non-native forbs are *Plantago lanceolata* and *Rumex acetosella.*

Figure 1: Angelo Coast Range Reserve (6 km length) meadow locations



The devastating grasshopper (*Melanoplus devastator*) is one of California's dominant pest grasshoppers that prefers to eat various legumes, brome, and barley grasses during the spring, but as annual grasslands dry, they have been found to feed on perennial grasses (*Stipa spp.),* tarweeds, (*Hemizonia spp.)* and grass seeds (Joern 1989, Pfadt, 1994, Porter and Redak 1997, Suttle 2005). The nymphs of this species can emerge as early as April and as late as July; they mature over the course of the summer to mate and oviposit in soils in the fall.

At Angelo Coast Range Reserve, a xerophytic, non-native katydid (*Tessellana tessellata*), a numerically dominant import from southern Europe, was first described in California in 1955 (Rentz 1963). Within its home range, this katydid is found in semi-arid grasslands with average temperatures ranging from 5-25 °C (Biyoekolojisi S. P. C. O. T. 2006). The katydid nymphs emerge in March or April. Adults mate throughout the summer and oviposit on dry grass stems from July through October (Biyoekolojisi S. P. C. O. T. 2006, Rentz 1963). I observed these katydids to eat perennial grasses, a variety of forbs, and seeds of *Plantago lanceolata.*

Schizocosa mccooki, (Family: Lycosidae) is a medium to large sized wolf spider (9.6- 22.7 mm) that is typically found in a variety of western but primarily open habitats. It is the dominant meadow wolf spider in our system and typically resides in burrows along the edges of the meadows (Suttle, 2005). It is an important predator of juvenile grasshoppers (Oedekoven and Joern, 1998). The male spiders are abundant in June and July and the females are most abundant from June through August. Ambient wolf spider density is 1 per 2 ½ m^2 within the meadows (Suttle, 2005).

Herbivore arthopod microhabitat use

Sweep-net surveys of the native and non-native grass assemblages (large patches of the meadow that had >50% or ≤ 30% native plant cover) in summer of 2011 revealed that the devastating grasshopper (*Melanoplus devastator)* was the dominant invertebrate herbivore in the non-native assemblages, while the katydid (*Tessellana tessellata)* dominated the native assemblages (Table 1). The effect of native vegetation on Orthopteran assemblages was significant ($F(3,18) = 4.78, p < 0.05$; Wilk's $\Lambda = 0.557$, partial $\eta^2 = 0.44$).

Table 1: Orthopteran densities (per m^2) and average size in native and non-native assemblages.

	Grasshoppers (*Melanoplus devastator*)		**Katydids** (*Tessellana tessellata*)	
Assemblage	**Mean**	**S.D.**	**Mean**	**S.D.**
Non-native	0.10	0.13	0.12	0.04
Native	0.06	0.10	0.47	0.13
Body Size	**Length**	**Stage**	**Length**	**Stage**
July 2011	9 mm	3	11 mm	5

Experimental design

H 1: Microclimate will be cooler in native and non-native habitats

To better understand microclimates in native perennial vs. European annual grasses, I monitored native and non-native assemblage temperatures within 0.25 m^2 microsites from July 4 – August 4, 2010, separate from the experiment described below, using an Onsite Weather Logger ("Spider 49", O.W.L. by EME Systems, T. Allen, Berkeley CA.). Assemblage temperatures were monitored at seven heights, from the 17cm to 60cm above ground surface (at 7cm intervals) with probes attached to metal flag poles. Temperatures were recorded within 4 native and 3 non-native dominated habitats between July 4 and 16th and within 3 native and 4 non-native dominated habitats between July 16th and August 4th. Native microhabitats were dominated by mixtures of *Elymus glaucus, Danthonia californica, Bromus carinatus*, and minor amounts (<10%) of *Verbena lasiostachys and Bromus hordeaceus.* Non-native microhabitats were dominated by mixtures of *Bromus hordeaceus , Aira carophylla* and *Hypocherus glabra.* Non-native probes were on average, 9 meters from the meadow-woodland boundary and native probes averaged 10 meters from the meadow-woodland boundary.

Temperatures were monitored in each of the experimental enclosures described below with Oakton® humidity loggers and Ibutton® temperature loggers for comparison to this microhabitat study.

H2,3,4, and 5 *Plant damage will be differentially affected by spider presence or absence but will be less in cooler (native dominated) and restored habitats than in hotter (non-native dominated) habitats.*

To test whether spider presence or absence affects Orthopteran feeding behavior differently in un-manipulated native, un-manipulated non-native, and experimentally restored assemblages, I experimentally added and removed spiders from enclosures that were installed in 3 meadows. Six, 3x3m enclosures were installed in each meadow. Two enclosures were placed in patches where native grasses dominated, two in patches where European annual grasses dominated, and two were placed in experimental restoration enclosures within non-native dominated assemblages (described in the section below). I installed 50 cm aluminum flashing around and within each enclosure to retain spiders (Figure 2). The flashing was buried at least 10cm in the soil around each enclosure during May and June 2011. I also surrounded each enclosure with deer fencing (1.1 meters tall). Spider treatments were randomly assigned in June 2012. The 4-pen per enclosure design was used to maintain consistent environmental variation among the spider addition and removal treatments. All enclosures were also placed within 30 meters of the woodland-meadow border. In total, there were 72 pens (1.5 x1.5 meter no-spider and spider) in 18 enclosures (3x3 meter) in a total of three meadows. In addition, I surveyed herbivore damage in un-manipulated open pens (1.5 x 1.5 m) in 3 native-dominated and 3 non-native dominated areas of each of the three meadows.

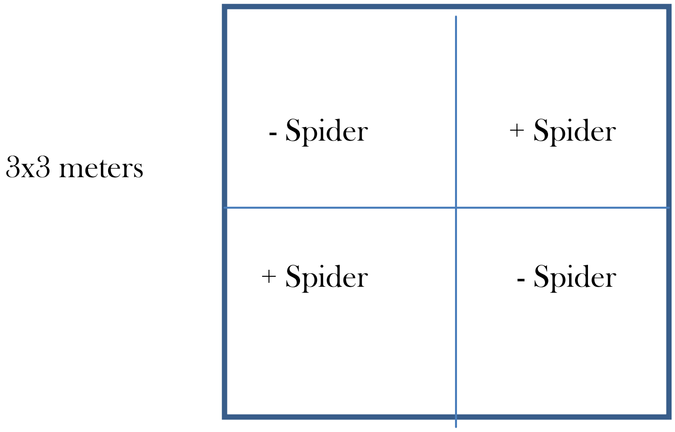


Figure 2: An experimental meadow enclosure (N=18) with four pens (N= 72). Each 3x3 enclosure was divided into 4 (1.5 x 1.5m) pens with aluminum flashing, for the spider addition and removal.

Restored enclosures

Newly grown "plugs" (3-4 cm in diameter) of *Elymus glaucus, Festuca californica, Festuca idahoensis, and Elymus multisetus* were established in a greenhouse environment for 3-5 months in the fall and winter of 2011 and 2012, in 20 ounce paper cups. In May and June 2011, I planted the plugs in two (3x3 m) areas of non-native annual assemblages in each of the three meadows close to the woodland boundary to ensure consistent shade and moisture and facilitate survival. Non-native plants were weeded from the planted areas to reduce competition. Plugs were placed in the ground by first stabbing the ground in a cross-hatch pattern with an OST® Tree Planter and loosening the soil to a 25cm depth. After placing the grass plugs in the ground, the soil was tamped down around the plant to ensure soil to root connection. Each (3x3 m) restored area received twelve *Elymus glaucus* and four *Festuca sp.* in May 2011. Between the months of June and August 2011, these plots were watered five days a week. These plugs were allowed a year to establish.

In January 2012, to better mimic a more fully restored assemblage, I supplemented restored areas with one or two (two if the tussocks were smaller than 10 cm diameter) *Danthonia californica* "tussocks" (cut squarely to a 25 cm depth) harvested from the adjacent field and also planted 3 additional "plugs" of *Elymus multisetus* in each pen.

Vegetation characteristics

At the onset of the experiment in July 2012, I measured the percent cover of vegetation in each pen using point frame counts. The point frame is a standing frame that holds 10 vertically aligned pins, 5cm apart which are lowered into the vegetation. Plants species touched by each point were recorded at ground level, 10 cm, and 20 cm above ground. The vegetation, free space, and bare ground were measured with the frame held at two perpendicular angles per plot. The percent cover of plant species was assessed by the following formula: Cover of Spp A (# hits of Spp A/ total # of points per plot) x 100. Vegetation cover was analyzed by plant species and by native or non-native type. Non-native plots had between 0-25% native; un-manipulated native plots had 45-100% native, and experimentally restored plots had between 30-96% native plant cover (See Table 2). Experimental plots in which the cover of native plants did not fall into the above categories were removed from subsequent analysis; thirteen pens were removed from analysis, most of which were restored pens that did not meet an acceptable threshold of percent native cover. Un-manipulated open plots in either non-native or native dominated areas of the grassland (n=14) ranged between 0-71% native plant cover.

Table 2: Percentage of Plant-types and Heights by Assemblage and Plot-type

	Native and Non-native Plant Assemblage Characteristics (%)						Plant Height Characteristics (cm) (%)			
	NNAG*	NNF*	NF*	NPG*	NNPG*	BG*	0	5	10	20
Non-native	61.1	19.9	4	12.3	0.8	1.9	2.3	66.3	30.2	1.2
Native	34.8	1.1	1.2	58.4	4.4	0.1	0.1	44	38.8	17.1
Restored	41.3	5.7	2.7	49.5	0	0.7	0.7	53.3	35.5	10.4
Control	62.1	4.6	4.8	28	0	0.4	0.4	68.8	25.8	5

**Abbreviations: NNAG= non-native annual grass; NNF = non-native forb; NF = native forb; NPG= native perennial grass; NNPG = non-native perennial grass; BG = bare ground.*

Herbivore damage

I tagged and measured ten undamaged leaves of plant species that were commonly abundant, and some of which were known food sources for Orthopterans, in each of the experimental pens and open plots prior to spider treatment. Tagged native plant species were *Danthonia californica, Elymus glaucus, Hemizonia congesta, Eschscholizia californica,* and *Elymus multisetus.* Tagged non-native plants were *Plantago lanceolata, Rumex acetosella,* and *Cynosurus echinatus.* Tagged stems were uniformly distributed among the living plants ($\geq$ 5 plants) and as evenly as possible throughout the 1.5m^2 plot (Hudewenz et al. 2012). After the five week experiment, I collected the leaves and froze them for later analysis. I measured invertebrate chewing damage to leaves by; 1) the proportion of native and non-native leaves damaged per plot and, 2) the amount removed per leaf. Percent damage was estimated by comparing amount removed per leaf to leaf templates of similar size (placed under a protective cover of thick clear tape on white paper) that were undamaged leaves of the same species. The amount of chewing damage per leaf was measured as a comparable portion on an undamaged leaf using Image J software. I used ten representative preserved leaves of different sizes and shapes of each species for comparison (Nitschke et al 2010). The frequency of leaf damage per plot was calculated by dividing the total number of damaged stems by the total number of stems collected. Some markers were destroyed or missing due to animal activity. The average amount of damage per leaf was calculated by adding together the total amount of damage per plot across all stems collected and dividing by the total number of stems collected per plot.

Spider treatment

To mimic ambient spider density of approximately 1 individual per 2.25 m^{-2} (Suttle, 2005), I placed one field-collected *Schizocosa* spider in each experimental spider pen on a biweekly basis to maintain spider density during peak abundance (mid- June through July). Spiders were collected from several locations throughout the reserve with pitfall traps and by hand, at night, along meadow-woodland borders using a headlamp. For spider removal pens, all spiders were removed by hand and with an aspirator, and checked a weekly to ensure absence. All plant material within 15 cm of the interior and exterior edge of each plot was clipped to within 2 cm from the ground on a weekly basis to eliminate leaf bridges over flashing for spider escape or entry.

Statistical Analysis

To test for effects of spider, assemblage treatment, and meadow on both the frequency of undamaged stems and amount of chewing damage per damaged stem, I used GLM analyses (IBM® SPSS® Statistics version 20 2011). Meadow, assemblage (native, non-native, or restored), and spider treatment (spider or no-spider) were fixed factors and I included an interaction term between spider treatment and assemblage. I analyzed the frequency of damage to Hayfield Tarweed in relation to assemblage characteristics by using GLM analyses (IBM® SPSS® Statistics version 20 2011). For Hayfield Tarweed, in order to capture finer-scale variation within the treatments, meadow and spider treatment were fixed factors and, the percent cover of native perennial grass, non-native annual grass, non-native forbs and native forbs were covariates within the model. The assumptions for homogenous variance were met (Levene's Test for Equality of Error Variances F = 1.00, p =0.48). Assemblage temperature and humidity conditions were averaged over a daily and weekly basis.

Results

Temperatures in native and non-native microhabitats

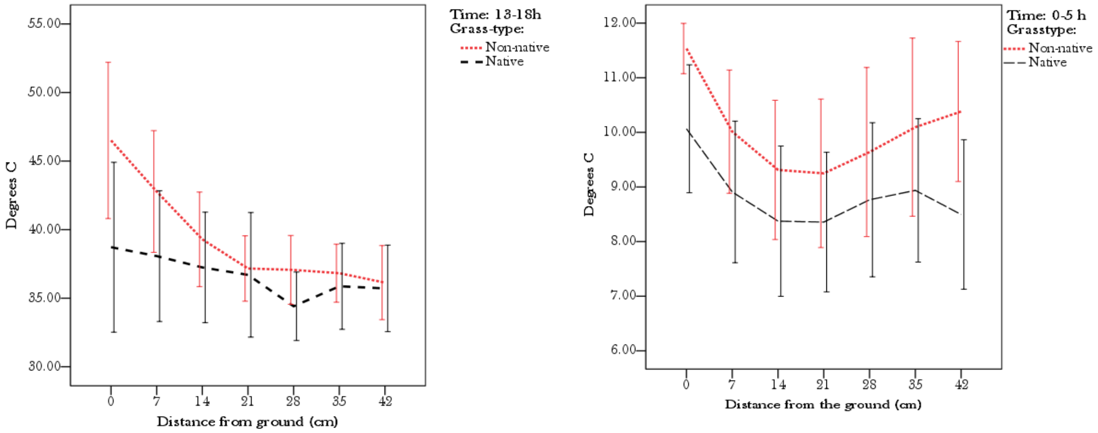
I found native assemblages were significantly cooler than non-native assemblages during the hottest (13-18 hrs) and coolest portions (0-5 hrs) of the day (Table 3). This difference was greatest closest to the ground surface (Figures 3-4).

Table 3: Temperatures (°C) in native and non-native assemblages

Time		**Non-native**			**Native**		
13-18 HRS		N	Mean	S.D.	N	Mean	S.D.
	Minimum*	47	28.0	7.6	48	24.9	6.8
	Maximum	47	51.4	8.1	48	50.4	6.0
	Mean*	47	**39.5**	**5.7**	**48**	**36.7**	**5.4**
0-5 HRS		N	Mean	S.D.	N	Mean	S.D.
	Minimum**	46	5.8	1.5	47	4.5	1.5
	Maximum*	46	16.1	6.7	47	13.8	3.5
	Mean**	46	**10.1**	**1.7**	**47**	**8.8**	**1.7**

** difference is significant at the p < 0.01 level

* difference is significant at the p < 0.05 level



Figures 3 - 4: Grassland temperature (°C) by distance from ground surface and assemblage type. Difference between assemblage types were greatest near the ground surface.

Temperature and light conditions in native, restored, and non-native enclosures

Contrary to the survey above, within enclosures, I found that native and restored enclosures were warmer than non-native enclosures. Over a 24 hour period, native and non-native plot temperatures were somewhat similar but restored plots were consistently warmer (Table 4). Native and restored plots were hottest and driest in the afternoon hours when diurnal Orthopteran activity peaks (Joern 2006). Native plots were cooler and moister than others during the night (1-6 hrs).

Table 4: Average Plot Temperatures and Daily Light Penetration (Watt hrs/day)

		24 hrs						13-18 hrs			1-6 hrs		
		Light	Degrees °C				% RH	°C		% RH	°C		% RH
Assemblage	N	Watt hrs	Avg	S.D.	Min.	Max.	Avg	Avg	S.D.	Avg	Avg	S.D.	Avg
Non-native	5280	6560	21	15	-0.94	61.5	52	35.0	11.1	37.7	7.5	3.4	61.1
Native	5280	6705	21	16	-0.91	60.0	50	36.6	10.3	5.5	6.7	3.6	80.8
Restored	4224	5930	22	16	2.11	63.5	53	40.2	12.01	17.1	8.4	2.9	74.7

Effects of spider presence, temperature, and prey growth stage on herbivore damage

Spider presence and ambient spider density (open plots) reduced the proportion of native leaves damaged by large invertebrate herbivores. The proportion of damaged native leaves was not significantly different between control and spider plots but both were significantly lower than in no spider plots (Figure 5).

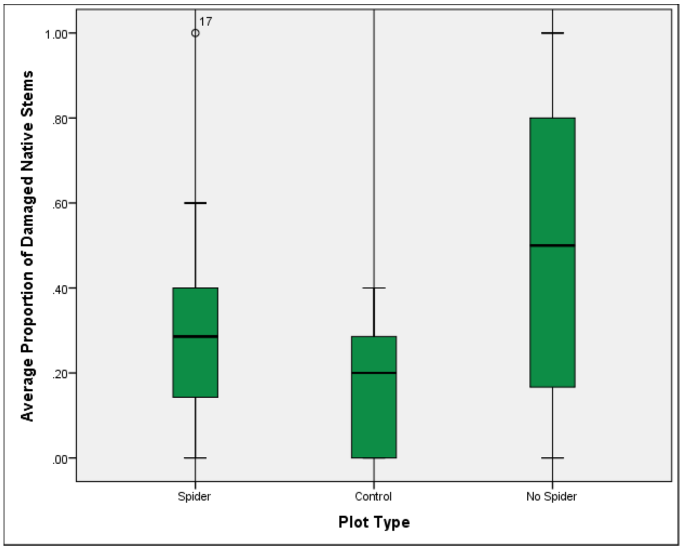


Figure 5: The percent of native plant stems damaged in the presence or absence of spiders, [GLM followed by Tukey's HSD post-hoc comparisons, $n = 71$, $F = 5.6$, $P < 0.01$; mean (Standard Error) No spider 0.44 (0.04), Spider 0.31 (0.04), Control (ambient spider density) 0.28 (0.05)].

GLM results revealed that spider presence did not reduce damage to all plant types when non-native plants were included in analysis (Table 5), and spiders had no effect on the average amount of damage per leaf.

Table 5: The Proportion of Damage by Plant Type and Plot Type

	Native Plants			Non-native Plants			All Plants		
Plot Type	Mean	N	S.D	Mean	N	S.D	Mean	N	S.D
Spider	0.31	24	0.23	0.34	16	0.32	0.35	27	0.20
Control	0.23	14	0.24	0.43	7	0.35	0.32	14	0.19
No Spider	0.44	27	0.32	0.31	17	0.31	0.43	30	0.27
Total	0.35	65	0.28	0.34	40	0.32	0.38	71	0.23

Spider and assemblage interactions Native plants were better protected from herbivore damage in the native-dominated assemblages when spiders were present, either stocked in pens, or at ambient densities in open, control plots [GLM, $n = 71$, $F = 2.8$, $p < 0.05$] (Table 6). There was also less herbivore damage to tagged native plants in non-native dominated plots when spiders were present, either in spider-stocked pens, or at ambient spider densities in open control plots.

Table 6: Plant Damage by Plot and Grass Assemblage

Native Plant Damage

	Spider (S)			No Spider (NS)				Control (Ambient)		
Assemblage	Mean	N	S.D.	Mean	N	S.D.	Δ S-NS	Mean	N	S.D.
Non-native	0.16	*5*	0.17	0.40	7	0.41	*0.25*	0.25	8	0.30
Native	0.31	11	0.13	0.48	8	0.36	*0.17*	0.20	6	0.14
Restored	0.40	8	0.32	0.44	12	0.25	*0.04*	-	-	-
Total	0.31	24	0.23	0.44	27	0.32	0.13	0.23	14	0.22

All Plant Damage

	Spider (S)			No spider (NS)			Δ S-NS	Control (Ambient)		
Assemblage	Mean	N	S.D.	Mean	N	S.D.		Mean	N	S.D.
Non-native	0.32	8	0.23	0.39	10	0.30	*0.08*	0.39	8	0.23
Native	0.35	11	0.17	0.45	8	0.32	*0.10*	0.24	6	0.10
Restored	0.38	8	0.22	0.44	12	0.24	*0.06*	-	-	-
Total	0.35	27	0.20	0.43	30	0.27	0.08	0.32	14	0.19

Effects of plant assemblage on herbivore damage

Contrary to expectations, rather than herbivore damage being lower in restored pens than in non-native pens, it was marginally higher than in non-native pens (Fig. 6). There was no significant difference between the proportion of native damaged stems in invaded and native assemblages, or between native and restored assemblages.

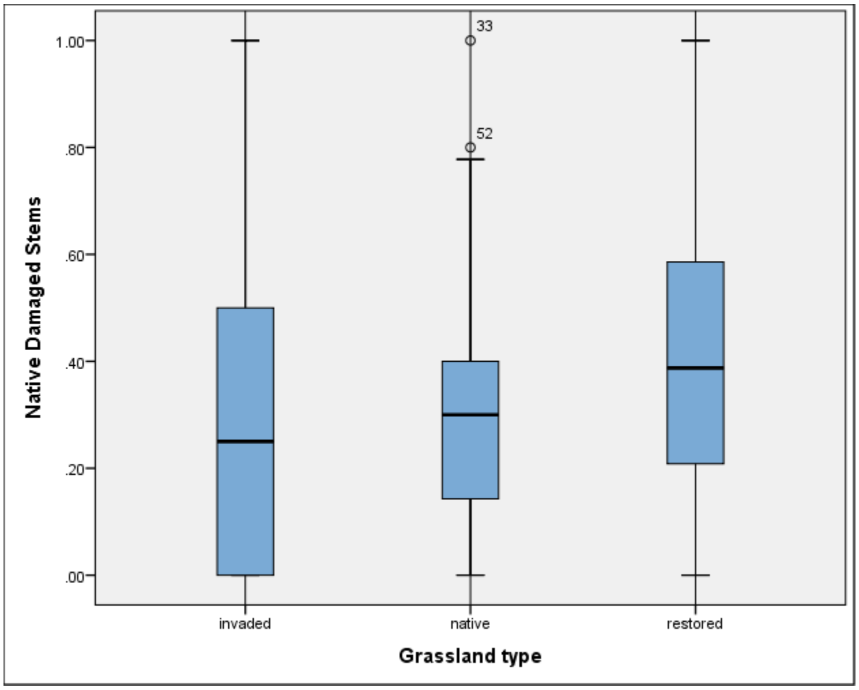


Figure 6: The average proportion of native stems damaged by assemblage, [GLM followed by Tukey's HSD post hoc comparisons for assemblage *n =71, F = 4.93, p=0.057*; mean (SE) Non-native 0.31 (0.04), Native 0.34 (0.04), Restored 0.42 (0.05)]

More native stems were damaged in restored pens but the proportion of *all* damaged stems was similar in native and non-native pens (Table 7). The proportion of all damaged stems was moderately but positively correlated with increasing cover of non-native annual grass (Fig. 7). Native stem damaged was not correlated with native or non-native plant cover.

Table 7: The average proportion of stems damaged (D) and the percent cover (%C) of plant-types by plot-type.

Plot-type		Average Number of Damaged Stems	Native Forbs		Non-native Forbs		Native Grass		Non-native Grass	
			D	%C	D	%C	D	%C	D	%C
Non-native	Mean (S.D.)	3.54 (2.6)	0.44 (0.4)	3(5)	0.37 (0.3)	19 (20)	0.32 (0.4)	3(6)	0.55 (0.09)	75 (18)
	N	26	11	23	17	23	6	23	3	23
Restored	Mean (S.D.)	4.1(2.3)	0.51 (0.3)	2(4)	0.54 (0.4)	6 (7)	0.43 (0.3)	44 (10)	0.17 (0.3)	39 (19)
	N	20	11	19	8	18	20	18	8	18
Native	Mean (S.D.)	3.4 (2.2)	0.29 (0.3)	1(4)	0.64 (0.3)	1(3)	0.37 (0.3)	48 (19)	0.50 (0)	31 (19)
	N	25	12	25	6	25	24	25	2	25
Total	Mean (S.D.)	3.65 (2.3)	0.41 (0.3)	2 (5)	0.46 (0.3)	9 (15)	0.39 (0.3)	31 (25)	0.31(0.3)	48 (27)
	N	71	34	67	31	66	50	66	13	66

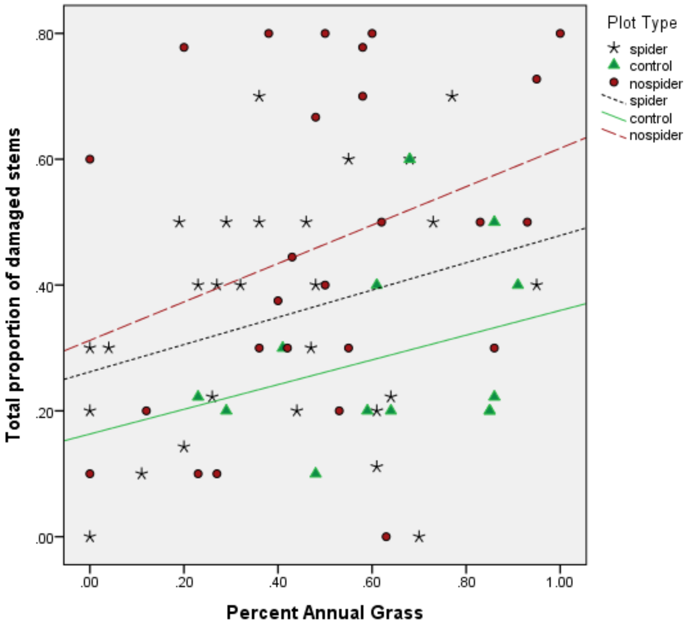
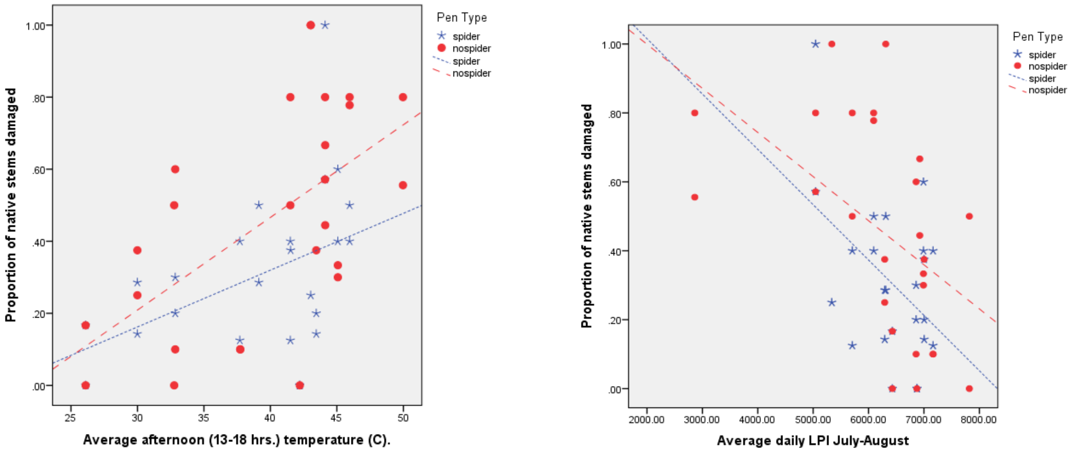


Figure 7: Plant Damage and Annual Grass Cover (%) by Plot type (r = 0.25, p = 0.041)

Overall, native plant damage was significantly correlated with average afternoon temperature (Fig. 8). Native plant damage was also negatively correlated with the light penetration index (LPI))(Fig. 9).



Figures 8: Native plant damage in relation to the average plot temperature ($r = 0.41$, $p < 0.01$) and Figure 9: Light penetration index ($r = -0.49$, $p < 0.001$).

Damage by plant species across meadow and plot-types

A few plant species sustained the larger proportion of overall plant damage (Table 8). The native species Blue Wild Rye (*Elymus glaucus*) and Hayfield Tarweed (*Hemizonia congesta*) were damaged at higher rates than they were marked in the field. Hayfield Tarweed damage increased with non-native annual grass cover, decreased with native perennial grass cover ($F = 6.03$, $p < 0.05$), and decreased with non-native forb cover ($F = 4.5$, $p = 0.05$), (Fig. 10). Spiders had a marginal effect in decreasing tarweed damage ($p = 0.085$).

The non-native species of Common Plantain (*Plantago lanceolata*) and Hedgehog Dogtail Grass (*Cynosurus echinatus*) were also damaged at slightly higher rates than they were marked in the field. California Oat Grass (*Danthonia californica*) evidenced the lowest frequency of damage by large invertebrate herbivores. There was no evidence of assemblage type or spider treatment on damage received to these plant species.

Table 8: Tagged Plant Species Damage

Plant Species	# Marked	% Damaged	% of all Marked	% of all Damaged
Non-native Plants				
C.echinatus	43	47	5	8
P.lanceolata	74	56	9	16
R.acetocella	108	31	13	13
Native Plants				
D.californica	173	25	20	17
E.californica	49	31	6	6
E.glaucus	190	55	22	40
E.multisetus	55	22	6	5
H. congesta	156	51	18	31

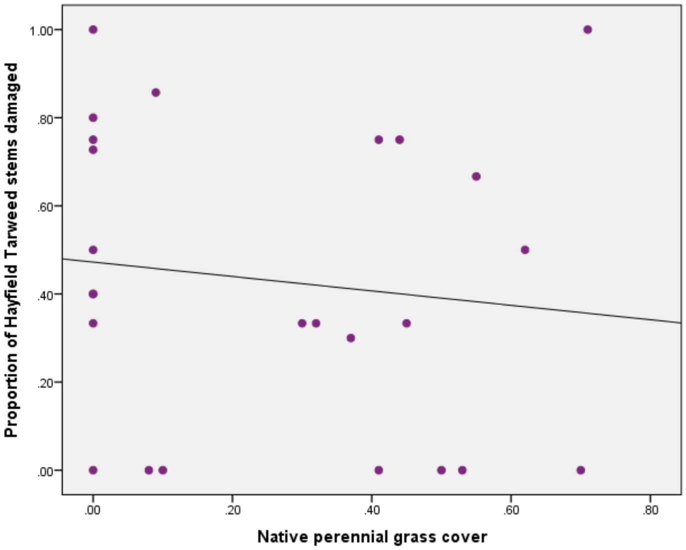


Figure 10: Hayfield Tarweed damage in relation to native perennial grass cover [GLM, *n =24, F = 5.6, p< 0.05*].

Meadow effects on the rate of damage: Across the three meadows, evidence of herbivore chewing damage was highest in the smallest meadow, Sprague (18,444 m^2), lower in the intermediate sized meadow, Angelo (25,898 m^2), and least in the largest meadow, Wilanor (72,578 m^2) (Fig. 11) .

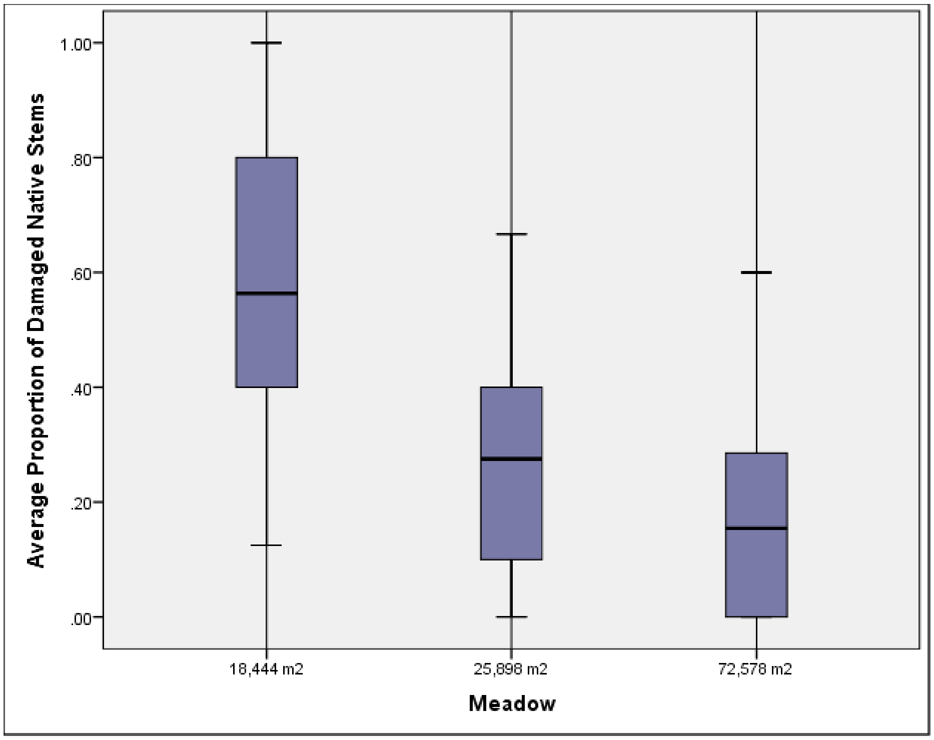


Figure 11: Native plant damage by meadow size [GLM, *n =71, F = 13.13, P <0.0001]*

Angelo meadow, the second largest meadow, was the warmest of the three meadows, followed by Sprague, and Wilanor, the largest meadow. The plot temperatures were most likely related to position of the plots in relation to the afternoon sun; those plots that received the most afternoon sun also had higher temperatures and higher rates of damage. Within Angelo Meadow, experimental blocks were placed closer to the central portions of this south-facing meadow than in the other two meadows. In Sprague Meadow, also south-facing, non-native and restored plots received more direct afternoon sunlight. Within the largest meadow, Wilanor, plots faced east and received more afternoon shade (Table 9). Restored plots were the hottest plots in two of the three meadows. It is likely that a combination of temperature, humidity, and plant food sources contributed to the amount of damage to plants within each meadow.

Table 9: Meadow and Plot Conditions and Plant Damage

			Plant Cover per plot		Damage to tagged stems		Temperature (°C)	
Meadow	Assemblage	Distance to forest (m)	% Native Cover	Canopy height (cm)	% Native stems	% All stems	24 HR	13-18 HRS
Sprague	*Non-native*	2.4	6	6.5	51	56	21.9	41.6
	Native	28.0	60	9.3	57	58	21.1	38.4
	Restored	1.3	52	7.2	72	65	21.9	46.7
	Average	10.6	37	7.6	60	60	21.6	42.2
Angelo	*Non-native*	24.0	0	5.6	5	20	20.7	42.2
	Native	22.0	57	9.7	26	27	22.5	41.8
	Restored	9.0	51	9.2	46	47	24.5	44.1
	Average	18.3	31	8.2	25	31	22.6	42.7
Wilanor	*Non-native*	2.0	16	6.9	13	37	20.5	27.4
	Native	2.3	72	9.4	21	23	20.4	33.4
	Restored	2.0	64	8.0	17	20	20.5	79.0
	Average	2.1	54	8.1	17	27	20.3	28.9

Discussion

I found mixed results on the temperature differences between native and non-native grassland patches (Hypothesis 1). Although an earlier and more detailed survey of temperatures in native and non-native microhabitats revealed that native assemblages are generally cooler than non-native assemblages, in restored pens, plot level albedo may have decreased as a result of soil disturbance and the removal of perennial non-native forbs. Enclosures located in native assemblages were warmer than those in non-native assemblages, but this may be due to largely to landscape factors. Restored enclosures were the warmest; microhabitat level disturbance may have contributed to this warmth.

I confirmed that spider presence reduced the amount of chewing damage to native plants. Evidence here suggests that the effect of spiders was stronger in cooler areas of the grassland, but the cooler areas of the grassland, in this case, were dominated by non-native plant species. Spiders may have had a stronger effect because the prey found here were predominately nymphal grasshoppers, or because of the cooler environment, or both factors. These results suggest that plants residing in native dominated areas suffered greater damage. This may be due to in part to the fact that these areas of the grassland are home to the bulk of non-native katydids, but also plants found in newly restored habitats, suffered greater damage. Furthermore, the somewhat warmer native assemblages that were further away from the shaded boundary had higher proportions of damaged stems than non-native pens. Evidence of damage to Hayfield Tarweed, which was evenly distributed throughout the assemblages, increased as non-native annual grass cover increased, suggesting that non-native assemblages may facilitate herbivore feeding on smaller populations of native plants.

The third hypothesis was confirmed; spider presence evidenced a stronger effect on native plant damage in non-native dominated areas of the grassland where nymphal grasshoppers are more abundant. This evidence is preliminary, however, and further research is needed to untangle the effects of temperature and prey body size on spider predation within the grassland. This data suggests that the earlier hatching and earlier maturation of the non-native katydids may help them escape spiders during their most active season and warrants further study of the effects of this katydid on California's remaining native grass stands.

Contrary to expectations, I was not able to confirm that restoring grassland reduced plant damage, instead, damage increased within the restored areas. These enclosures, although closest to the woodland boundary, had the highest temperatures. This data suggests that early stage restoration may prove to be a boon for hungry herbivores but a detriment to the predatory capacity of the grassland's dominant wolf spider. Early stage restoration is critical not only for plant establishment but also for greater damage from heat-loving arthropod herbivores that prefer native hosts.

Lastly, I confirmed the hypothesis that native plants experience greater herbivore damage in hotter areas of the grassland. Contrary to expectations, restored plots were the warmest, not non-native dominated plots, and native plants found here had the highest rates of herbivore damage. As warmer habitats, newly restored habitats benefited the least from spider presence; there was little to no difference in the amount of plant damage between spider and no-spider pens in restored pens. The overall amount of damage in restored pens was highest in comparison to pens in other grassland areas. In general, herbivore feeding increased with higher average afternoon temperatures but not with greater light intensity, as restored plots had the lowest light intensity. Given that I know from previous research (Joern 1990), Orthopterans prefer to reside in areas that help them reach maximal development and increase their digestive efficiency; it makes sense that warmer environments sustained higher levels of chewing damage.

Conclusion

Orthopteran damage increased with temperature but spider presence inhibited their feeding, as evidenced from the frequency of chewing damage to plant stems. Spiders were more effective at protecting native plants in cooler areas of the grassland, which, due to landscape positional difference, was dominated by non-native plants. However, non-native grass cover was also associated with greater native forb damage. Overall, Orthopteran foraging (both grasshoppers and katydids) had a stronger impact on the populations of native rather than non-native plants. Orthopteran interactions with spiders are effected by the nature of the plant assemblages in which they are found. This data suggests that across the grasslands, as temperatures increase, herbivore damage will also increase and native spider activity will be reduced, similar to findings from other research systems (Laws and Joern, 2013, Joern et al 2006). If indeed temperatures are higher in non-native assemblages of the grassland as anticipated, these higher temperatures could contribute to higher invertebrate feeding rates and reduced foraging by the dominant and native wolf spider.

Although not studied here, this continuous cycling of feeding during the hottest and driest time of year could contribute to weakening of the native plant systems and lead to poorer fertility and reduced competitive interactions with invasive plants. This study reveals that the impacts of predators that indirectly protect plants are context-dependent and are relevant to grassland restoration.

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Appendix 1:

Table 1: Plant species found in forest boundary to meadow interior transects within Sprague, White-House, and Wilanor meadows of the Angelo Coast Range Reserve

Non-native Transects		# Counts	% of plant population	**Native Transects**		# Counts	% of plant population
1	*Aira carophylla*	340	0.25	1	*Achillea millefolium*	6	0.00
2	*Bromus diandrus*	5	0.00	2	*Agrostis grandiflora*	5	0.00
3	*Bromus carinatus*	4	0.00	3	*Aira carophylla*	18	0.01
4	*Bromus laevipes*	5	0.00	4	*Bromus carinatus*	41	0.02
5	*Briza minor*	1	0.00	5	*Bromus diandrus*	44	0.02
6	*Bromus hordeaceus*	107	0.08	6	*Bromus hordeaceus*	132	0.06
7	*Convulvulus arvensis*	9	0.01	7	*Bromus laevipes*	8	0.00
8	*Clarkia sp.*	5	0.00	8	*Bromus tectorum*	3	0.00
9	*Carex pansa*	20	0.01	9	*Carex sp.*	314	0.13
10	*Cynosurus echinatus*	31	0.02	10	*Clarkia sp.*	7	0.00
11	*Danthonia californica*	329	0.24	11	*Convulvulus arvensis*	24	0.01
12	*Daucus carota*	2	0.00	12	*Croton setigerus*	1	0.00
13	*Elymus glaucus*	34	0.02	13	*Cynosurus echinatus*	23	0.01
14	*Croton setigerus*	7	0.01	14	*Danthonia californica*	512	0.22
15	*Galium aparine*	8	0.01	15	*Digitalis purpurea*	3	0.00
16	*Holcus lanatus*	4	0.00	16	*Elymus glaucus*	394	0.17
17	*Hypocherus glabra*	73	0.05	17	*Eschsholizia californica*	9	0.00
18	*Hypocherus radicata*	7	0.01	18	*Fragaria vesca*	9	0.00
19	*Lotus micranthus*	31	0.02	19	*Galium aparine*	151	0.06
20	*Lupinus bicolor*	16	0.01	20	*Geranium dissectum*	7	0.00
21	*Hemizonia congesta*	50	0.04	21	*Hemizonia congesta*	246	0.10
22	*moss*	16	0.01	22	*Holcus lanatus*	50	0.02
23	*Cirisium vulgare*	1	0.00	23	*Hypocherus glabra*	2	0.00
24	*Castilleja exserta*	1	0.00	24	*Iris douglasiana*	2	0.00
25	*Plantago lanceolata*	73	0.05	25	*Juncus sp.*	4	0.00
26	*Poa sp.*	3	0.00	26	*Lotus micranthus*	4	0.00
27	*Vulpia myuros*	180	0.13	27	*Lotus purshianus*	9	0.00
28	*Fragaria vesca*	4	0.00	28	*Lupinus formosa*	95	0.04
29	*Wyethia mollis*	2	0.00	29	*moss*	59	0.02
				30	*Perideridia bolanderia*	5	0.00
				31	*Plantago lanceolata*	5	0.00
				32	*Poa sp.*	4	0.00
				33	*Psuedotsuga menziesii*	1	0.00
				34	*Pteridium aquilinum*	7	0.00
				35	*Ranunculus sp.*	2	0.00

36	*Rubus discolor*	3	0.00
37	*Rumex acetosella*	13	0.01
38	*Solanum douglasii*	27	0.01
39	*Stachys sp.*	3	0.00
40	*Torilis arvensis*	21	0.01
41	*Trifolium cyathiferum*	2	0.00
42	*Trifolium sp.*	9	0.00
43	*Vicia sp.*	53	0.02
44	*Vulpia myuros*	33	0.01
45	*Wyethia mollis*	8	0.00

Table 2: Plant species found in patches of Walker, White-house and Wilanor meadow s of the Angelo Coast Range Reserve

Non-native patches		# Counts	*% of plant population*	Native patches		# Counts	*% of plant population*
1	*Achillea millefolium*	10	0.00	1	*Achillea millefolium*	21	0.01
2	*Aira carophylla*	462	0.19	2	*Agrostis pallens*	2	0.00
3	*Avena barbata*	6	0.00	3	*Aira carophylla*	107	0.05
4	*Briza minor*	9	0.00	4	*Briza minor*	8	0.00
5	*Brodea sp*	1	0.00	5	*Brodea sp*	2	0.00
6	*Bromus diandrus*	44	0.02	6	*Bromus carinatus*	2	0.00
7	*Bromus hordeaceus*	257	0.11	7	*Bromus diandrus*	24	0.01
8	*Bromus japonicus*	57	0.02	8	*Bromus hordeaceus*	185	0.08
9	*Carex sp.*	338	0.14	9	*Bromus japonicus*	56	0.02
10	*Clarkia sp*	6	0.00	10	*Calamagrostis bolanderi*	9	0.00
11	*Convolvulus arvensis*	3	0.00	11	*Carex sp.*	322	0.14
12	*Croton setigerus*	4	0.00	12	*Cirsium vulgare*	17	0.01
13	*Cynosurus echinatus*	5	0.00	13	*Convolvulus arvensis*	10	0.00
14	*Danthonia californica*	618	0.26	14	*Cynosurus echinatus*	8	0.00
15	*Daucus carota*	18	0.01	15	*Dactylis glomerata*	1	0.00
16	*Elymus glaucus*	13	0.01	16	*Danthonia californica*	1029	0.44
17	*Elymus multisetus*	1	0.00	17	*Elymus glaucus*	235	0.10
18	*Eschscholizia californica*	23	0.01	18	*Eschscholizia californica*	3	0.00
19	*Galium aparine*	74	0.03	19	*Galium aparine*	24	0.01
20	*Geranium dissectum*	13	0.01	20	*Geranium dissectum*	7	0.00
21	*Hemizonia congesta*	42	0.02	21	*Hemizonia congesta*	27	0.01
22	*Holcus lanatus*	29	0.01	22	*Hypochaeris glabra*	5	0.00
23	*Hordeum brachyantherum*	9	0.00	23	*Lotus micranthus*	11	0.00
24	*Hypochaeris glabra*	9	0.00	24	*Lotus purshianus*	8	0.00
25	*Lotus micranthus*	23	0.01	25	*Perideridia bolanderi*	36	0.02
26	*Lotus purshianus*	1	0.00	26	*Plantago lanceolata*	23	0.01
27	*Lupinus bicolor*	2	0.00	27	*Poa sp.*	4	0.00
28	*Lupinus formosa*	2	0.00	28	*Rumex acetosella*	7	0.00
29	*Perideridia bolanderi*	2	0.00	29	*Sanicula crassicaulis*	3	0.00
30	*Plagiobothrys nothofulvus*	1	0.00	30	*Scutellaria californica*	6	0.00
31	*Plantago lanceolata*	50	0.02	31	*Stachys ajugoides*	6	0.00
32	*Poa sp*	8	0.00	32	*Torilis arvensis*	2	0.00
33	*Rumex acetosella*	4	0.00	33	*Trifolium campestre*	14	0.01
34	*Sanicula crassicaulis*	10	0.00	34	*Trifolium cyathiferum*	1	0.00
35	*Scutellaria californica*	9	0.00	35	*Vicia americana*	25	0.01
36	*Torilis arvensis*	1	0.00	36	*Vulpia myuros*	79	0.03
37	*Trichostema lanceolatum*	91	0.04	37	*Wyethia mollis*	2	0.00

38	*Trifolium campestre*	6	0.00
39	*Vicia sp.*	5	0.00
40	*Vulpia myuros*	131	0.05

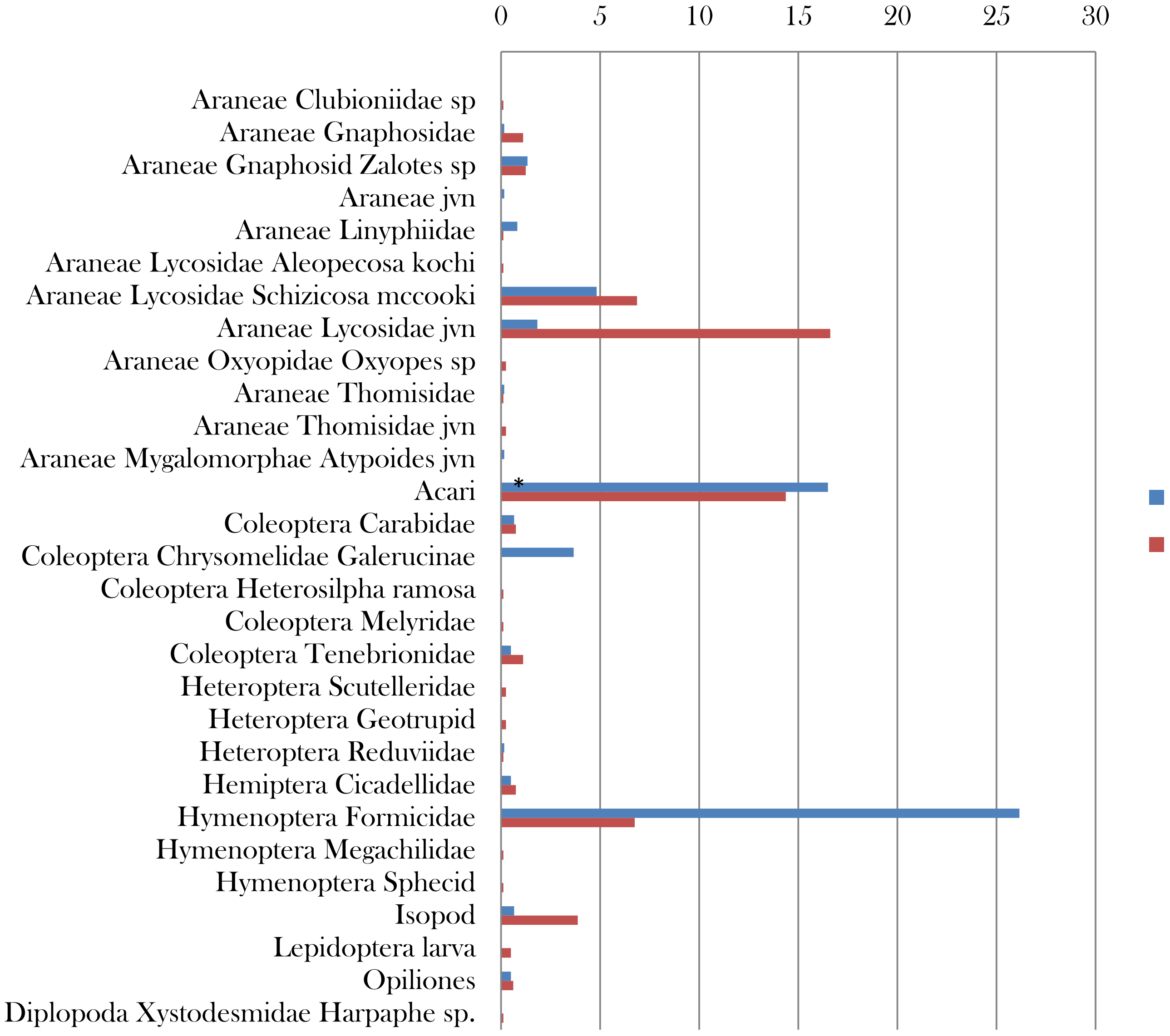

Figure 1: Arthropods Captured in Pitfall Traps

Table 3: Functional Groups of Species Captured in Pitfall Traps along Transects (30m)

Predators	**Non-native**	**Native**
Araneae	N	N
Aleopecosa kochi	0	1
Araneae juvenile	1	2
Clubioniidae	0	1
Gnaphosidae	9	19
Linyphiidae	5	1
Lycosidae juvenile	11	133
Lycosidae S.mccooki	29	55
Oxyopidae	0	2
Thomisidae	1	1
Coleoptera *Carabidae*	4	6
Heteroptera		
Geocoridae		2
Reduviidae	1	1
Hymenoptera Sphecidae		1
Opiliones	3	5
Vulnerable arthropods	N	N
Orthoptera *Grillidae* nymph	0	2
Araneae juveniles	12	135
Lepidoptera larva	0	4
Scavenging arthropods	N	N
Acari	99	115
Archaeognatha	6	8
Coleoptera		
Heterosilpha ramosa	0	1
Tenebrionidae Coelocnemis sp.	1	1
Tenebrionidae Iphthiminus serratus	2	5
Hymenoptera *Formicidae*	157	54
Diplopoda *Harpaphe sp.*	0	1
Isopoda	4	31

Figure 2: Arthopods observed by transect type

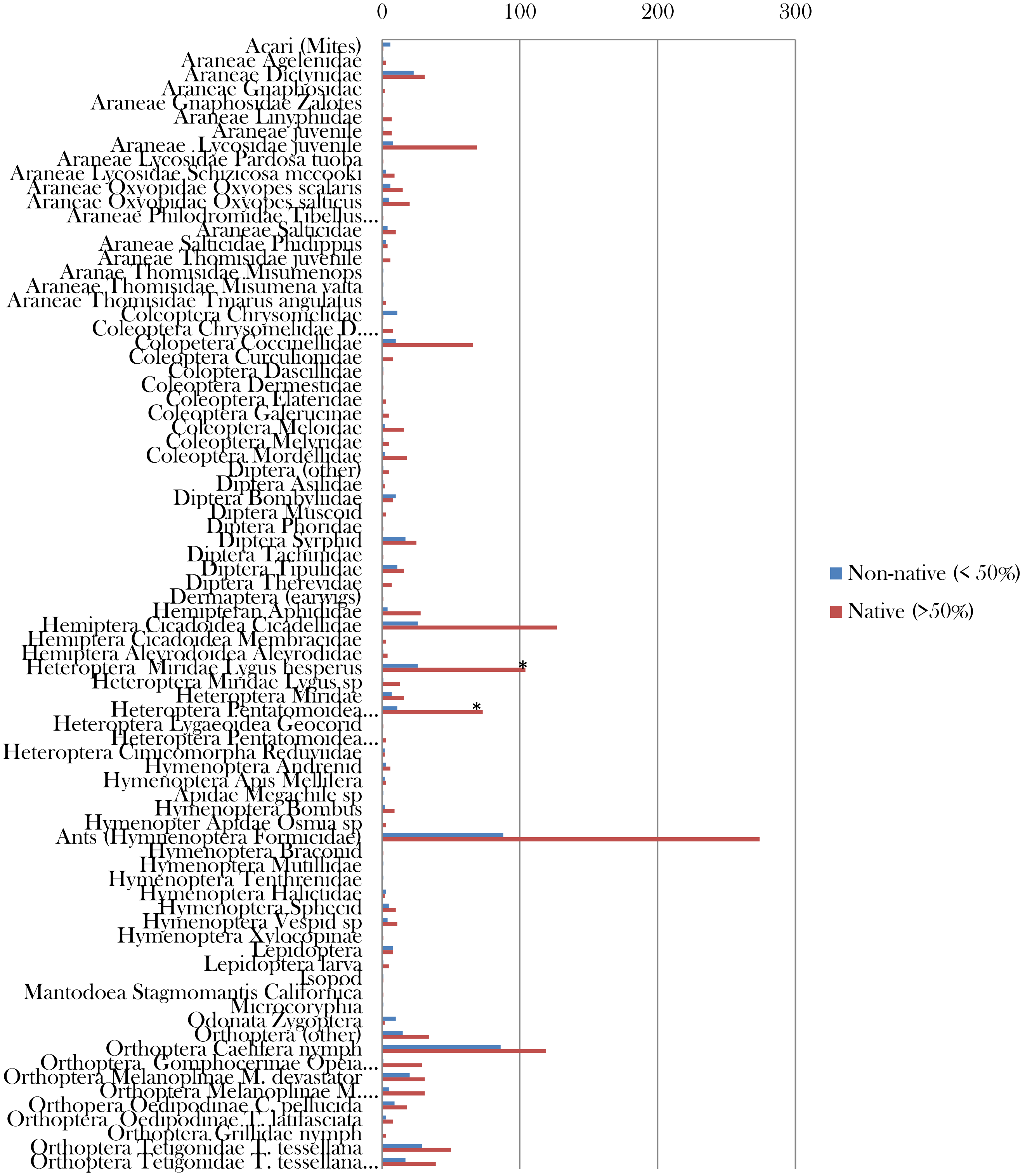

Table 4: Functional groups of species observed in transects (30m)

Pollen/nectar feeders	**Non-native**	**Native**
Hymenoptera	N	N
Anthophila, Andrenidae	3	6
Anthophila, Apis	2	3
Anthophila, Bombus	2	9
Anthophila, Halictidae	3	2
Anthophila, Megachile	1	0
Anthophila, Osmia	0	3
Anthophila, Xylocopinae	0	1
Ichneumonidae, Braconidae	0	1
Symphyta, Tenthredinidae	1	0
Coleoptera		
Meloidae	2	16
Mordellidae	2	18
Diptera		
Bombyliidae	10	8
Syrphidae	17	25
Predators	Non-native	Native
Araneae	N	N
Agelenidae	1	3
Araniella sp.	1	0
Dictynidae	23	31
Gnaphosidae	0	3
Araneae juvenile	9	85
Linyphiidae	0	7
Lycosidae Pardosa tuoba	0	1
Lycosidae Schizocosa mccooki	3	9
Oxyopidae	11	36
Philodromidae	0	1
Salticidae	7	14
Thomisidae	3	3
Colopetera *Coccinellidae*	10	66
Diptera		
Asilidae	1	2
Tachinidae	0	1
Stratyiomyidae	0	7
Heteroptera		
Geocoridae	0	1
Reduviidae	2	2

Hymenoptera Sphecidae	5	10
Mantodea	0	1
*Sap-feeders (***Heteroptera***)*	N	N
Cicadellidae	26	127
Lygus sp.	27	117
Membracidae	0	3
Miridae	7	16
Pentatomidae	0	3
Scutelleridae	11	73
Scavengers		
Acari	6	1
Archaeognatha	1	0
Coleoptera *Dermestidae*	0	1
Dermaptera	0	1
Hymenoptera *Formicidae*	88	274

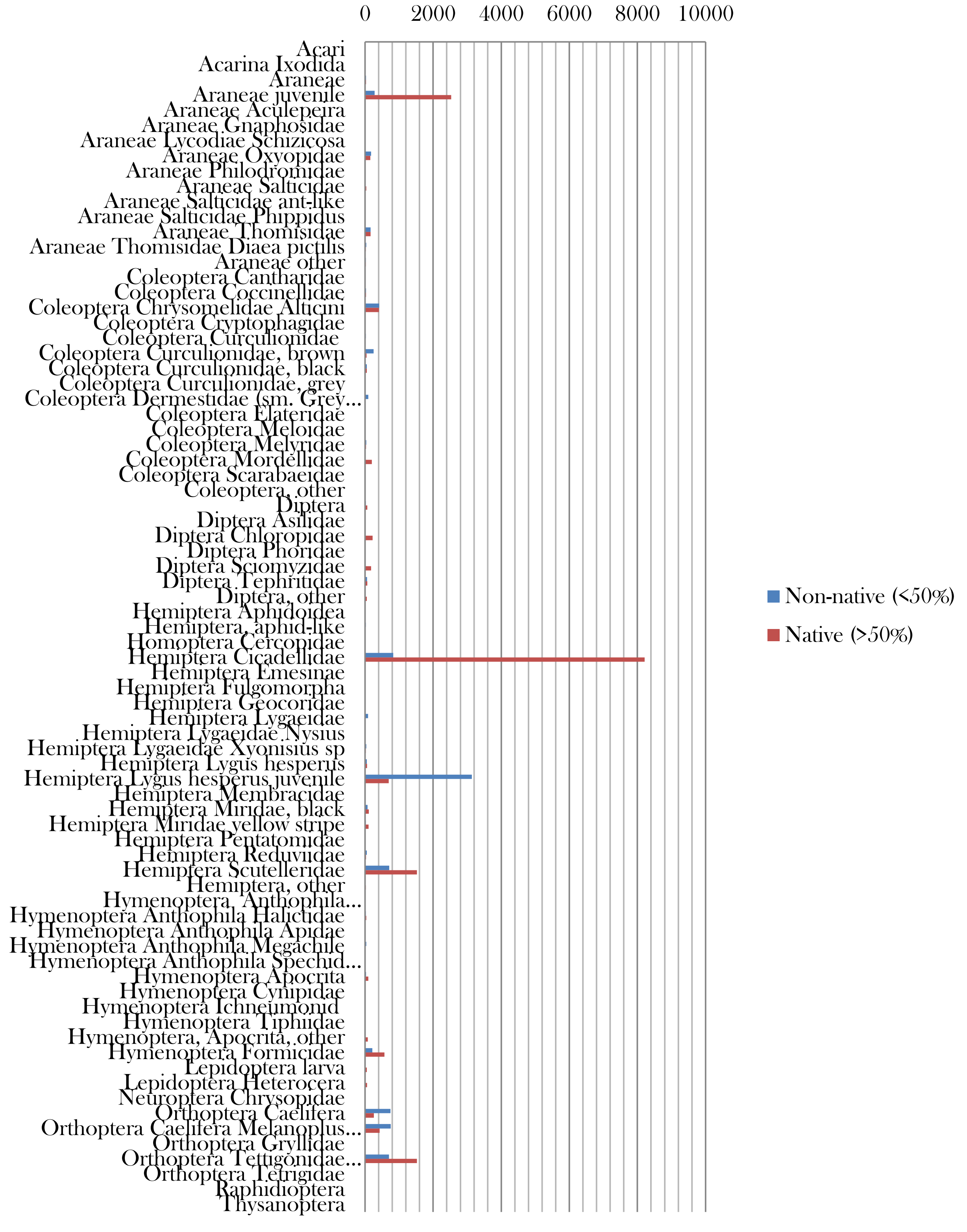

Figure 3: Arthropods captured in sweep-net surverys

Table 5: Functional groups of species captured in grassland sweep-net surveys		
Pollen and nectar feeders	**Non-native**	**Native**
Hymenoptera		
Anthophila, Andrenidae	4	3
Anthophila, Apis	5	0
Anthophila, Bombus	1	0
Anthophila, Megachile	2	1
Anthophila, Osmia	32	13
Apocrita	59	158
Coleoptera		
Meloidae	3	8
Mordellidae	3	196
Lepidoptera, Heterocera	14	59
Predators (excluding spiders)	**Non-native**	**Native**
Coleoptera		
Carabid chlaenus	0	1
Carabidae(other)	1	0
Coccinellidae	28	27
Melyridae Collops sp.	36	27
Heteroptera		
Geocoridae	15	15
Reduviidae	30	13
Diptera		
Asilidae	2	12
Stratiomyidae	0	1
Sciomyzidae	0	174
Neuroptera		
Chrysopidae	1	3
Raphidioptera	1	5
Mantodea	1	1
Hymenoptera, *Pompilidae*	0	1
Sap-feeders (Heteroptera)	Non-native	Native
Aphididae	19	1
Cercopoidea	1	16
Cicadellidae	825	8209
Cicadomorpha	1	0
Coreidae	1	0
Emesinae	4	0

Fulgaroidea	13	15
Lygaeidae Xyonysius sp	39	23
Lygus (1)	1	0
Lygus (2)	0	13
Lygus (3)	10	4
Lygus (4)	78	3
Lygus (5)	0	1
Lygus hesperus	3186	753
Membracidae	17	9
Miridae (black)	75	114
Nysius sp.	11	1
Pentatomidae	17	11
Scutelleridae (1)	134	322
Scutelleridae (2)	578	1203
Stenotus binotatus	19	102

Appendix 2:

Table 1: Spiders observed in transects		
Spiders Identified	Non-native (<50%)	Native (> 50%)
Agelenidae	1	3
Dictynid	23	31
Gnaphosidae		
Orodrassus sp.	0	1
Zalotes sp.	0	1
Juvenile (unid)	1	7
Linyphiidae	0	7
Lycosidae		
Pardosa tuoba	0	2
Schizocosa mccooki	3	9
Juvenile lycosid	8	69
Oxyopidae		
Oxyopes salticus	5	20
Oxyopes scalarus	6	15
Philodromidae	1	3
Philodromidae ***Tibellus sp.***	0	1
Salticidae	7	14
Thomisidae		
Misumena vaita	1	0
Misumenops sp.	1	0
Juvenile Thomisidae	0	6
Total	***57***	**189**

Table 2: Spiders Captured in Pitfall Traps		
Spiders Identified	Non-native (< 50%)	Native (> 50%)
Aleopecosa	0	1
Atypoides	1	0
Clubioniidae	0	1
Gnaphosidae		
Orodrassus sp.	0	3
unidentified Gnaphosidae	1	2
Zalotes sp.	8	10
Juvenile Gnaphosidae	0	4
Lycosidae		
Juvenile Lycosidae	11	133
Schizocosa mccooki	29	55
Oxyopidae		
Oxyopes salticus	0	1
Oxyopes scalarus	0	1
Thomisidae	0	1
Misumenops sp.	1	0
Juvenile Thomisidae	0	2
Unidentified species	1	0
Total	**52**	**214**

Table 3: Spiders from Sweep-net surveys		
Spiders Identified	Non-native (< 50%)	Native (> 50%)
Araneae	7	8
Araneidae *Aculepeira sp.*	1	3
Dictynidae	1	1
Gnaphosidae	2	4
Juvenile spiders	283	2530
Linyphiidae	0	1
Lycosidae *Schizocosa mccooki*	2	3
Juvenile lycosid	1	1
Miturgidae	0	1
Oxyopidae sp.	175	158
Philodromidae *Tibellus oblungus*	2	7
Salticidae	17	40
Salticidae (ant mimic)	0	2
Salticidae *Phippidus sp.*	0	2
Thomisidae	159	160
Thomisidae *Diaea pictilis*	33	22
Unidentifiable	22	25
Total	**705**	**2968**