CHANGES IN ARTHROPOD ABUNDANCE AND DIVERSITY WITH INVASIVE GRASSES

A Thesis

by

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ABSTRACT

Changes in Arthropod Abundance and Diversity with Invasive Grasses

(August 2011)

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Invasive grasses can alter plant communities and can potentially affect arthropods due to specialized relationships with certain plants as food resources and reproduction sites. Kleberg bluestem (*Dichanthium annulatum*) is a non-native grass and tanglehead (*Heteropogon contortus*) is native to the United States, but recently has become dominant in south Texas. I sought to: 1) quantify changes in plant and arthropod communities in invasive grasses compared to native grasses, and 2) determine if grass origin would alter effects. I sampled vegetation and arthropods on 90 grass patches in July and September 2009 and 2010 on the King Ranch in southern Texas. Arthropod communities in invasive grasses were less diverse and abundant, compared to native grasses; I also documented differences in presence and abundance of certain orders and families. Because arthropods play integral roles in pollination, decomposition, and as food resources for wildlife, such declines are likely to have significant cascading effects.

DEDICATION

I dedicate this thesis to everyone who helped me along the way. I want to thank my parents for all their unconditional love and support, Shannon for being the best friend I could ever have, and Dave for so many reasons I cannot possibly list them all here. Without you guys I never could have done this.

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CHAPTER I: EFFECTS OF INVASIVE PLANTS ON ARTHROPOD COMMUNITIES AND FUNCTIONAL GROUPS: A REVIEW

ABSTRACT

Invasive plants often alter the structure and composition of vegetation communities, with concomitant effects on arthropods. To reveal general patterns and better understand changes, I examined 39 peer-reviewed scientific articles that investigated effects of invasive plants on arthropod communities and functional groups. Nearly half (19/39) of studies examined community-level changes; 13 documented decreases in total arthropod abundance and richness at various taxonomic levels or changes in species composition, and 6 studies documented increases or no change in community-level measures. Decreases in herbivore abundance, richness, or composition were documented in 24 studies, for both specialist and generalist groups; 4 studies reported increases in abundance of some generalist herbivores, particularly certain families or species of Orthoptera. Abundance of certain pollinator groups decrease with invasive plants in 3 studies. Responses of arthropod predators to invasive plants also varied; 6 studies documented decreases in predator abundance, presence, or richness, but 3 studies reported increases in certain predaceous arthropods. These increases in abundance were related to changes in vegetation structure that benefitted predators: increased predator mobility with simplified vegetation, avoidance of tidal flooding with increased ground litter, and larger webs and increased web-building activity in invasive plants. Detritivores increased in abundance with increased ground litter and decaying vegetation in 7 studies; whereas 6 studies documented decreases

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Format and Style follow Conservation Biology in abundance or richness. Changes in presence and abundance of various functional groups may have implications for trophic dynamics within the arthropod community. Although many studies have examined the influence of invasive plants on arthropods, knowledge gaps still remain, specifically concerning generalist herbivores, pollinators, non-arachnoid predators, and parasitoids. Invasive plants alter arthropod communities in diverse ways; these changes could have far-reaching, cascading effects on higher trophic levels that depend on arthropods as food resources and on ecosystem processes, such as decomposition and pollination.

INTRODUCTION

The introduction and spread of invasive plants is a source of conservation concern worldwide (Vitousek et al. 1996; Blossey 1999; Didham et al. 2005). Invasive plants often can out-compete native plants, resulting in lower vegetation diversity and abundance (Pimentel et al. 1999; Bakker & Wilson 2001). Some invasive plants have characteristics that aid in propagation or establishment; many successful invaders are able to grow quickly and establish before native plants, utilize poor soil conditions, and tolerate disturbance and variable climatic conditions (Celarier & Harlan 1955; Kelly & Skipworth 1984; Vitousek et al. 1996; Bodle & Hanlon 2001; Rutman & Dickson 2002; Herrera & Dudley 2003). In some cases, invasive plants create unfavorable growing conditions for native plants via allelopathy or by altering availability of soil nutrients (Christian and Wilson 1999; Stermitz et al. 2003). Plants introduced into novel areas also generally lack the natural herbivores found in their native ranges and thus can become dominant (i.e., enemy release hypothesis, Keane & Crawley 2002; Tallamy 2004). Increased dominance by invasive plants can alter vegetation structure and composition, historic fire regimes, nutrient cycling, and habitat quality for wildlife species (Vitousek 1990; Vitousek et al. 1996; Blossey 1999; Christian & Wilson 1999). An estimated 5,000 species of plants have been introduced into the United States; however, a relatively small percentage of these species negatively impact the ecosystems they invade (Simberloff 1981; Morse et al. 1995).

Although most invasive plants in the United States are non-native, a few plant species have increased in distribution and dominance in their native ecosystems (Vitousek et al. 1996; Bockelmann & Neuhaus 1999; Lynch & Saltonstall 2002; Buelow 2009). Tanglehead (*Heteropogon contortus*) is a warm season bunchgrass that historically has been distributed sparsely throughout the southern United States (Hatch et al. 1999; USDA 2007). However, the distribution and dominance of tanglehead in many areas of South Texas has increased within the last decade (F. Smith, personal communication). Changes in land management practices or shifting rainfall patterns may be responsible for this increase (Tothill 1966; Orr & Paton 1997), although the mechanism currently is unknown. *Elymus athericus* (no common name) also has spread rapidly in its native range, and greatly altered vegetation structure of many wetlands in Europe; this increased spread may be due to increases in nitrogen in wetland soils and the ability of *E. athericus* to monopolize this resource (Bockelmann & Neuhaus 1999; Leport et al. 2006). Common reed (*Phragmites australis*) also has increased in abundance, and as with tanglehead and *E. athericus*, environmental and landscape changes have been proposed to explain these increases (Saltonstall 2002). Although common reed previously was assumed to be non-native, it is now considered native to areas of the United States, including New England and parts of the San Francisco Bay estuary (Orson

1999; Goman & Wells 2000; Saltonstall 2002). Increases in dominance and distribution of these native plants can result in changes in vegetation structure and composition similar to those created by non-native plants (Slobodchikoff & Doyen 1977; French & Major 2001; Herrera & Dudley 2003; Cuda et al. 2007; Wilkie et al. 2007; Wu et al. 2009), such that the origin of the plant is of little importance.

Invasive plants often alter structural characteristics of vegetation communities (Slobodchikoff & Doyen 1977; Breytenbach 1986; Herrera & Dudley 2003). Increases in abundance of many invasive plants can result in increased vegetation cover, a concomitant decrease in bare ground (French & Major 2001; Standish 2004; Topp et al. 2008; Wolkovich et al. 2009), as well as increases in vegetation biomass and density (Cable 1971; Cox et al. 1990; Toft et al. 2001; Standish 2004; Lindsay & French 2006; Spyreas et al. 2010). Increases in vegetation biomass often are associated with subsequent increases in the amount and depth of litter and decomposing vegetation (Lambrinos 2000; Toft et al. 2001; Standish 2004; Petillon et al. 2005; Topp et al. 2008; Wolkovich et al. 2009). Vegetation height may increase or decrease with plant invasions, depending on the plant species and level of dominance (Slobodchikoff & Doyen 1977; Toft et al. 2001; Hickman et al. 2006; Topp et al. 2008; Spyreas et al. 2010). These structural changes can affect microclimates within vegetation, altering ambient temperatures and the amount of light and moisture available (French & Major 2001; Standish 2004; Lindsay & French 2006; Wolkovich et al. 2009).

Increased dominance by invasive plants clearly alters the composition of vegetation communities (Cox et al. 1988; Hickman et al. 2006; Sands et al. 2009; Wu et al. 2009). Many invasive plants have been associated with overall decreases in diversity of native plants (Slobodchikoff & Doyen 1977; Herrera & Dudley 2003; Cuda et al. 2007; Wilkie et al. 2007; Wu et al. 2009; Spyreas et al. 2010), including decreases in the abundance and diversity of forbs (Flanders et al. 2006; Hickman et al. 2006; Sands et al. 2009). Other studies also have detected a marked decrease in the abundance and diversity of woody plants in areas dominated by an invasive plant (Jonas et al. 2002). In one study, the increased cover of several invasive grasses actually facilitated growth in a native shrub (*Artemisia californica*), although this seems to be relatively uncommon (Wolkovich 2009).

Invasive plants may modify soil characteristics as well (Standish 2004; Kappes et al. 2007; Wolkovich et al. 2009), which can contribute to further changes in composition of native plant communities. Increased dominance of invasive plants may be associated with increased total root mass, increased soil moisture, and changes in soil nutrients – increases in nitrogen and decreases in calcium and potassium (Slobodchikoff & Doyen 1977; Witkowski 1991; Standish 2004; Gratton & Denno 2005; Kappes et al. 2007). Invasive plants also may alter soil salinity and pH, creating environments where native plants can no longer grow (Windham & Lathrop 1999; Kappes et al. 2007).

ARTHROPODS

Arthropods fulfill a diversity of ecological roles within natural ecosystems, in addition to providing economic benefits in agricultural systems (Wilson 1987; Isaacs et al. 2009). Arthropods function as prey resources for many taxa, as important predators, and as pollinators and seed dispersers (Bond & Slingsby 1984; Wilson 1987; Isaacs et al. 2009). Arthropods also are important for decomposition and nutrient cycling, creating nutrient-rich soils for plants (Seastedt & Crossley 1984). Changes in vegetation and soil characteristics resulting from plant invasions may be especially detrimental for arthropods because of their relative limited mobility and because many species require specific host plants as food or as sites for reproduction (Wilson 1987; Kremen et al. 1993; Niemela & Mattson 1996; Tallamy 2004; Burghardt et al. 2008). Soil moisture, ambient temperature, light intensity, and pH are also important determinants of the distribution and reproductive success of certain arthropod taxa, and these structural changes resulting from invasive plants may modify habitat quantity and quality (Niemela & Mattson 1996, Antvogel & Bonn 2001; de Souza & de Souza Modena 2004; Lassau et al. 2005).

Numerous researchers have documented changes in overall arthropod abundance, biomass, species composition, diversity, and richness at several levels of taxonomic organization, including order, family, morphospecies, and species with increased dominance by invasive plants (Table 1.1). In general, these community-level measures of abundance, richness, and diversity decreased in areas dominated by invasive plants relative to areas dominated by native plants (Slobodchikoff & Doyen 1977; Samways et al. 1996; Herrera & Dudley 2003; Ernst & Cappucino 2005; Gratton & Denno 2005; Hickman et al. 2006; Levin et al. 2006; Gerber et al. 2008; Wolkovich et al. 2009; Wu et al. 2009; Litt & Steidl 2010, Simao et al. 2010, Table 1.1), however there are a few examples where overall abundance or species richness increased, did not change, or depended on season or trapping method (Jonas et al. 2002; Greenwood et al. 2004; Harris et al. 2006; Fork et al. 2010, Table 1.1). When a single species of invasive plant dominates and the plant community becomes more homogeneous,

Table 1.1. Summary of literature (39 papers) examining changes in arthropod communities with invasive plants.

Reference	Invasive plant	Abundance	Biomass	Richness	Diversity	Spp[a] comp[b]
Slobodchickoff & Doyen 1977	*Ammophila arenaria*	–			– spp	
Samways et al. 1996	many spp of plants/trees			– spp	– spp	
Lambrinos 2000	*Cortaderia jubata*	–				Δ
Jonas et al. 2002	*Bromus inermis*	varied by trap		varied by trap	varied by trap	
Herrera & Dudley 2003	*Arundo donax*	−50% aerial spp	−50% aerial spp	−50% tax[c] aerial spp	− Shannon's	
Greenwood et al. 2004	*Salix x rubens*	− canopy spp			– mspp[d]	Δ
Harris et al. 2004	*Ulex europaeus*	no Δ		+ spp		Δ
Standish 2004	*Transcendentia fluminensis*	− (weak trend)		− RTU[e] (weak)		Δ
Ernst & Capuccino 2005	*Vincetoxicum rossicum*	–				
Gratton & Denno 2005	*Phragmites australis*	–		– spp	– spp	
Hickman et al. 2006	*Bothriochloa ischaemum*		−25%			
Levin et al. 2006	*Spartina alterniflora* X *Spartina foliosa*	−75%	−57%			Δ
Lindsay & French 2006	*Chrysanthemoides monilifera* ssp. *rotundata*	no Δ				Δ
Gerber et al. 2008	*Fallopia* spp.	−40%	−60%	−20-30% in mspp		
Wolkovich et al. 2009	several grasses	–				

Table 1.1. Continued

Reference	Invasive plant	Abundance	Biomass	Richness	Diversity	Spp[a] comp[b]
Wu et al. 2009	*Spartina anglica*	+ in mixed sites		− fam[f] & spp		Δ
Fork 2010	*Conium maculatum* & *Phalaris aquatica*	no Δ		no Δ in order		
Litt & Steidl 2010	*Eragrostis lehmanniana*	−		− fam & mspp		
Simao et al. 2010	*Microstegium vimineum*	− 39%		− spp		

[a] Species.

[b] Composition (dominant species making up total arthropod community).

[c] Taxonomic richness.

[d] Morphospecies.

[e] Recognizable taxonomic unit.

[f] Family.

vegetation structure and microclimate conditions are simplified, such that a diversity of arthropods cannot find appropriate habitat conditions (Breytenbach 1986; Haddad et al. 2001). Vegetation communities that provide heterogeneous structure at many scales can support a more diverse arthropod community. For example, monotypic ground litter supported fewer species of arthropods and provided less diverse composition and structure for those species that persisted (Hansen 2000). Arthropods also have different microclimate requirements depending on life stage, seeking optimal conditions for larval development, protection from desiccation and extreme temperatures, and overwinter survival (Phillips et al. 1991; Pickett and Bugg 1998; Boughton 1999; Morris 2000). Even when microclimate conditions are less important, thick stands of invasive plants potentially can impede flight, reducing mobility and available habitat (Samways et al. 1996). Overall, these changes associated with invasive plants can affect various functional groups differently depending on their specific requirements for food resources, reproduction, and microclimate.

Functional Groups: Herbivores

Because many phytophagous arthropods are host-specific to varying degrees, native arthropod herbivores may not recognize or be able to use novel plants as food resources (Ehrlich & Raven 1965; Strong et al. 1984; Tallamy 2004). Because the energy in invasive plants may be largely unavailable (Tallamy 2004), overall abundance of herbivorous arthropods may decrease (Ernst & Cappucino 2005; Gerber et al. 2008, Simao et al. 2010, Table 1.2). Because a more diverse vegetation community can support a more diverse community of herbivorous arthropods (Niemela & Mattson 1996), shifts in plant composition also can result in changes in species composition or decreases in

Table 1.2. Summary of literature (39 papers) examining changes in arthropod functional groups with invasive plants

		Functional Groups		
Reference	Invasive plant	Herbivores	Predators	Detritivores
Herrera & Dudley 2003	*Arundo donax*	few observed in invasive		
Ernst & Capuccino 2005	*Vincetoxicum rossicum*	− abund of herbivores & pollinators		
Gratton & Denno 2005	*Phramites australis*	Δ in spp[a] comp[b]		+ abund[c]
Levin et al. 2006	*Spartina alterniflora* X *Spartina foliosa*	− density	no Δ	+ density
Lindsay & French 2006	*Chrysanthemoides monilifera* ssp. *Rotundata*			+ abund
Kappes et al. 2007	*Reynoutria* spp.	− abund	+ abund	+ abund
Gerber et al. 2008	*Fallopia* spp.	− in abund & mspp[d] rich[e]		
Wu et al. 2009	*Spartina anglica*	Δ in herbivore spp comp		
Simao et al. 2010	*Microstegium vimineum*	− 31%	− 61% (includes parasitoids)	

[a] Species.
[b] Composition (dominant species making up total arthropod community).
[c] Abundance.
[d] Morphospecies.
[e] Richness.

richness (Ernst & Cappucino 2005; Gerber et al. 2008; Wu et al. 2009).

Arthropod herbivores that specialize on one or a few select plants as food resources or for reproduction may be most negatively affected by the loss of native forbs and other plant species associated with the introduction and spread of an invasive plant (Ehrlich & Raven 1965; Williamson 1996; Tallamy 2004). Switching to a new host plant may be extremely difficult; the native herbivore generally does not share an evolutionary history with the invasive plant and may not be able to adapt quickly to using the novel plant as a food resource (Auerbach & Simberloff 1988; Novotny et al. 2003; Tallamy 2004). Many species in the orders Hemiptera (true bugs) (including suborders Auchenorrhyncha and Sternorrhyncha) and Lepidoptera (moths, butterflies, and skippers), and a few Thysanoptera (thrips) and Coleoptera (beetles) species are considered host-specific during some or all life stages (Triplehorn & Johnson 2005). Some researchers detected a complete absence (Derraik et al. 2001) or an overall decline in the abundance of hemipterans (Lambrinos 2000; Litt & Steidl 2010; Spyreas et al. 2010), whereas others documented changes in the composition of hemipteran families or species (Samways et al. 1996; Wilkie et al. 2007; Litt & Steidl 2010; Simao et al. 2010) when an invasive plant dominates the vegetation community (Table 1.3). For example, presence of Coreidae (leaf-footed bugs) and Lygaeidae (seed bugs) and abundance of Coreidae and Cicadellidae (leaf-hoppers) decreased with increased dominance of an invasive grass (Litt & Steidl 2010, Table 1.3). Researchers in one study detected a positive relationship between cover of the invasive grass and cicadellid abundance and species richness, but this resulted from the growth of a native shrub, which was facilitated by conditions created by the invasive grass (Wolkovich 2009, Table 1.3). Many

Table 1.3. Summary of literature (39 papers) examining changes in arthropod orders with invasive plants

Reference	Invasive plant	Acari	Aranae	Coleoptera	Collembola
Slobodchickoff & Doyen 1977	*Ammophila arenaria*			− spp[a] rich[b] of 1 fam[c]	
Samways et al. 1996	several spp of plants/trees			1 sp only in inv[d] 5 fams only in nat[e]	
Crisp et al. 1998	several plants			Δ in comp[f]	
Lambrinos 2000	*Cortaderia jubata*		+ abund[g]		
Toft et al. 2001	*Transcendentia fluminensis*			no Δ in abund/comp	
Jonas et al. 2002	*Bromus inermis*			+ abund − fam div[h]	
Herrera & Dudley 2003	*Arundo donax*			Δ comp (seasonal)	
Harris et al. 2004	*Ulex europaeus*			+ detrivore abund − herbivore abund[i]	
Standish 2004	*Transcendentia fluminensis*			Δ comp	
Gratton & Denno 2005	*Phramites australis*		− 80% abund (web-builders)		
Petillon et al. 2005	*Elymus athericus*		+ abund 1 sp − abund 1 sp		
Lindsay & French 2006	*Chrysanthemoides monilifera* ssp. *rotundata*	− abund	− abund		
Gerber et al. 2008	*Fallopia* spp.		− mspp[j] rich		
Topp et al. 2008	*Reynoutria* spp.			− abund/spp rich + detritivore abund	
Pearson 2009	*Centaurea maculosa*		+ abund of some spp		
Wolkovich 2009	several grass spp		+ abund/spp rich		
Wolkovich et al. 2009	several grass spp	− abund 1 fam			+ abund 1 fam − abund 2 fams
Fork 2010	*Conium maculatum* & *Phalaris aquatica*			no Δ	
Litt & Steidl 2010	*Eragrostis lehmanniana*			− mspp rich −abund − pres/abund of 1 fam	
Petillon et al. 2010	*Elymus athericus*		+ in abund 1 sp		
Simao et al. 2010	*Microstegium vimineum*		- abund	- abund of 1 fam (seasonal)	

Table 1.3. Continued

Reference	Invasive plant	Diptera	Hemiptera	Hymenoptera
Breytenbach 1986	*Hakea sericea*	+ spp div		− ant spp div
Samways et al. 1996	several spp of plants/trees		spp only in nat	1 fam only in nat ant spp only in nat
Wheeler 1999	*Eragrostis curvula*		+ abund/dist[k] 2 spp	
Lambrinos 2000	*Cortaderia jubata*		− abund	− abund
Webb et al. 2000	*Ammophila arenaria*	+ abund		− ant spp/mspp rich
Derraik et al. 2001	*Agrostis capillaris* & *Anthoxanthum odoratum*		many spp only in nat	
French & Major 2001	*Acacia saligna*			Δ ant spp comp − ant mean abund
Toft et al. 2001	*Transcendentia fluminensis*	no Δ in spp rich & abund[l] + abund of 1 sp		
Harris et al. 2004	*Ulex europaeus*	Δ in spp comp[l] + spp rich[l] & 1 fam		
Gratton & Denno 2005	*Phramites australis*	− abund of 1 sp		
Wilkie et al. 2007	*Chrysanthemoides monilifera* spp. *rotundata*		Δ in spp comp	
Ostoja et al. 2009	*Bromus tectorum*			+ ant abund, fg[m] div − in ant spp div
Wolkovich 2009	several grass spp		+ abund/spp rich 1 fam	
Wolkovich et al. 2009	several grass spp			− abund of 2 spp + abund of other spp
Fork 2010	*Conium maculatum* & *Phalaris aquatica*			− abund & spp rich
Litt & Steidl 2010	*Eragrostis lehmanniana*	− abund, abund of 1 fam + abund 1 fam	− overall abund −abund of 2 fams	
Simao et al. 2010	*Microstegium vimineum*		− abund of 1 fam (seasonal)	
Spyreas et al. 2010	*Phalaris arundinacea*		− abund	

Table 1.3. Continued

Reference	Invasive plant	Lepidoptera	Neuroptera	Orthoptera	Thysanoptera
Bock et al. 1986	*Eragrostis lehmanniana* & *E. chloromelas*			− grasshopper abund Δ spp comp	
Samways & Moore 1991	*Cupressus arizonica & Pinus roxburghii*			+ spp rich/abund (for 1 plant) − sp rich (1 plant)	
Samways et al. 1996	several sp of plants/trees			no abund Δ in inv 1 sp only in nat	
Lambrinos 2000	*Cortaderia jubata*			none in inv	
Derraik et al. 2001	*Agrostis capillaris* & *Anthoxanthum odoratum*	some only in nat	only in nat		most only in nat
Jonas et al. 2002	*Bromus inermis*			+ abund, spp rich + Shannon div	
Harris et al. 2004	*Ulex europaeus*	no Δ spp rich			
Standish 2004	*Transcendentia fluminensis*			none in inv	
Lindsay & French 2006	*Chrysanthemoides monilifera* ssp. *Rotundata*				− abund
Burghardt et al. 2008	several sp of non-native ornamentals	− larval abund − larval spp rich			
Litt & Steidl 2010	*Eragrostis lehmanniana*	− mspp rich		− overall abund −abund of 1 fam + in abund of 1 fam	

[a] Species.
[b] Richness.
[c] Family.
[d] Invasive.
[e] Native.
[f] Composition (dominant species making up total arthropod community)..
[g] Abundance.
[h] Diversity.

Table 1.3. Continued

[i] 1 sp of weevil excluded.
[j] Morphospecies.
[k] Distribution.
[l] Only for fungus gnats.
[m] Functional group.

Lepidoptera species are specialist herbivores, particularly during the larval stage (Ehrlich & Raven 1965; Burghardt et al. 2008); researchers in one study found that abundance and species richness of Lepidoptera larvae was lower on non-native plants (Burghardt et al. 2008, Table 1.3 [p. 12]). Some studies have documented an absence of, or decrease in, abundance of thrips (order Thysanoptera) in areas dominated by invasive plants (Derraik et al. 2005; Lindsay & French 2006, Table 1.3 [p. 12]), however little research has focused on Thysanoptera in a non-agricultural setting. Few researchers have considered specialist Coleoptera species, particularly the family Curculionidae (weevils), although researchers in one study indicated these beetles were found only on their specific host plants (Harris et al. 2004, Table 1.3 [p. 12]). If host plants are replaced by an invasive plant, species of specialist herbivores may no longer persist (Tallamy 2004).

Pollinators also may be affected by invasive plants (Ernst & Cappucino 2005, Table 1.2 [p. 10]*)*; introductions of an invasive plant species can change functional relationships between pollinator and plant (Breytenbach 1986). With increased dominance of an invasive plant, there may be concomitant decreases in abundance of flowering plants and of nectar, an extremely important food source for many pollinating arthropods (Hickman et al. 2006; Lopezaraiza-Mikel et al. 2007, Sands et al. 2009). Species richness and overall abundance of pollinating arthropods may decline with reduced food resources (Kruess and Tscharntke 2002). For example, the order Hymenoptera (sawflies, bees, wasps, and ants) includes many pollinators, and may decrease in abundance with the increased dominance of an invasive plant (Lambrinos 2000; Ernst & Capuccino 2005; Triplehorn & Johnson 2005; Fork 2010 Tables 1.2 [p. 10] & 1.3 [p. 12]). If an invasive plant does provide flowers, the novel plant may favor generalist arthropods and exclude specialists (Lopezaraiza-Mikel et al. 2007). Even if patches of native plants can be maintained, the number of pollinators typically decreases with increased distance from native vegetation (Carvalheiro et al. 2010). Such fragmentation effects could cause small patches of diverse native vegetation to be largely unvisited by pollinators if they are surrounded by invasive plants.

Invasive plants may be less detrimental to generalist herbivores because, in theory, they may be more likely to incorporate a novel plant into their diet easily and effectively (Tallamy 2004). In practice, many generalist herbivores have difficulty utilizing invasive plants as food because of low tissue nitrogen and high lignin and starch content (Haddad et al. 2001) and may still prefer certain native plants, however these effects are not well understood (Morris 2000; Tallamy 2004; Schaffner et al. 2011). Some researchers observed an overall decrease in abundance of herbivorous beetles in areas dominated by invasive plants (Crisp et al. 1998; Topp et al. 2008), whereas in other studies, researchers reported no differences in abundance or richness (Toft et al. 2001, Table 1.3 [p.12]). These diverse responses may be explained by variation in the families comprising the community. Declines in species richness and overall abundance of the family Tenebrionidae (darkling beetles), and decreased presence of Elateridae (click-beetles) have been documented in vegetation dominated by certain invasive plants (Slobodchikoff & Doyen 1977; Herrera & Dudley 2003; Litt & Steidl 2010, Table 1.3 [p. 12]). I found a surprising absence of studies examining potential effects of invasive plants on leaf beetles (Chrysomelidae), another common generalist herbivore. Responses of Orthoptera to invasive plants were more well-documented, but variable (Table 1.3 [p. 12]); some researchers detected lower overall abundance (Bock et al. 1986; Litt & Steidl

2010), lower species richness (Jonas et al. 2002) or an absence of Orthoptera in areas dominated by invasive plants (Lambrinos 2000; Standish 2004), whereas researchers in other studies documented an increase in abundance (Samways & Moore 1991; Samways et al. 1996, Table 1.3 [p. 12]). The response of certain orthopteran families or species to invasive plants also varied; researchers in one study in Arizona documented an increase in abundance of the family Tettigoniidae (katydids) and a decrease in Acrididae (short-horned grasshoppers) (Litt & Steidl 2010) and another group of researchers in Arizona detected a lower abundance of 8 species of Orthoptera and a greater abundance of 1 species in areas dominated by invasive plants (Bock et al. 1986, Table 1.3 [p. 12]). The order Orthoptera contains a diversity of species, including some omnivores that feed on dead plant material and live prey (Triplehorn & Johnson 2005); these species may benefit from or be unaffected by structural changes in vegetation associated with invasive grasses, such as increases in detritus.

Other arthropod groups, such as adult lepidopterans, require specific plants for reproduction rather than as food resources (Gilbert & Singer 1975; Thompson and Pellmyr 1991). Adult preferences for certain plant species may be based on chemical aspects that provide cues for oviposition or specific structural characteristics that will maximize larval growth and development, such as plant size, proximity to other host plants, and availability of specific microclimate conditions (Thompson & Pellmyr 1991; Haribal & Renwick 1998). Relatively few plant species may provide the conditions appropriate for successful reproduction and thus, a decrease in diversity of plant species could be detrimental for lepidopterans and other taxa (Tallamy & Shropshire 2009).

Functional Groups: Predators

Arthropod predators may be affected indirectly by invasive plants (Gratton & Denno 2005; Pearson 2009; Petillon et al. 2010); decreases in abundance and diversity of other arthropod taxa may result in decreases in overall abundance and richness of predators because of a lack of prey (Hunter & Price 1992; Gratton & Denno 2005; Gerber et al. 2008; Mgobozi et al. 2008, Table 1.2 [p. 10]). Aranae (spiders), some Opilonies (harvestmen), most Neuroptera (lace-wings), some Coleoptera, Acari (mites), and Hymenoptera, and a few Diptera (flies) species are predaceous (Triplehorn & Johnson 2005). Decreases in the abundance of predators in areas dominated by invasive plants have been detected for Carabidae (ground beetles) and Coleoptera overall, as well as for the family Anystidae in the order Acari (mites) (Herrera & Dudley 2003; Topp et al. 2008; Wolkovich et al. 2009). Other groups of arthropod predators, including Neuroptera, are less likely to be present in areas dominated by invasive plants (Derraik et al. 2005, Table 1.3 [p. 12]).

Decreases in presence or abundance are not systematic among arthropod predators; variation in prey preferences may drive diverse responses. Presence of some hymenopteran families such as Vespidae (social wasps) may increase with increased dominance of an invasive plant because they feed on a wide variety of arthropods, whereas abundance of other hymenopteran families such as Pompilidae (spider wasps) may decrease because of reductions in abundance and diversity of spiders, their main food resource (Samways et al. 1996; Triplehorn & Johnson 2005; Litt & Steidl 2010, Table 1.3 [p. 12]). Researchers examined the impacts of invasive plants on parasitoids in only 1 study (another type of predator mostly from the order Hymenoptera), finding a decrease in overall abundance, potentially driven by a lack of host species present in invasive grass (Simao et. al 2010). Clearly, more study needs to be done on invasive plants, and this group of arthropod predators.

Some spiders and other predators (e.g., order Opiliones, some Diptera) also may be affected by the structural changes in vegetation associated with an invasive plant (Herrera & Dudley 2003; Gratton & Denno 2005; Petillon et al. 2005; Kappes et al. 2007; Pearson 2009; Wolkovich 2009, Table 1.3 [p. 12]). For example, some species of spiders can exploit the increase in ground litter or simplified vegetation associated with an invasive grass increasing in abundance and causing a shift in spider species composition (Pearson 2009; Petillon et al. 2010, Table 1.3 [p. 12]). In one study an overall increase in predator abundance was observed in areas dominated by an invasive plant, however the predator group in this study consisted only of Opiliones (an order with detritivorous species) which may have benefitted from the simplified structure and increased detritus associated with the invasive plant (Triplehorn & Johnson 2005; Kappes et al. 2007). A species of Dolichopodidae (long-legged flies) was the most common non-arachnid predator in native plant-dominated sites and was virtually absent from invasive plant-dominated sites (Gratton & Denno 2005); this change may be related to a decrease in prey because the simplified vegetation structure favored concealed-feeding herbivores that may be largely unavailable to predators (Gratton & Denno 2005, Table 1.3 [p. 12]). Changes in predaceous arthropod communities associated with invasive plants are complicated and require more investigation, especially for non-arachnid predator groups.

Functional Groups: Detritivores

Of all the functional groups, detritivores are likely to benefit most from the introduction and spread of an invasive plant (Gratton & Denno 2005). Detritivores are represented by species from several orders including Collembola (spring-tails), Acari, Microcoryphia (bristle-tails), several Opiliones, and some Coleoptera and Diptera (Triplehorn & Johnson 2005). Increases in ground litter and decaying vegetation associated with many species of invasive plants can provide more food and preferred microclimate conditions for detritivores (Sukava & Huhta 1998; Longcore 2003; Levin et al. 2006, Table 1.2 [p. 10]). Several researchers detected an increase in the abundance of detritivores in areas dominated by invasive plants (Gratton & Denno 2005; Levin et al. 2006; Lindsay & French 2006; Topp et al. 2008; Litt & Steidl 2010, Tables 1.2 [p. 10] & 1.3 [p. 12]). Increases in invasive plants could lead to an ecosystem-wide shift – from a food web based on primary productivity of plants to one dependent on detritus (Gratton & Denno 2006; Levin et al. 2006).

Although many detritivores may benefit from invasive plants, others may decrease in overall abundance or be completely absent from invaded sites (Lambrinos 2000; Jonas et al. 2002; Petillon et al. 2005; Lindsay & French 2006, Tables 1.2 [p. 10] & 1.3 [p. 12]). For example, abundance of globular springtails (Collembola, Sminthuridae) increased, but abundance of two elongate-bodied springtails (Collembola, Entomobryidae and Isotomidae) decreased in areas dominated by invasive plants (Wolkovich et al. 2009, Table 1.3 [p. 12]). A similar pattern was observed for certain families of fungus gnats; abundance of the family Keroplatidae increased whereas abundance of other families (Mycetophilidae and Ditomyiidae) did not change with an invasive plant (Toft et al.

2001, Table 1.3 [p. 12]). This variability in response within taxa is not well understood, but may be due to changes in the microclimate created by the invasive plant that benefit some groups but are detrimental for others (Toft et al. 2001; Wolkovich et al. 2009).

Ants

Ants (order Hymenoptera, family Formicidae) do not fit neatly into a single functional group and can be classified as herbivores, predators, and detritivores; the effects of invasive plants on this family are relatively well-studied and are as variable as their ecological roles (Triplehorn & Johnson 2005; Table 1.3 [p. 12]). Decreases in total abundance, diversity, and richness of morphospecies and species of ants have been documented with increases in invasive plants (Breytenbach 1986; Webb et al. 2000; French & Major 2001; Ostoja et al. 2009; Fork 2010, Table 1.3 [p. 12]). Some ant species may benefit from invasive plants, if they can utilize available food resources or microclimate conditions; such species can become dominant and increase in abundance (Ostoja et al. 2009; Wolkovich et al. 2009, Table 1.3 [p. 12]). Because ants represent a diversity of functional groups and are relatively easy to identify to the species level, research on this family can provide great insights into how an invasive plant affects an arthropod community (Wolkovich et al. 2009).

CONCLUSION

Arthropods are important contributors to a variety of ecosystem processes and fill a diversity of niches and functional roles (Wilson 1987). The specific effects of invasive plants on arthropods are complex and reflect this breadth in form and function. Researchers in many studies focus on the effects of invasive plants at the level of taxonomic order or family; within those arthropod groups, diverse genus- or species-specific responses may be masked. As a result, future research should focus at the lowest level of taxonomic or functional resolution possible. Additional research also is necessary to understand how generalist herbivores, pollinators, parasitoids, and non-arachnid predators are affected by invasive plants (Tallamy 2004; Gratton & Denno 2005; Lopezaraiza-Mikel et al. 2007; Simao et al. 2010*).* These taxa comprise a large part of the diet of many different species of reptiles, amphibians, small mammals, and birds, including many declining grassland birds (Wiens & Rotenberry 1979; Wilson 1987; Blossey 1999; Tallamy 2004). As invasive plants continue to increase in presence and dominance with changes in land-use and climatic conditions, a better understanding of effects on the arthropod community and subsequent changes is needed to conserve arthropod abundance and diversity, ensure the survival of many wildlife species, and maintain ecological processes (Wilson 1987; Vitousek et al. 1996; Blossey 1999; Didham et al. 2005).

CHAPTER II: CHANGES IN ARTHROPOD COMMUNITIES WITH NON-NATIVE AND NATIVE INVASIVE GRASSES

ABSTRACT

Increased dominance by invasive grasses can alter composition and structure of vegetation communities. Arthropods may be particularly affected by these changes due to specialized relationships with plants as food resources and for reproduction. To better understand the effects of invasive plants, I compared diversity and abundance of arthropods in areas dominated by Kleberg bluestem, tanglehead, and a diversity of native grasses. Kleberg bluestem (*Dichanthium annulatum*) is an introduced Old World grass that dominates grasslands in south Texas and tanglehead (*Heteropogon contortus*) is native to south Texas, but recently has increased in distribution and dominance in certain areas, behaving like an invasive species. I selected 90 total grass patches dominated by Kleberg bluestem, tanglehead, or diverse native grasses, 30 patches each, on the King Ranch, Kleberg County, Texas. I quantified vegetation structure and composition and collected arthropods using pitfall traps and vacuum sampling on 1-m^2 plots during July and August 2009-2010. Richness of arthropod orders decreased by 14%, richness of insect families decreased by 17%, abundance of all arthropods and 8 orders decreased, and presence of 12 families decreased in invasive grasses, relative to native grasses; presence of 1 order and 3 families increased. The variable responses I documented were related to the diversity of functional roles and consequent habitat requirements. Although many taxa responded to both invasive grasses similarly, 1 order and 6 families were less likely to occur in tanglehead compared to Kleberg bluestem. Because arthropods play integral roles in pollination, decomposition, and as food resources for many wildlife

species, such declines in abundance and diversity of arthropods are likely to have significant cascading effects throughout ecosystems dominated by invasive plants. Although complete eradication of invasive grasses is unlikely, conservationists can focus on maintaining or increasing vegetation heterogeneity to sustain diverse and abundant arthropod communities and essential ecosystem processes.

INTRODUCTION

Invasive plants are one of the leading causes of habitat degradation and species loss (Wilson 1992; Vitousek et al. 1996; Wilcove et al. 1998). Approximately 5,000 species of non-native plants have been introduced to and are now established in the United States (Morse et al. 1995). Within this group, approximately 1,500 species are considered invasive, in that they dominate their novel ecosystems, displace many native species of plants, and alter plant community composition (Vitousek et al. 1996; Pimentel et al. 1999). Invasive plants also often alter the structure of plant communities by modifying the cover of bare ground, forbs, and woody vegetation (French & Major 2001; Standish 2004; Flanders et al. 2006; Hickman et al. 2006; Sands et al. 2009; Wolkovich et al. 2009). These changes in the vegetation community can lead to concomitant changes in ecosystem processes and diversity of native fauna (Vitousek et al. 1996; Pimentel et al. 1999).

Arthropods may be particularly affected by the changes in vegetation composition associated with an invasive plant because many arthropod species rely on specific plants as sites for reproduction and food resources (Wilson 1982; Kremen et al. 1993; Niemela & Mattson 1993; Tallamy 2004). Many phytophagous arthropods are host-specific, to some degree, and they may be able to forage or reproduce successfully only on the plant lineages with which they co-evolved (Bernays & Graham 1988; Tallamy 2004). Invasive plants may have defenses that prevent native arthropod herbivores from feeding or arthropods may not recognize the novel plant as a potential food resource (Ehrlich & Raven 1965; Strong et al. 1984; Tallamy 2004). Changes in vegetation composition resulting from plant invasions also may influence the diversity and composition of herbivorous arthropods by favoring generalists that can feed successfully on a variety of plants (Samways et al. 1996; Tallamy 2004).

Arthropods also may be affected by changes in vegetation structure resulting from increased dominance of invasive plants (Samways & Moore 1991; Lagerlöf & Wallin 1993; Crisp et al. 1998; Toft et al. 2001; Standish 2004; Lindsay & French 2006; Spyreas et al. 2010). Reductions in bare ground and vegetation heterogeneity and increased vegetation biomass and plant height often associated with invasive plants can modify the microclimate by increasing humidity and soil moisture, and decreasing temperature (Samways 1977; Lagerlöf & Wallin 1993; Samways et al. 1996; Lassau et al. 2005); microclimatic and soil conditions are important determinants of the distribution of certain arthropod taxa (Niemela et al. 1993, Antvogel & Bonn 2001; de Souza & de Souza Modena 2004). These structural and microclimate changes associated with invasive plants could benefit some arthropods, providing increased detritus, shelter from predators, and protection from desiccation, especially in early, more vulnerable life stages (Samways 1977; Gratton & Denno 2005; Wilson & Wheeler 2005). However, the overall decrease in vegetation heterogeneity associated with the dominance of an invasive plant has generally resulted in reduced arthropod diversity because many of the characteristics required to create habitat for a variety of species are absent (Samways et al. 1996; Collinge et al. 2003; Herrera & Dudley 2003; Wolkovich et al. 2009; Wu et al. 2009).

Old World bluestem (OWB) grasses are native to Europe, Asia, and parts of Australia and Africa (Bisset & Sillar 1984; Hickman et al. 2006; Harmony et al. 2007; Ortega et al. 2007). This group of grasses includes King Ranch bluestem (*Bothriochloa ischaemum*), Caucasian bluestem (*Bothriochloa bladhii*), Kleberg bluestem (*Dichanthium annulatum*), and Angleton bluestem (*Dichanthium aristatum*) (Muntz & Drawe 1983; Bisset & Sillar 1984; Harmony et al. 2007). These grasses were introduced purposefully to the southern and central Great Plains regions of the United States as early as the 1920s (Celarier & Harlan 1955; Berg et al. 1993) for their supposed high forage quality, high tolerance to grazing, and ability to establish and grow rapidly in a new environment (Hickman et al. 2004; Schmidt et al. 2008). Although many of these characteristics proved accurate, the grazing quality of these grasses is much lower than originally thought (Ortega et al. 2007). OWB grasses have leaves for only a short period; these leaves decline in forage quality as they reach maturity and contain little green organic material (Dabo et al. 1988; Ortega et al. 2007). Despite low forage value, OWB grasses were and continue to be a popular choice to re-vegetate former croplands (Schmidt & Hickman 2006). As OWB grasses increase in dominance, the diversity of native flora and fauna may decrease, but specific effects of OWB grasses on different taxa are not well known (Hickman et al. 2006).

Unlike OWB grasses, tanglehead (*Heteropogon contortus*) is a grass species native to Texas and parts of the southwestern United States (USDA 2007). This species recently has increased in distribution and dominance in certain areas of South Texas where previously it was a much smaller component of the vegetation community (F. Smith, personal communication), and as such, appears to be behaving like an invasive species by increasing homogeneity in vegetation structure and composition. Tanglehead may be able to out-compete non-native plants, such as Kleberg bluestem, as it can form dense stands when dominant (E. Cord, personal observation). Although the mechanisms for these changes are not well understood, several explanations have been posed. Tanglehead thrives in drought conditions, even in areas with disturbance, and changes in land management practices or shifting rainfall patterns may be responsible for this increase in dominance (Tothill 1966; Orr & Paton 1997; Goergen & Daehler 2002). In addition, much of South Texas was reseeded in the 1950s with a mixture of grasses from Australia, including Rhodesgrass (*Chloris gayana*), silky bluestem (*Andropogon sericeus*), and tanglehead (Burr 1955). With these plantings, tanglehead was introduced to areas of Texas where it had not been found previously and potential differences between Australian and U.S. strains also may explain its current behavior (Burr 1955). Because increases in tanglehead are a relatively new phenomenon, the consequences of this invasion for flora and fauna are unclear.

I sought to quantify changes in the vegetation and arthropod communities resulting from increased dominance of invasive grasses and determine if the origin of these two invasive plants (Kleberg bluestem and tanglehead) would influence the effects. I quantified how presence, abundance, and richness of orders and families changed in areas dominated by native and invasive grasses. In addition, I examined the range of responses for the diversity of arthropod functional groups represented, as I thought this information might provide insight into potential mechanisms underlying changes, as well a greater understanding of how trophic relationships within the arthropod community may be affected by invasive plants. Changes in abundance and diversity of the arthropod community also can have cascading effects for higher trophic levels for taxa such as birds and small mammals (Wiens & Rotenberry 1979; Wilson 1987; Abell 1999; Litt & Steidl 2011).

METHODS

Study Area

I selected study plots in the South Texas Plains vegetation community, on the Santa Gertrudis division of the King Ranch near Kingsville, Texas (27.49°N, 97.88°W) in the Enmedio pasture (2,590.4 ha). The study area was comprised of a mixture of grasses, but predominant native grasses included seacoast bluestem (*Schizachyrium scoparium* var. *littorale*), little bluestem (*Schizachyrium scoparium* var. *scoparium*), sandbur (*Cenchrus incertus*), knotroot bristle grass (*Setaria parviflora*), red lovegrass (*Eragrostis secundiflora*), and tanglehead (*Heteropogon contortus*), and predominant nonnative grasses included Kleberg bluestem (*Dichanthium annulatum*) and buffelgrass (*Cenchrus ciliaris*). Common forbs included lemon beebalm (*Monarda citriodora*), wooly croton (*Croton capitatus* var. *lindheimeri*), purple nightshade (*Solanum xanti*), and scarlet pimpernel (*Anagallis arvensis* ssp. *arvensis*) and common woody species included honey mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), and granjeno (*Celtis erhenbergiana*). Soil types included clay loam, sandy, sandy loam, and tight sandy loam. Throughout the study period, the Enmedio pasture was grazed continuously at 1 animal unit/8.1 hectares/year and managed for brush control via herbicide, fire, and mechanical methods.

Plot Selection

I randomly selected 90 patches of grass for sampling; I used GIS software and restricted selection based on a series of criteria. Determination of sample size was based on balancing sufficient replication with the ability to sample all plots in a relatively short time frame such that samples would be comparable and identify all collected specimens in a timely manner. I selected 30 patches each in areas with >50% estimated cover of: 1) Kleberg bluestem, 2) tanglehead, or 3) a mixture of native grass species, to serve as controls. Patches were separated by ≥30 m, were ≥25 m from all roads and deer feeders, and were not sprayed, burned, or cleared during our study or for at least a year prior to study initiation. Patches varied in size (small – <5 m in diameter, medium – 5-15 m, and large – >15 m, 10 of each in each grass community) and composition of the surrounding vegetation; patch size varied to address another research question. I established 1 m^2-plots placed randomly within each grass patch (1 plot on small patches, 2 plots on medium, and 3 plots on large) and marked each plot location with a GPS and pin flag. Because of a change in dominant vegetation between 2009 and 2010 on 12 patches (1 Kleberg bluestem, 3 tanglehead, and 9 native grasses), I selected replacement patches, which I sampled in 2010.

Sampling

I sampled vegetation and arthropods on all plots in all patches in July and September of 2009 and 2010 to capture variation associated with growing season and precipitation (*n* = 360 patch samples, 90 patches in each of 4 sampling seasons). I sampled vegetation prior to collecting arthropods to avoid any changes in vegetation caused by arthropod sampling methods. I divided each 1-m^2 plot into four quarters and estimated aerial cover (%) by plant species, cover of bare ground, and cover of dead vegetation for each quarter. I averaged cover estimates over all four quarters to generate cover estimates for each species in each plot.

Because most arthropod sampling methods result in some taxonomic bias (Greenslade 1964; Luff 1975), I used two sampling methods for a more complete assessment of the arthropod community: pitfall traps and vacuum sampling. Pitfall traps are an effective way to estimate diversity and abundance of ground dwelling arthropods, such as certain beetles (Greenslade 1964; Luff 1975; Melbourne 1997; Standen 2000), but vegetation cover may influence sampling efficiency (Melbourne 1999). Vacuum sampling effectively samples volant insects and insects found on vegetation (Standen 2000). This combination of methods allowed me to sample effectively the overall community as well as specific orders of interest, including Hemiptera and Orthoptera, which may be particularly affected by changes in vegetation composition due to specific plant preferences or dependency on certain hosts.

I randomly placed two pitfall traps in each 1-m^2 plot, with the rim of the trap level with the soil surface. Traps were 0.27-l tapered plastic cups filled halfway with propylene glycol and left undisturbed for 24 hours. I collected and combined the contents of both traps in a plastic bag and stored them for later sorting and identification. After collecting pitfall traps, I waited 24 hours before vacuum sampling to mitigate any potential effects of this disturbance. I conducted vacuum sampling between 8:00 and 11:00 am to avoid excess moisture on the vegetation and maximize the number of arthropods collected; I sampled each 1-m² plot for 120 sec using a modified ES-230 shred 'N' vac (Echo Incorporated. Lake Zurich, IL). I transferred captured arthropods to a plastic bag containing cotton balls soaked in ethyl acetate to reduce predation and froze samples for later sorting and identification. I combined pitfall and vacuum samples and identified arthropods to taxonomic order and insects to taxonomic family based on Triplehorn and Johnson (2005), with one exception. The order Hemiptera is comprised of 3 suborders (Heteroptera, Auchenorrhyncha, and Sternorrhyncha); I examined Hemiptera as a whole, as well as focused on the combination of suborders Auchenorrhyncha (free-living hemipterans) and Sternorrhyncha (plant-parasitic hemipterans), hereafter referred to as "Homoptera". I used this approach because these subgroups may be differentially affected by invasive plants – many Homoptera feed nearly exclusively on plant fluids and are considered host-specific to some degree (Triplehorn & Johnson 2005), whereas many Heteroptera feed on a variety of liquid foods from both plants and animals (von Dohland and Moran 1995).

Data Analysis

I averaged vegetation and arthropod variables over all plots in each grass patch, to remove the effect of variable patch size. For vegetation, I computed average plant species richness and vegetation cover by class: invasive grasses (Kleberg bluestem, tanglehead, buffelgrass, and others), native grasses (excluding tanglehead), forbs, bare ground, and dead vegetation (grasses and forbs). I computed average order richness for all arthropods, overall abundance of all arthropods (excluding Formicidae), and family richness of all insects (excluding larvae and unidentifiable moths). I excluded ants from the overall abundance values because variation in ant abundance was large and unpredictable; I felt this variability mainly was a result of random trap placement. Finally, I quantified presence and average abundance of each order and family. I used presence to indicate that an area provided habitat for a taxa and abundance as a gauge of habitat quality. Presence and abundance provide complementary information about habitat and examining both metrics allow for a more complete understanding of patterns within a study system (Fletcher et al. 2005). I examined changes in presence for orders and families that occurred in ≥10% (36) of the 360 total patch samples (i.e., 90 grass patches x 4 sampling seasons) and changes in abundance for orders and families that occurred in ≥75% (270) of total patch samples. Therefore, I analyzed presence of 7 orders and 37 families and abundance of 8 orders, 1 subgroup, and 3 families.

I used a generalized linear mixed model approach for all analyses and selected the appropriate distribution and link function for each continuous, binary, or discrete response variable (Littell et al. 2006); I transformed continuous response variables where needed to meet assumptions. I used a normal distribution with an identity link for all vegetation variables and a Poisson distribution with a log link for arthropod richness and abundance variables due to the high variation and skewed nature of these data. I treated patches as subjects to account for repeated measurements taken on the same patches over time; for each analysis I evaluated 4 possible covariance structures (compound symmetric, first-order autoregressive, first-order autoregressive moving average, and toeplitz), and selected one based on Akaike’s information criterion adjusted for small sample bias (AIC_c) (Littell et al. 2006).

I examined changes in vegetation and arthropod variables based on grass community (native grasses, Kleberg bluestem, tanglehead), seasonal changes based on timing of sampling (early or late in the growing season based on month sampled – July and Sept), and the interaction between grass community and season, denoting some seasonal variation in the differences among grasses. Because rainfall was extremely variable during our study, which could affect vegetation and arthropod communities greatly, I also explored precipitation effects. I incorporated average rainfall recorded for the two-week period prior to the sampling date for the sampled pasture, based on the idea that this time lag would be required for most arthropods to respond to rainfall (Dunham 1978; Tanaka & Tanaka 1982; Frampton et al. 2000). As such, I also explored changes in vegetation and arthropod variables based on rainfall and the interaction between grass community and rainfall, where precipitation effects on vegetation or arthropods differed by grass community, resulting in a full model with 3 simple effects (grass community, rainfall, and season) and 2 interactive effects (grass community × rainfall and grass community × season). To generate the best estimates of effects, I used backwards variable selection to eliminate any interaction terms where $p > 0.10$, but I retained all single terms in the final model. To quantify differences among grass communities and seasonal changes, I present least squares means and 95% confidence intervals in the text and tables. For effects involving rainfall, I present back-transformed slopes in the text and predicted values in graphs.

RESULTS

Vegetation

I observed a total of 67 plant species during all sampling periods, including 14 species of native grasses, 5 species of non-native grasses, 44 species of forbs, 2 species of succulents, and 2 species of woody plants (Appendix A). The most common native grass was tanglehead (*Heteropogon contortus*, 51.1% of 360 samples), followed by common sandbur (*Cenchrus spinifex*, 29.2%). Not surprisingly, the most common non-native grass was Kleberg bluestem (*Dichanthium annulatum*, 61.1% of samples). Wooly croton (*Croton capitatus* var. *lindheimeri*) was the most common forb (48.6% of samples), prickly pear was the most common succulent (*Opuntia engalmanni*, 2.5%), and huisache (*Acacia minuata*, 8.9%) was the most common woody plant (Appendix A).

GRASS COMMUNITY

Vegetation composition and structure differed by grass community (Table 2.1). Vegetation species richness and forb cover were highest in areas dominated by native grasses, compared to areas dominated by invasive grasses (Table 2.2 [p. 37]). Early in the growing season, bare ground was also slightly greater in areas dominated by native grasses; however I did not detect differences late in the growing season (Tables 2.1 & 2.2 [p. 37]). Cover of dead vegetation was greatest in areas dominated by native grasses and tanglehead, relative to Kleberg bluestem (Table 2.2 [p. 37]).

Table 2.1. Factors affecting vegetation species richness and cover based on generalized linear mixed models, $n = 360$ patch samples, 2009-2010, Kleberg County, Texas, USA.

	Grass[a]		Rainfall[b]		Season[b]		Grass × Season[ac]	
Vegetation variable	F[e]	P	F[f]	p	F[d]	P	F[e]	p
Species richness (/m^2)	8.74	0.0003	37.78	<0.0001	49.98	<0.0001		
Cover (%)								
Bare ground	8.26	0.0050	37.14[g]	<0.0001	8.26[e]	0.0050	5.12	0.0077
Forbs	10.50	<0.0001	46.57	<0.0001	31.53	<0.0001		
Dead vegetation	7.05	0.0014	234.45	<0.0001	68.88	<0.0001		

[a] Numerator degrees of freedom (*df*) = 2.

[b] Numerator *df* = 1.

[c] I removed interaction terms where $p > 0.10$. I did not detect a grass community × rainfall interaction for any variables.

[d] Denominator *df* = 101.

[e] Denominator *df* = 99.

[f] Denominator *df* = 256.

[g] Denominator *df* = 254.

Table 2.2. Least square means (above) and 95% confidence intervals (below) for vegetation richness and cover by grass community based on generalized linear mixed models, *n* = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

Vegetation variable	Season*	Native grasses	Kleberg bluestem	Tanglehead
Species richness (/m^2)		4.6	3.3	3.5
		4.2 to 5.1	2.8 to 3.8	3.0 to 4.0
Cover (%)				
Forbs		19.0	10.9	11.9
		15.9 to 22.9	9.0 to 13.1	9.8 to 14.3
Bare ground	Early	2.3	1.6	1.6
		1.8 to 2.9	1.3 to 2.1	1.3 to 2.1
	Late	2.0	2.5	2.4
		1.6 to 2.6	2.0 to 3.2	1.9 to 3.0
Dead vegetation		12.4	8.3	11.8
		10.6 to 14.7	7.0 to 9.8	10.0 to 14.0

* When I detected a grass community × season interaction, I provide means for early and late in the growing season separately.

RAINFALL

Rainfall increased over the four sampling periods and was highest in 2010 (July 2009 = 0.00 cm, September 2009 = 12.78 cm, July 2010 = 18.97 cm, and September 2010 = 19.81 cm), which also affected vegetation composition and structure (Table 2.1 [p. 36]). Vegetation species richness increased 0.06 species/m^2 (95% CI = 0.04 to 0.08) and forb cover increased 4.2% (2.9 to 5.4) with each additional cm of rainfall. In contrast, cover of bare ground decreased 3.5% (95% CI = −4.5 to −2.4) and dead vegetation decreased 8.3% (−9.3 to −7.2) with each additional cm of rainfall.

SEASON

I also observed seasonal changes in vegetation (Table 2.1 [p. 36]). Vegetation species richness was higher early in the growing season (4.3 species/m^2, 95% CI = 4.0 to 4.7) compared to later (3.3, 3.0 to 3.7). Forb cover also was higher early in the growing season (15.4%, 13.5 to 17.5) relative to later (7.4, 6.5 to 8.4); whereas, cover of dead vegetation increased later in the growing season (15.4%, 13.5 to 17.5) compared to earlier (2.0, 6.5 to 8.4).

Arthropods

I captured 68,450 total arthropods, representing 24 orders and 129 families (Appendix B). Hymenopterans (bees, wasps, and ants) were present in nearly all samples (99.7%) and composed 41.4% of total arthropod abundance (Appendix B). Dominance of hymenopterans mainly was due to the abundance of ants (family Formicidae), which comprised 39.9% of all individuals sampled (Appendix B). Hemipterans were also common and abundant; I collected true bugs in 86.1% of all samples, which accounted for 11.3% of total abundance (Appendix B).

GRASS COMMUNITY

In general, arthropod communities in areas dominated by native grasses were more diverse and had at least one additional order of arthropods relative to areas dominated by invasive grasses, but the exact magnitude differed by season (Tables 2.3 [p. 41]& 2.4 [p. 43]). Native grass-dominated areas also had approximately 3 additional families of insects, compared to areas dominated by Kleberg bluestem and tanglehead (Table 2.4 [p. 43]). Abundance of arthropods always was greater in areas dominated by native grasses, but the magnitude the differences among grass communities depended on rainfall (Table 2.3 [p. 41]). Abundance of arthropods changed little with rainfall in areas dominated by native grasses (−0.7%, −1.7 to 0.0) or Kleberg bluestem (−1.0%, −2.2 to 0.0), but decreased 2.2% (−3.4 o −1.1) with every 1-cm increase in rainfall in tanglehead-dominated areas (Fig. 1).

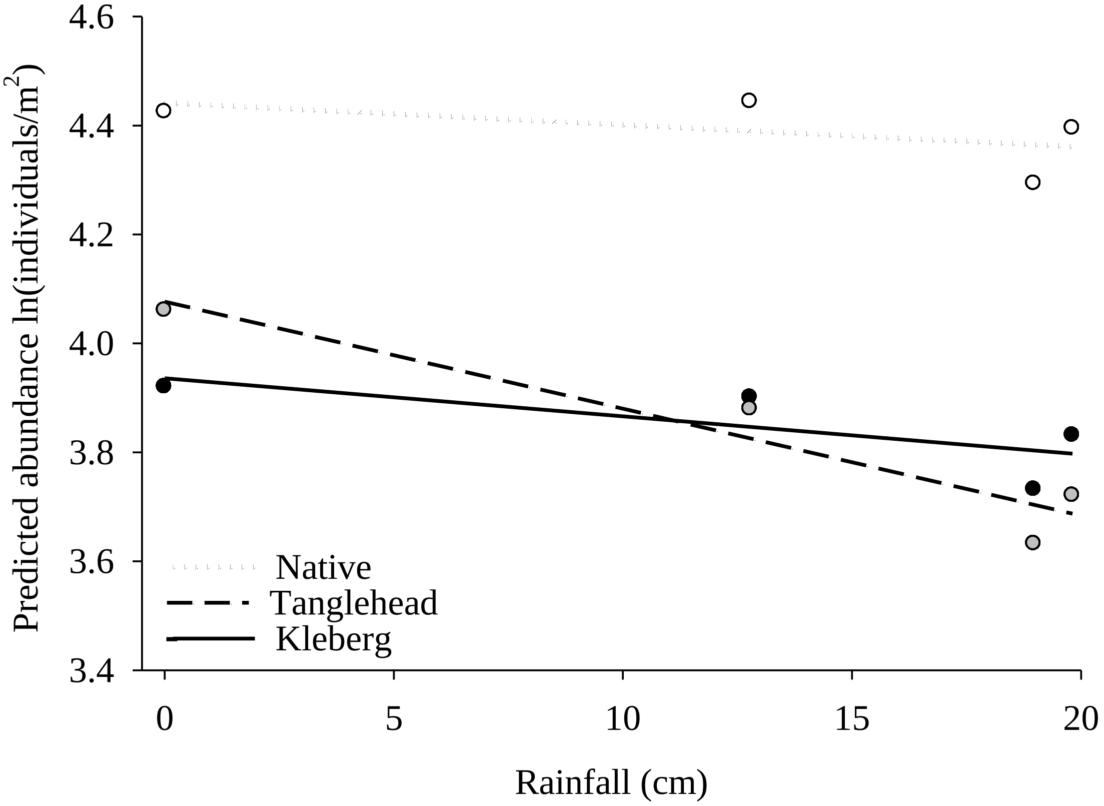

Figure 1. Changes in predicted average abundance of all arthropods (excluding Formicidae) with rainfall, by grass community, 2009-2010, Kleberg County, Texas, USA.

Table 2.3. Factors affecting arthropod abundance and richness for the overall community and by order and family, based on generalized linear mixed models, *n* = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

	Grass[a]		Rainfall[b]		Season[b]		Grass × Rainfall[a]		Grass × Season[ac]	
Variable	*F* [f]	*p*	*F*	*p*	*F*	*P*	*F*	*p*	*F*	*p*
Community										
Abundance[d] (total/m^2)	10.53	<0.0001	12.62[g]	0.0005	3.15[e]	0.0604	2.55[g]	0.0804		
Order richness (/m^2)	7.64	0.0008	6.54[g]	0.0111	38.59[f]	<0.0001			4.80[f]	0.0103
Family richness (/m^2)	2.65	0.0002	111.15[h]	<0.0001	2.65[e]	0.1066				
Orders & families (#/m^2)										
Acari	19.98	<0.0001	173.04[h]	<0.0001	0.06[e]	0.9780				
Aranae	15.84	<0.0001	188.07[h]	<0.0001	10.90[e]	0.0013				
Coleoptera	7.44	0.0010	16.51[g]	<0.0001	65.37[f]	<0.0001			5.82[f]	0.0041
Collembola	0.10	0.9047	30.80[g]	<0.0001	0.64[e]	0.4270	2.29[g]	0.1039		
Entomobryidae	0.18	0.8389	23.92[g]	<0.0001	9.80[e]	0.0023	2.52[g]	0.0822		
Diptera	0.15	0.8603	36.36[i]	<0.0001	43.15[f]	<0.0001	3.52[i]	0.0310	4.76[f]	0.0107
Hemiptera	15.64	<0.0001	24.50[i]	<0.0001	4.83[f]	0.0303	6.17[i]	0.0024	5.48[f]	0.0055
Homoptera[j]	47.53	<0.0001	4.43[h]	0.0363	39.44[e]	<0.0001				
Hymenoptera[c]	5.33	0.0063	40.49[g]	<0.0001	18.28[f]	<0.0001			4.29[f]	0.0163
Formicidae	3.72	0.0278	1.76[g]	0.1860	3.78[e]	0.0547	4.72[g]	0.0097		
Orthoptera	2.40	0.0958	0.36[g]	0.5466	1.08[e]	0.3016				
Gryllidae	0.20	0.0504	9.51[h]	0.0023	0.20[e]	0.6590				

[a] Numerator degrees of freedom (*df*) = 2.

[b] Numerator *df* = 1.

[c] I removed interaction terms where $p > 0.10$.

[d] Does not include family Formicidae.

Table 2.3. Continued

[e] Denominator $df = 101$.
[f] Denominator $df = 99$.
[g] Denominator $df = 254$.
[h] Denominator $df = 256$.
[I] Denominator $df = 252$.
[j] Includes suborders Auchenorrhyncha and Sternorrhyncha within order Hemiptera.

Table 2.4. Least square means (above) and 95% confidence intervals (below) for richness of the overall arthropod community and abundance of orders and families by grass community based on generalized linear mixed models, *n* = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

Variable	Season[a]	Native grasses	Kleberg bluestem	Tanglehead
Community				
Order richness (/m^2)	Early	9.6	8.3	8.2
		9.1 to 10.7	7.8 to 8.8	7.7 to 8.7
	Late	10.1	9.5	9.2
		9.5 to 10.6	9.0 to 10.1	8.7 to 9.7
Family richness (/m^2)		16.8	13.9	13.3
		15.5 to 18.1	12.8 to 15.2	12.2 to 14.5
Orders & families (#/m^2)				
Acari		6.4	3.1	3.6
		5.1 to 8.0	2.3 to 4.1	2.7 to 4.7
Aranae		7.8	5.7	4.7
		6.8 to 8.8	4.9 to 6.6	4.0 to 5.5
Coleoptera	Early	2.5	2.3	2.3
		1.9 to 3.3	1.7 to 3.0	1.8 to 3.1
	Late	10.0	5.1	5.2
		8.6 to 11.7	4.1 to 6.3	4.3 to 6.4
Diptera	Early	7.8	4.2	3.1
		6.1 to 10.0	3.1 to 5.9	2.1 to 4.5

Table 2.4 Continued

Variable	Season[a]	Native grasses	Kleberg bluestem	Tanglehead
Diptera	Late	10.8	9.9	9.4
		8.8 to 13.2	7.9 to 12.4	7.4 to 11.9
Hemiptera	Early	10.1	4.1	4.0
		7.3 to 14.0	2.3 to 7.1	2.4 to 6.8
	Late	27.8	3.7	4.7
		22.6 to 34.3	2.2 to 6.3	2.4 to 7.6
Homoptera[b]		13.4	3.2	3.4
		11.0 to 16.3	2.3 to 4.6	2.4 to 4.7
Hymenoptera[c]	Early	2.8	1.2	1.6
		2.3 to 3.5	0.8 to 1.6	1.2 to 2.2
	Late	0.9	0.9	1.1
		0.7 to 1.3	0.7 to 1.3	0.8 to 1.5
Orthoptera		3.6	2.6	3.5
		2.9 to 4.4	2.1 to 3.3	2.8 to 4.3
Gryllidae		2.5	1.7	2.7
		2.0 to 3.3	1.2 to 2.3	2.1 to 3.5

[a] When I detected a grass community × season interaction, I provide means for early and late in the growing season separately.
[b] Includes suborders Auchenorrhyncha and Sternorrhyncha within order Hemiptera.
[c] Does not include family Formicidae.

Presence of 2 of 7 orders of arthropods differed by grass community (Table 2.5). Lepidoptera (moths and butterflies) were least likely to occur in tanglehead, compared to native grasses and Kleberg bluestem (Table 2.6 [p. 49]). Presence of Isopoda (sowbugs and pillbugs) was somewhat higher in invasive grasses relative to native grasses, but the exact differences depended on season (Table 2.6 [p. 49]).

Presence of 20 of 34 insect families differed by grass community, including 7 of 11 Coleoptera families (beetles), 5 of 7 Diptera families (flies), 4 of 7 Hemiptera families (true bugs), 3 of 6 Hymenoptera families (sawflies, bees, wasps, and ants), and 1 of 3 Orthoptera families (grasshoppers, crickets, and katydids, Table 2.5). Chrysomelidae (leaf beetles), Curculionidae (weevils), Chironomidae (non-biting midges), Chloropidae (grass flies), Drosophilidae (vinegar flies), Sciaridae (dark-winged fungus gnats), Cercopidae (spittle bugs), Cicadellidae (leaf hoppers), and Pachygronthidae (seed bugs) were most likely to occur in native grasses, relative to invasive grasses (Table 2.6 [p. 49]. Scarabeidae (scarab beetles) were somewhat more likely to occur in native grasses and tanglehead, relative to Kleberg bluestem; Miridae (plant bugs) and Tettigoniidae (katydids) were more likely to occur in native grasses and Kleberg bluestem, compared to tanglehead (Table 2.6 [p. 49]). In contrast, presence of Mordellidae (tumbling flower beetles) was higher in Kleberg bluestem (Table 2.6 [p. 49]). Presence of Latridiidae (minute brown scavenger beetles), Phalacridae (shining flower beetles), Scraptiidae (false flower beetles), and Dolichopodidae (long-legged flies) differed by grass community, but the differences depended on sampling season (Table 2.6 [p. 49]). Presence of these beetles and flies was higher in native grasses relative to invasive grasses in at least one

Table 2.5. Factors affecting presence of arthropod orders and families based on generalized linear mixed models, n = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

	Grass^a		Rainfall^b		Season^b		Grass × Season^{ac}	
Variable (% plots present)	F^e	p	F	p	F	P	F^e	p
Coleoptera								
Carabidae	0.25	0.7764	55.00^f	<0.0001	5.48^d	0.0212		
Chrysomelidae	2.65	0.0037	0.66^f	0.4171	3.97^d	0.0419		
Curculionidae	15.86	<0.0001	21.03^f	<0.0001	40.64^d	<0.0001		
Elateridae	0.89	0.4150	1.40^f	0.2380	15.66^d	0.0001		
Latridiidae	4.63	0.0120	3.22^g	0.0741	0.43^e	0.5139	2.80	0.0656
Mordellidae	2.68	0.0738	4.08^f	0.0455	11.87^d	0.0008		
Phalacridae	2.45	0.0919	4.10^g	0.0440	2.14^e	0.1464	3.89	0.0236
Scarabeidae	2.51	0.0866	0.34^f	0.5589	5.94^d	0.0166		
Scraptiidae	2.02	0.1382	7.08^g	0.0083	0.34^e	0.5600	2.75	0.0689
Staphylinidae	1.71	0.1860	12.77^f	0.0004	6.73^d	0.0109		
Tenebrionidae	0.23	0.7958	9.20^f	0.0027	1.80^d	0.1831		
Collembola								
Hypogastruridae	0.75	0.4761	3.22^f	0.0086	0.25^d	0.6155		
Sminthuridae	1.08	0.3452	1.01^f	0.9315	36.02^d	<0.0001		
Diptera								
Cecidomyiidae	0.04	0.9633	30.03^f	<0.0001	17.78^d	<0.0001		
Chironomidae	8.38	0.0004	27.12^f	<0.0001	2.84^d	0.0948		

Table 2.5. Continued

Variable (% plots present)	Grass^{a}		Rainfall^{b}		Season^{b}		Grass × Season^{ac}	
	F^{e}	p	F	p	F	P	F^{e}	p
Chloropidae	5.93	0.0037	63.00^{f}	<0.0001	8.42^{d}	0.0046		
Dolichopodidae	2.57	0.0819	6.03^{g}	0.0147	42.82^{e}	<0.0001	5.23	0.0007
Drosophilidae	8.18	0.0005	6.04^{f}	0.0147	0.93^{d}	0.3384		
Phoridae	0.08	0.9230	15.03^{f}	0.0001	2.49^{d}	0.1178		
Sciaridae	9.44	0.0002	3.31^{f}	0.0701	4.74^{d}	0.0318		
Hemiptera								
Aphidae	0.00	0.9972	0.16^{f}	0.6924	0.25^{d}	0.6197		
Cercopidae	6.40	0.0004	22.19^{f}	<0.0001	6.40^{d}	0.0129		
Cicadellidae	10.87	<0.0001	52.26^{f}	<0.0001	8.54^{d}	0.0043		
Membracidae	1.80	0.1700	21.81^{f}	<0.0001	56.33^{d}	<0.0001		
Miridae	3.03	0.0530	59.33^{f}	<0.0001	57.27^{d}	<0.0001		
Pachygronthidae	11.05	<0.0001	11.72^{f}	0.0007	0.33^{d}	0.5665		
Rhyparochromidae	0.43	0.6513	13.02^{f}	0.0004	27.83^{d}	<0.0001		
Hymenoptera								
Braconidae	2.80	0.0655	28.15^{f}	<0.0001	6.09^{d}	0.0152		
Eurytomidae	4.42	0.0145	35.22^{g}	<0.0001	13.73^{e}	0.0003	3.67	0.029
Halictidae	0.58	0.5636	11.76^{f}	0.0007	0.02^{d}	0.8952		
Mutilidae	0.64	0.5287	2.53^{f}	0.1126	3.65^{d}	0.0588		
Pteromalidae	5.19	0.0072	64.00^{f}	<0.0001	0.22^{d}	0.6404		
Sphecidae	0.43	0.6513	0.57^{f}	0.4525	8.79^{d}	0.0038		

Table 2.5. Continued

	Grass[a]		Rainfall[b]		Season[b]		Grass × Season[ac]	
Variable (% plots present)	*F*[e]	*p*	*F*	*P*	*F*	*P*	*F*[e]	*p*
Isopoda	0.18	0.8360	9.46[g]	0.0023	0.24[e]	0.6218	3.04	0.0522
Isoptera	2.25	0.1110	1.51[f]	0.2201	1.10[d]	0.2971		
Lepidoptera	4.97	0.0087	0.32[f]	0.5695	1.14[d]	0.2883		
Microcoryphia	0.55	0.5778	13.78[f]	0.0003	0.57[d]	0.4529		
Orthoptera								
Acrididae	0.20	0.8183	31.16[f]	<0.0001	7.64[d]	0.0068		
Tetrigidae	2.31	0.1050	17.40[f]	<0.0001	9.32[d]	0.0029		
Tettigoniidae	0.08	0.0006	32.19[f]	<0.0001	16.96[d]	<0.0001		
Pseudoscorpiones	0.21	0.8125	10.96[f]	0.0011	9.15[d]	0.0032		
Psocoptera	0.14	0.8698	6.05[f]	0.0146	8.88[d]	0.0036		
Thysanoptera	0.84	0.4354	2.25[f]	0.1345	0.06[d]	0.8086		

[a] Numerator degrees of freedom (*df*) = 2.

[b] Numerator *df* = 1.

[c] I removed interaction terms where *p* > 0.10. I did not detect a grass community × rainfall interaction for any variables.

[d] Denominator *df* = 101.

[e] Denominator *df* = 99.

[f] Denominator *df* = 256.

[g] Denominator *df* = 252.

Table 2.6. Least square means[a] (above) and 95% CIs (below) for arthropod presence by order and family by grass community based on generalized linear mixed models, n = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

Variable	Season[b]	Native grasses	Kleberg bluestem	Tanglehead
Coleoptera				
Chrysomelidae		34.0	19.5	24.3
		25.1 to 44.1	12.6 to 29.0	16.6 to 34.1
Curculionidae		55.5	20.9	18.1
		44.3 to 66.2	13.8 to 30.5	11.6 to 27.1
Latridiidae	Early	54.9	55.7	33.4
		43.4 to 65.9	44.6 to 66.3	23.8 to 44.6
	Late	60.3	45.7	47.8
		48.6 to 70.9	35.1 to 56.8	36.9 to 58.8
Mordellidae		18.6	23.2	10.6
		11.7 to 28.3	15.3 to 33.5	5.8 to 18.7
Phalacridae	Early	10.2	5.6	23.7
		4.6 to 21.2	1.9 to 15.2	13.9 to 37.4
	Late	30.0	13.3	14.8
		18.8 to 44.3	6.2 to 26.4	7.2 to 28.0
Scarabeidae		11.0	6.0	14.3
		6.6 to 17.6	3.1 to 11.5	9.2 to 21.5
Scraptiidae	Early	10.0	11.4	12.9
		4.6 to 20.6	5.4 to 22.5	6.4 to 24.4
	Late	13.8	21.4	20.8
		6.6 to 26.6	12.1 to 35.2	2.9 to 13.6
Diptera				
Chironomidae		16.2	9.4	4.2
		9.7 to 25.7	5.2 to 16.5	1.9 to 8.5
Chloropidae		47.4	24.6	31.0
		37.3 to 57.7	17.2 to 33.9	22.5 to 40.9
Dolichopodidae	Early	3.5	3.6	10.7
		0.9 to 12.2	0.9 to 12.2	5.0 to 21.2
	Late	68.8	20.6	31.2
		55.5 to 79.6	12.4 to 32.0	20.9 to 43.9

Table 2.6. Continued

Variable	Season[b]	Native grasses	Kleberg bluestem	Tanglehead
Drosophilidae		35.9	24	13.4
		27.8 to 44.9	17.2 to 32.5	8.5 to 20.6
Sciaridae		35.8	11.6	22.2
		27.5 to 45.1	7.0 to 18.6	15.5 to 30.7
Hemiptera				
Cercopidae		2.8	0.7	1.1
		0.8 to 8.7	0.2 to 2.9	0.3 to 3.9
Cicadellidae		94.7	71.6	76.6
		89.1 to 97.5	57.4 to 82.5	63.2 to 86.2
Miridae		24.5	18.4	10.8
		15.5 to 36.6	11.0 to 29.2	5.9 to 19.0
Pachygronthidae		29.7	10.3	6.5
		21.4 to 39.6	5.7 to 17.7	3.2 to 13.0
Hymenoptera				
Braconidae		26.4	13.8	19.5
		18.6 to 36.0	8.5 to 21.6	12.9 to 28.4
Eurytomidae	Early	46.0	9.6	16.0
		28.9 to 64.0	4.2 to 20.7	7.9 to 29.9
	Late	8.1	8.1	6.3
		3.9 to 16.3	3.9 to 16.3	2.8 to 13.6
Pteromalidae		29.9	29	15.4
		20.9 to 40.9	20.1 to 39.9	9.8 to 23.5
Isopoda	Early	17.7	12	26.2
		9.5 to 30.5	5.6 to 23.9	15.9 to 39.9
	Late	14.9	20.9	13.4
		8.0 to 25.9	12.4 to 32.9	7.0 to 24.0
Lepidoptera		47.4	47.1	26.8
		37.2 to 57.8	36.8 to 57.7	18.5 to 37.1
Orthoptera				
Tettigoniidae		14.8	8.9	4.3
		8.9 to 23.6	4.9 to 15.5	2.1 to 8.6

[a] Measured as the percentage of plots where the taxa was present.

[b] When I detected a grass community × season interaction, I provide means for early and late in the growing season separately.

season, but was similar to or lower than Kleberg bluestem or tanglehead in another season (Table 2.6 [p. 49]). Presence of several families of parasitic wasps (Hymenoptera) also differed by grass community; the families Braconidae and Eurytomidae were most likely to occur in native grasses compared to invasive grasses, the latter at least during part of the growing season, whereas Pteromalidae were less likely to occur in tanglehead, compared to native grasses and Kleberg bluestem (Tables 2.5 [p. 46] & 2.6 [p. 49]).

Abundance of all individual orders of arthropods I examined varied with grass community (8 orders, 1 subgroup, Table 2.3 [p. 41]). Acari (mites and ticks), Aranae (spiders), and Homoptera (cicadas, hoppers, aphids, and scales) were more abundant in areas dominated by native grasses, compared to Kleberg bluestem and tanglehead (Table 2.4 [p. 43]). Orthoptera (grasshoppers and crickets) were most abundant in native grass- and tanglehead-dominated areas, relative to Kleberg bluestem (Table 2.4 [p. 43]) and Coleoptera, Diptera, Hemiptera, and Hymenoptera (excluding ants) also were more abundant in areas dominated by native grasses, but the magnitude differed by sampling season (Tables 2.3 [p. 41] & 2.4 [p. 43]). Abundance of Collembola (spring-tails) and Diptera differed by grass community, but the magnitude depended on rainfall (Table 2.3 [p. 41]). Collembolan abundance decreased with rainfall, by 2.7% in native grasses (−4.9 to −0.4), 5.7% in Kleberg bluestem (−8.0 to −3.2), and 5.2% in tanglehead (−7.5 to −2.8, Table 2.3 [p. 41]). At the lowest rainfall (0.0 cm, July 2009), the number of Collembola was similar for all three grass communities, but as rainfall increased the number of Collembola was highest in native grasses (Fig. 2). Dipteran abundance increased 8.8% in native grasses (5.9 to 11.7) and 4.4% in Kleberg bluestem (1.3 to 7.6) with every additional cm of rainfall, but did not change in tanglehead (3.3, −0.1 to 6.7, Table 3 [p. 41], Fig. 3 [p. 53]).

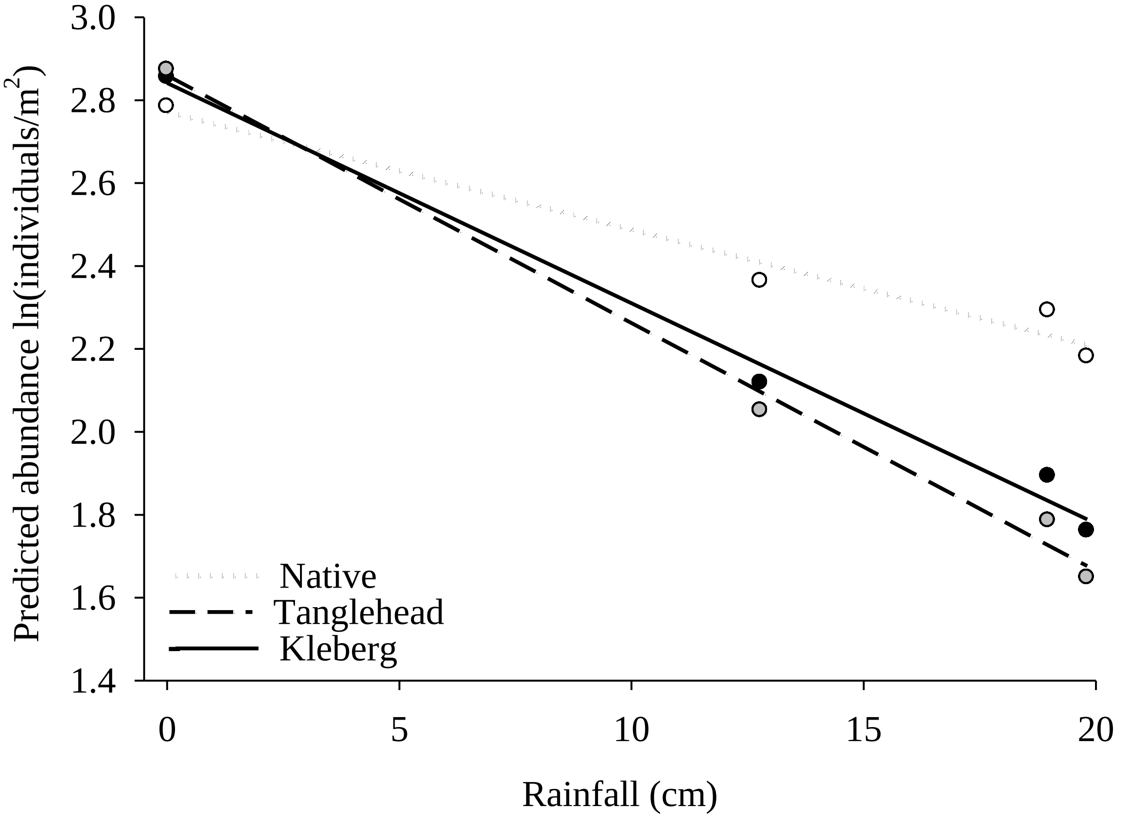

Figure 2. Changes in predicted average abundance of Collembola with rainfall, by grass community, 2009-2010, Kleberg County, Texas, USA.

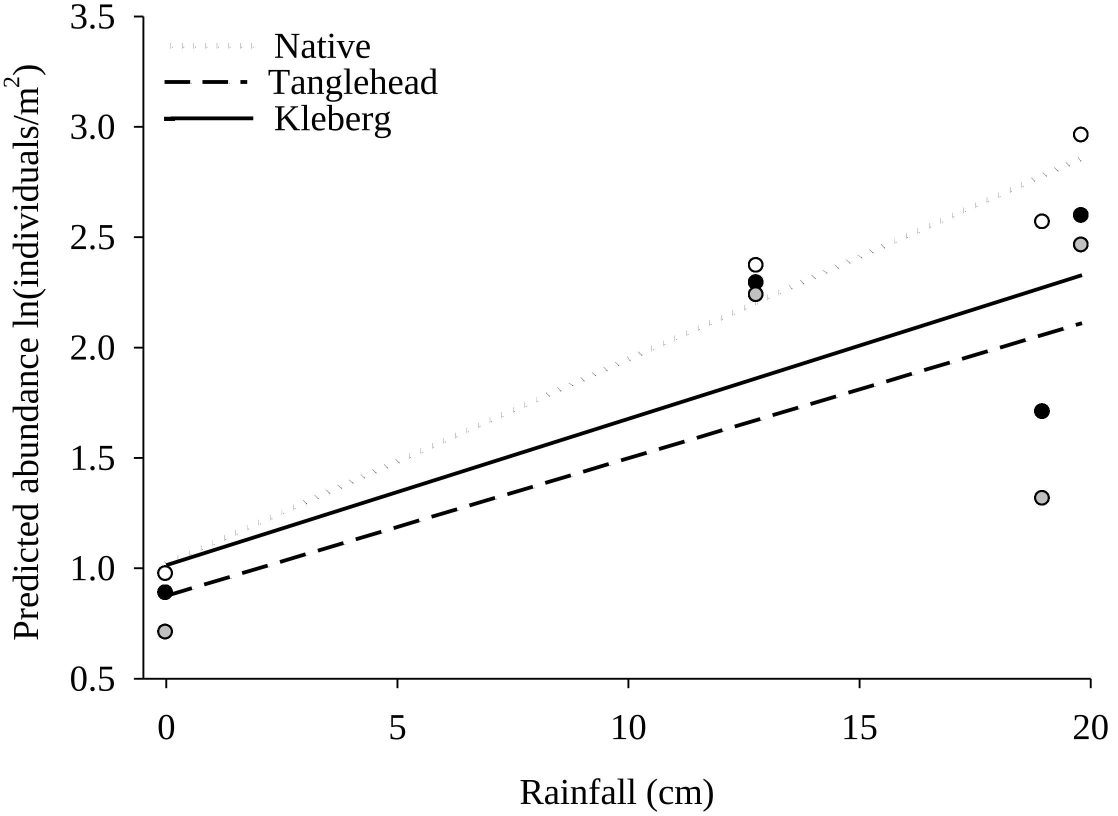

Figure 3. Changes in predicted average abundance of Diptera with rainfall, by grass community, 2009-2010, Kleberg County, Texas, USA.

I also detected grass-related differences in abundance for all 3 insect families examined (Table 2.3 [p. 39]). Gryllidae (crickets, Orthoptera) were most abundant in native grasses and tanglehead, relative to Kleberg bluestem (Table 2.4 [p. 41]). Abundance of Entomobryidae (slender springtails, Collembola) and Formicidae (ants, Hymenoptera) differed by grass community, but also depended on rainfall. Abundance of entomobryids was similar for all three grass communities at the lowest rainfall value, but was higher in native grasses as rainfall increased (Fig. 4). Entomobryid abundance decreased 4.9% in Kleberg bluestem (−7.4 to −2.4) and 5.1% in tanglehead areas (−7.6 to −2.6) with every

1-cm increase in rainfall, with little decrease in native grasses (−1.9, −4.2 to 0.5, Table 2.3 [p. 41]). Abundance of Formicidae decreased 5.0% in tanglehead (−7.9 to −2.1) with every 1-cm increase in rainfall, but changed little in native grasses (0.5, −2.4 to 3.4) or Kleberg bluestem (0.7, −2.9 to 4.4, Table 2.3 [p. 41], Fig. 5 [p. 55]).

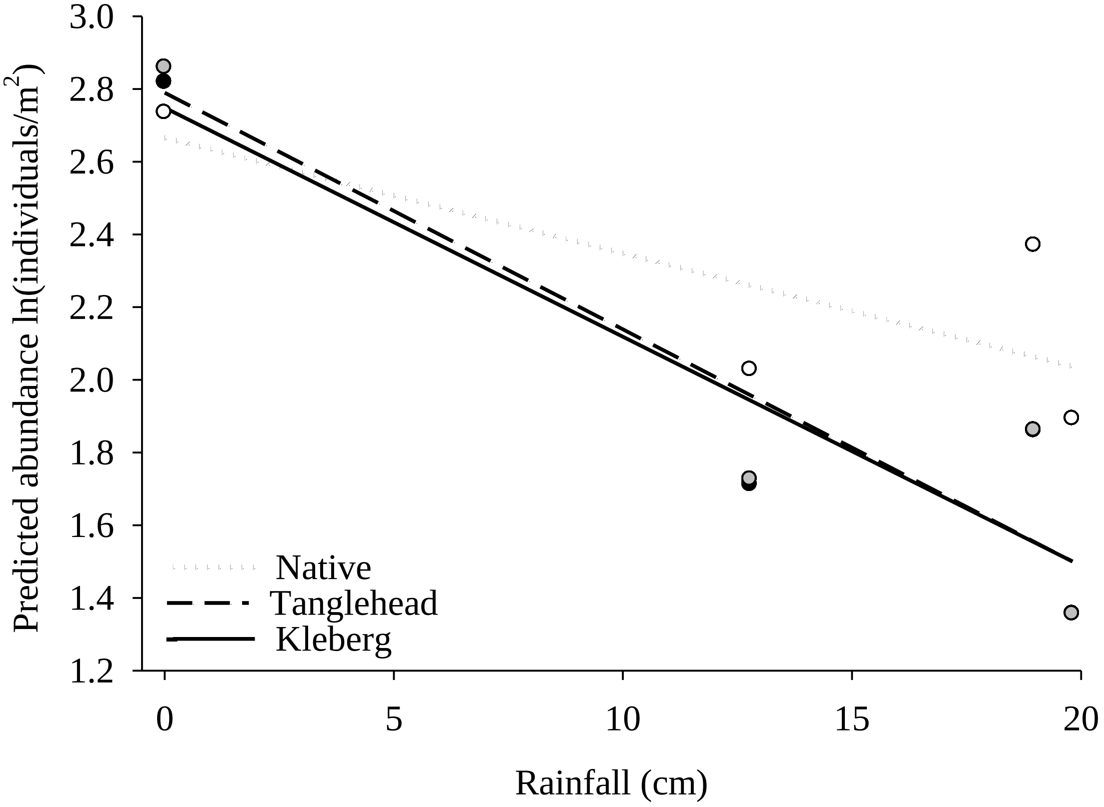

Figure 4. Changes in predicted average abundance of Entomobryidae (order Collembola) with rainfall, by grass community, 2009-2010, Kleberg County, Texas, USA.

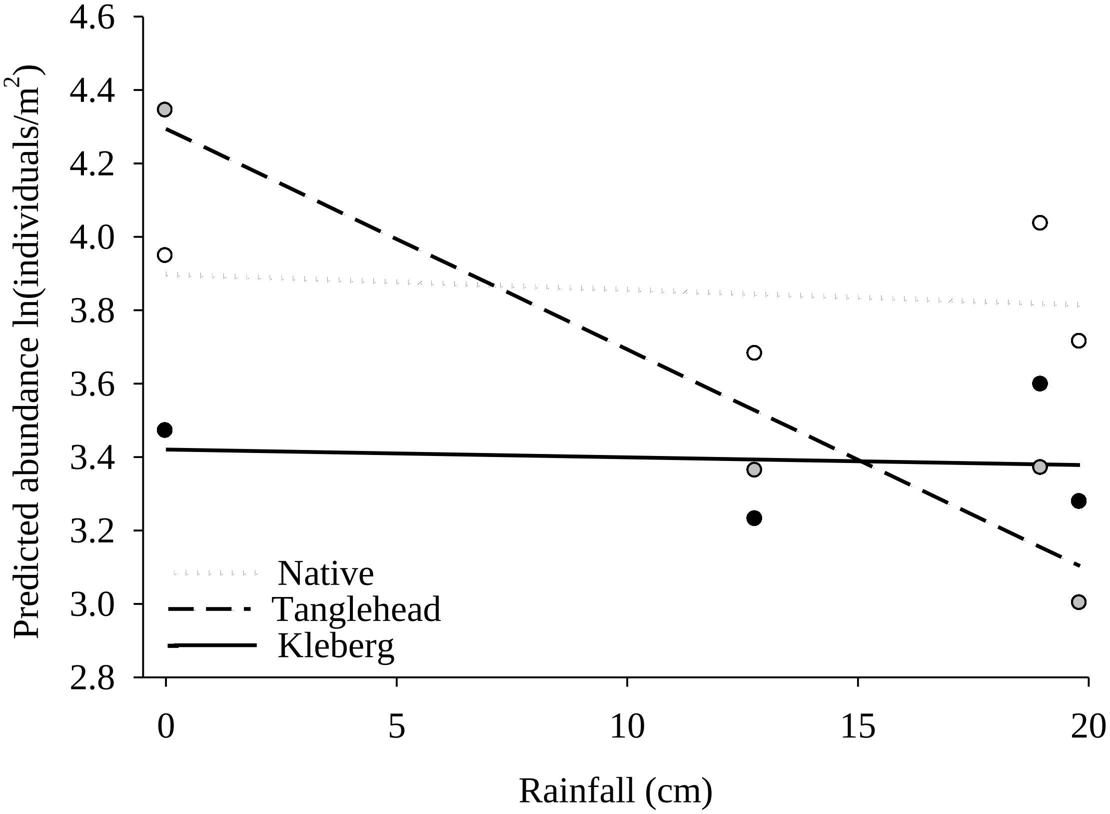

Figure 5. Changes in predicted average abundance of Formicidae (order Hymenoptera) with rainfall, by grass community, 2009-2010, Kleberg County, Texas, USA.

RAINFALL

I detected independent effects of rainfall on the presence of 4 of 6 arthropod orders and many arthropod families (Table 2.5 [p. 46]). With every 1-cm increase in rainfall, presence of Isopoda increased by 7.1% (2.5 to 11.2) and Microcoryphia (bristletails) by 7.2% (3.3 to 11.1), whereas presence of Psocoptera (bark lice) decreased by 16.2% (−27.2 to −3.5) and Pseudoscorpiones (false scorpions) by 16.7% (−27.2 to −3.5, Table 2.5 [p. 46]). Increased rainfall also resulted in increased presence of 8 of 11 coleopteran families (Carabidae [ground beetles, 14.0% increase with each additional cm of rainfall, 10.1 to 18.0], Mordellidae [5.5, 0.1 to 11.1], Staphylinidae [rove beetles, 12.3, 5.4 to 19.7], and Latridiidae [3.1, −0.3 to 6.6], 1 of 3 collembolan families (Hypogastruridae [7.7%, 1.9 to 13.8], all 7 dipteran families (Cecidomyiidae [gall midges, 55.4%, 29.2 to 86.6], Chironomidae [24.6, 14.7 to 35.5], Chloropidae [17.0, 12.5 to 21.6], Dolichopodidae [7.3, 1.4 to 13.5], Drosophilidae [4.8, 0.9 to 8.8], Phoridae [hump-backed flies, 7.9, 3.9 to 12.4], and Sciaridae [3.7, −0.3 to 7.8], 4 of 7 hemipteran families (Cicadellidae [31.9%, 22.3 to 42.2], Membracidae [tree hoppers, 32.5, 17.7 to 49.2], Miridae [28.0, 20.2 to 36.3], and Rhyparochromidae [seed bugs, 35.0, 14.6 to 58.9], 3 of 6 hymenopteran families (Braconidae [12.4, 7.6 to 17.4], Eurytomidae [another parasitic wasp family, 21.5, 13.9 to 29.6], and Pteromalidae [27.4, 20.1 to 35.3], 3 of 4 orthopteran families (Acrididae [short-horned grasshoppers, 8.9, 5.6 to 12.2], Tetrigidae [pygmy grasshoppers, 10.7, 5.5 to 16.2], and Tettigoniidae [27.2, 17.0 to 38.3]; and the only thysanopteran (thrips) family (Phlaeothripidae [4.1, −0.1 to 8.3], Table 2.5 [p. 46]). Rainfall resulted in decreased presence of 3 coleopteran families (Curculionidae [−9.7%, −13.6 to −5.7], Phalacridae [−4.1, −8.0 to −0.1], and Scraptiidae [−3.9, −10.0 to −1.6], 1 hemipteran family (Pachygronthidae [−7.7, −11.8 to −3.3], and 1 hymenopteran family (Halictidae [sweat bees, −6.9, −10.6 to −3.0], Table 2.5 [p. 46]).

Variation in rainfall independently affected diversity and abundance of some arthropods (Table 2.3 [p. 41]). Order richness increased 0.4% (0.1 to 0.7) and family richness increased 2.6% (2.1 to 3.1) with each additional cm of rainfall (Table 3 [p. 41]). Abundance of Aranae increased 10.5% (8.9 to 12.2), Hymenoptera (without Formicidae) increased 6.2% (4.2 to 8.1), and Homoptera increased 3.0% (0.2 to 6.0, Table 2.3 [p.

41]); however, abundance of Acari decreased 14.0% (−15.9 to −12.0), Coleoptera decreased 3.2% (−4.8 to −1.7), and Gryllidae decreased 3.3% (−5.4 to −1.2) with every 1-cm increase in rainfall (Table 2.3 [p. 41]).

SEASON

The arthropod community also varied seasonally (Tables 2.3 [p. 41] & 2.5 [p. 46]). Several families were more likely to occur early in the growing season including 1 of 7 families of Diptera, 4 of 7 families of Hemiptera (suborders Heteroptera, Auchenorrhyncha, and Sternorrhyncha), 3 of 6 families of Hymenoptera, and 2 of 4 families of Orthoptera (Tables 2.5 [p. 46] & 2.7). Aranae, Formicidae, and Entomobryidae were more abundant earlier in the growing season compared to later (Tables 2.3 [p. 41] & 2.8). In contrast, some orders and several families were more likely to occur later in the growing season including 7 of 11 coleopteran families, 1 of 2 collembolan families, 3 of 7 dipteran families, 1 of 3 orthopteran families, pseudoscorpions, and psocopterans (Tables 2.5 [p. 46] & 2.7). Abundance of all arthropods and of Homoptera increased later in the growing season compared to earlier (Tables 2.3 [p. 41] & 2.8).

Table 2.7. Least square means* (above) and 95% CIs (below) for arthropod presence by order and family by season (early or late in the growing season) based on generalized linear mixed models, *n* = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

Variable	Early	Late
Coleoptera		
Carabidae	35.2	49.2
	27.3 to 44.0	40.9 to 57.6
Chrysomelidae	20.9	30.7
	15.1 to 28.2	23.6 to 28.9
Curculionidae	11.3	57.9
	6.7 to 18.3	48.8 to 66.5
Elateridae	4.1	26.2
	1.8 to 9.2	18.7 to 35.5
Mordellidae	11.1	24.6
	7.0 to 17.2	18.1 to 32.4
Scarabeidae	6.1	15.7
	3.3 to 11.0	10.6 to 22.7
Staphylinidae	10.4	20.6
	6.1 to 17.2	14.2 to 28.8
Collembola		
Sminthuridae	10.9	46.7
	6.9 to 16.7	38.6 to 55.0
Diptera		
Cecidomyiidae	49.8	94.3
	30.6 to 69.0	84.6 to 98.0
Chironomidae	6.9	10.8
	3.7 to 12.7	6.7 to 17.1
Chloropidae	41.8	26.5
	33.4 to 50.7	20.3 to 33.8
Sciaridae	16.9	27.2
	11.8 to 23.5	20.6 to 34.9
Hemiptera		
Cercopidae	0.8	2.0
	0.2 to 2.9	0.6 to 6.5

Table 2.7. Continued

Variable	Early	Late
Cicadellidae	92.5	69.4
	82.5 to 97.0	59.0 to 78.2
Membracidae	18.7	1.4
	9.2 to 34.3	0.5 to 3.8
Miridae	43.3	5.3
	31.5 to 55.9	3.1 to 8.9
Rhyparochromidae	10	1.6
	3.7 to 24.3	0.5 to 5.0
Hymenoptera		
Braconidae	25.1	14.8
	18.4 to 33.1	10.2 to 20.8
Mutilidae	14	7.1
	9.1 to 20.9	3.9 to 12.7
Sphecidae	16.4	5.2
	11.3 to 24.0	2.7 to 9.8
Orthoptera		
Acrididae	57.8	41.7
	49.0 to 66.1	33.9 to 50.0
Tetrigidae	20.8	8.4
	14.6 to 28.7	5.1 to 13.5
Tettigoniidae	4.9	14
	2.5 to 9.2	9.1 to 21.0
Pseudoscorpiones	2.3	34.6
	0.4 to 12.1	22.7 to 48.9
Psocoptera	1.5	33.5
	0.2 to 9.8	20.7 to 49.3

[*] Measured as the percentage of plots where the taxa was present.

Table 2.8. Least square means (above) and 95% CIs (below) for arthropod abundance, for the overall community and by order and family by season (early or late in the growing season) based on generalized linear mixed models, *n* = 360 patch samples, 2009-2010, Kleberg County, Texas, USA.

Variable	Early	Late
Community		
Average abundance[a] (total/m^2)	52.8	58.8
	48.4 to 57.6	54.0 to 63.9
Orders & families (#/m^2)		
Aranae	6.6	5.3
	5.9 to 7.5	4.7 to 5.9
Collembola		
Entomobryidae	9.8	6.2
	8.2 to 11.3	5.0 to 7.6
Homoptera[b]	2.9	9.7
	2.1 to 4.0	7.9 to 12.0
Hymenoptera		
Formicidae	42.4	30.6
	34.3 to 52.6	24.0 to 39.2

[a] Does not include family Formicidae.
[b] Includes suborders Auchenorrhyncha and Sternorrhyncha within order Hemiptera.

DISCUSSION

As one plant species dominates the vegetation community, vegetation richness, bare ground, and structural heterogeneity decrease; this pattern has been observed with invasions of several nonnative plants (Slobodchikoff & Doyen 1977; French & Major 2001; Herrera & Dudley 2003; Standish 2004; Cuda et al. 2007; Wilkie et al. 2007; Topp et al. 2008; Wolkovich et al. 2009; Wu et al. 2009; Spyreas et al. 2010), as well as with several native invasive plants such as *Elymus athericus* (no common name) and *Phragmites australis* (common reed) (Bockelmann & Neuhaus 1999; Saltonstall 2002). I documented a similar change – vegetation was less diverse, both structurally and compositionally, in areas dominated by invasive grasses relative to areas dominated by native grasses; these changes were similar regardless of the varying origins of the invasive plants I examined. In general, grass-related differences in vegetation persisted despite influences of rainfall and growing season, although increased rainfall later in the growing season in both years lead to overall increases in plant growth and decreases in bare ground.

Changes in vegetation composition and structure with dominance by invasive grasses were associated with changes in the overall arthropod community. Richness and abundance of arthropods were lower in areas dominated by invasive grasses, relative to areas dominated by a diversity of native grasses, a pattern echoed in other studies that have examined invasive plants and arthropods (Gerber et al. 2008; Wu et al. 2009; Litt & Steidl 2010; Simao et al. 2010). Variation in soil type may have played a role in some of these results, particularly for certain groups of soil-dwelling arthropods that might be less affected by changes in standing vegetation (Brussaard 1997). These overall reductions were a result of many orders and families that were least likely to occur or least abundant in invasive grass-dominated areas (Slobodchikoff & Doyen 1977; Breytenbach 1986; Samways et al. 1996; Toft et al. 2001; Jonas et al. 2002; Lindsay & French 2006; Wolkovich et al. 2009, Wu et al. 2009; Litt & Steidl 2010). However, for some arthropod families, the probability of occurrence was lower in native grasses or comparable between native grasses and one of the invasive grasses. This diversity in the direction and magnitude of responses is likely related to the diversity of functional groups represented in the arthropod community and the diversity of habitat characteristics these groups of species require to complete their life cycles (Phillips et al. 1991; Pickett and Bugg 1998; Boughton 1999; Morris 2000).

Arthropod Functional Groups

Herbivorous arthropods depend on a variety of plants for food and reproduction, are host-specific to varying degrees (Tallamy 2004; Burghardt et al. 2008), and thus are most likely to be affected by changes in plant composition and structure. As a result, increases in presence and abundance of several groups of arthropod herbivores (e.g., many Hemiptera [including all Auchenorrhyncha and Sternorrhyncha], some Coleoptera, and some Diptera) I observed in areas dominated by native grasses were likely a response to increased vegetation species richness and cover of forbs (Lambrinos 2000; Derraik et al. 2001; Harris et al. 2006; Litt & Steidl 2010; Spyreas et al. 2010). Similarly, many groups of pollinating species (e.g., Lepidoptera, Hymenoptera) were less likely to occur or less abundant in at least one of the invasive grasses where overall forb cover, and likely abundance of flowering forbs, was lower. Generalist herbivores, such as Orthoptera, may be less affected by compositional and structural shifts in vegetation, but may be affected by forage quality; Orthoptera were least abundant in Kleberg bluestem, but had similar values in tanglehead and native grasses. Although many orthopterans may prefer native grasses as food (Tallamy 2004), many gryllid crickets are considered scavengers (Triplehorn & Johnson 2005). Gryllidae comprised 77% of orthopteran abundance and like the order as a whole, were less abundant in Kleberg bluestem; these species may be more affected by the decrease in dead vegetation observed in Kleberg bluestem than by the grass's origin.

Vegetation changes in areas dominated by invasive grasses are also likely to affect presence and abundance of some arthropod detritivores (Gratton & Denno 2005; Levin et al. 2006; Lindsay & French 2006; Kappes et al. 2007). Although increased dominance by invasive plants often results in increases in ground litter and decomposing vegetation (Lambrinos 2000; Toft et al. 2001; Standish 2004; Petillon et al. 2005; Topp et al. 2008; Wolkovich et al. 2009), I observed the lowest cover of dead vegetation in Kleberg bluestem areas and similar amounts in tanglehead and native grasses. A reduction in overall food resources could contribute to reductions in presence and abundance I detected in Kleberg bluestem for some predominantly detritivorous insect families such as Gryllidae and Sciaridae, as well as the beetle family Scarabeidae, which contains many detritivorous species (Triplehorn & Johnson 2005). Conversely, Drosophilidae, a fly family that includes many detritivores (Triplehorn & Johnson 2005), occurred most often in native grasses. This apparent contradiction may be more related to a change in composition and quality of the ground litter instead of a change in litter quantity, as forbs could be a larger component of litter in areas dominated by native grasses. Although adults of species in the beetle families Phalacridae, Latridiidae, and

Mordellidae often can be located on flowers, these groups have larvae that feed on decaying vegetation and fungus or contain certain species that are wholly detritivorous (Triplehorn & Johnson 2005); these families generally were more likely to occur in native grasses for at least part of the growing season, a pattern that previously has been documented for phalacrid beetles (Simao et al. 2010). Scraptiid beetles also have detritivorous larvae, but some species of these beetles have been associated with rotting woody vegetation (Triplehorn & Johnson 2005). Although the dominant woody species were similar between areas dominated by the two invasive grasses, huisache occurred in 11% of patches dominated by Kleberg bluestem and only 7% of patches dominated by tanglehead. Some invasive grasses may inhibit the growth of woody plants (Jonas et al. 2002), which could reduce the occurrence of these beetles in areas dominated by tanglehead.

Although I expected that changes in the plant community associated with invasive grasses would result in reductions in presence and abundance for many arthropod groups that depend directly on plants as food, I also documented less predictable, grass-related changes in arthropod predators, such as Aranae (spiders) and Acari (mites), possibly resulting from cascading effects (Gratton & Denno 2005). Increased abundance of spiders and mites in native grasses potentially are a result of the overall increase in the number and diversity of arthropods, providing a more abundant source of prey (Gratton & Denno 2006). In addition, arthropod predators may be influenced by changes in vegetation structure associated with invasive plants; increased vegetation cover may impede mobility or reduce availability of preferred microclimates (Sukava & Huhta 1998; Longcore 2003; Petillon et al. 2005) and result in reduced presence or abundance of mites and spiders, although predators benefitting from structural changes associated with invasive plants has also been observed (Pearson 2009).

Parasitoid arthropods (e.g., certain Hymenoptera and some Diptera) also may benefit indirectly from native grasses, such that more diverse vegetation and a more abundant and diverse arthropod community may mean that a diversity of preferred hosts are available and abundant (Simao et al. 2010). Some families of parasitic wasps (e.g., Braconidae, Eurytomidae, and Pteromalidae) that attack a variety of host arthropods (Triplehorn & Johnson 2005) were less likely to occur in one or both invasive grasses, relative to native grasses; preferred hosts may have been less abundant or absent in areas dominated by invasive grasses, although species-level identification would be required to examine this change further. The family Eurytomidae, although mostly parasitic, does contain some phytophagous species (Claridge 1961; Triplehorn & Johnson 2005), and the overall decrease in vegetation diversity with invasive grasses also may explain why this family was more likely to occur in native grasses for at least part of the growing season.

Native and Non-native Invaders

In general, I documented similar effects on abundance and presence of many arthropod groups in tanglehead and Kleberg bluestem, including abundance of 3 orders, presence of 7 families, and family and order richness. However, Lepidoptera, Tettigoniidae (Orthoptera), Miridae (Hemiptera), Pteromalidae (Hymenoptera), Drosophilidae (Diptera), Chironomidae (Diptera), Latridiidae (Coleoptera), and Scraptiidae (Coleoptera), were least likely to occur in tanglehead, during all or part of the growing season. Because these groups vary in functional roles and ecological niches, the reasons underlying this reduced presence are unclear.

Some groups are flower or nectar feeders for at least part of their life cycles (Triplehorn & Johnson 2005), so I considered the possibility that the dominant forb species in Kleberg bluestem and tanglehead differed, thus favoring different arthropod groups. However, when I examined the forb species that occurred most commonly in each invasive grass community, 8 of 10 forb species were present in a similar percentage of samples (Appendix 3). Dolichopodidae, a family of predaceous flies, was more likely to occur in tanglehead early in the growing season. Larvae of these flies can be predators, scavengers, or leaf-miners depending on species and often prefer moist and decaying vegetation (Pollett et al. 2004); tanglehead areas had higher cover of dead vegetation compared to Kleberg bluestem and overall vegetation cover compared to native grasses, potentially creating more favorable environmental conditions for reproducing dolichopodids. Total abundance and abundance of ants also declined with increasing rainfall in only tanglehead-dominated areas (Figs. 1 [p. 40] & 5 [p. 55]), such that precipitation may be affecting tanglehead differently. Although tanglehead is not a novel plant species in this ecosystem, increased distribution and dominance of this plant may be equally, if not more, detrimental for some groups of arthropods than Kleberg bluestem, a widespread non-native species. Additional research on the mechanisms underlying the increase in tanglehead dominance and subsequent changes in population dynamics, community composition, trophic structure, and ecosystem processes are needed to understand fully the implications of this native invader.

Rainfall and Seasonal Variability

Rainfall plays a prominent role in growth of vegetation, as well as of arthropod populations (Dunham 1978; Frampton et al. 2000). For many orders and families of arthropods, increased rainfall resulted in increased presence and abundance (Tanaka & Tanaka 1982; Mackay et al. 1986; Frampton et al. 2000); however, some groups decreased in abundance (Goolsby et al. 2005; Anu et al. 2009). Even where I documented relatively small changes for each additional cm of rainfall, these estimated changes become substantial when the range of rainfall I observed (0-20 cm) is considered.

I detected an overall decline in arthropod abundance with increased rainfall (Fig. 1), which was most pronounced in areas dominated by tanglehead. This decline, although somewhat surprising, was driven mainly by changes in abundance and dominance of Acari and Collembola. When rain was absent (July 2009, rainfall = 0.0 cm), I sampled 5,341 individual Acari (all mites) and 2,478 individual Collembola overall, which comprised 54.7% and 25.4% of the total abundance of arthropods, respectively. Abundance and dominance of these groups decreased with increased rainfall; when rainfall was highest (September 2010, rainfall = 19.8 cm), I only sampled 107 Acari and 265 Collembola, comprising only 1.1% and 2.8% of the total abundance of arthropods. Decreasing abundance and activity with relatively high rainfall has been documented for some species of mites and collembolans (Goolsby et al. 2005; Onzo et al. 2005; Anu et al. 2009), although rainfall also may have altered trap effectiveness. At the outset of this study, South Texas was under severe drought conditions (NDMC 2011). With such extremely dry conditions, more soil may have blown into pitfall traps and resulted in higher abundance of Acari and Collembola collected, relative to later sampling seasons. I also detected an overall decline in abundance of Coleoptera and the occurrence of 4 beetle families (i.e., Curculionidae, Phalacridae, Scraptiidae, and Tenebrionidae), these groups may have been sampled less effectively with increasing vegetation cover (Greenslade 1964) or this decrease may be related to an increase in predators (spiders) with rainfall.

Because vegetation growth, temperature, and other climatic conditions vary over the growing season, abundance and presence of certain arthropod orders and families also often display similar variation (Tanaka & Tanaka 1982; Pearson & Derr 1986). In general, I found that total abundance of arthropods increased over the growing season, which may be a function of seasonal vegetation growth and increased rainfall (Tauber et al. 1986; Wolda 1978). In addition, habitat requirements may vary for arthropods throughout their life cycles (Triplehorn & Johnson 2005), such that the effects of invasive plants and the differences I quantified among grass communities vary over the growing season. For example, I detected an overall increase in abundance of Coleoptera in native grasses later in the growing season, which may be driven by increased presence of a few beetle families. In contrast, Hymenoptera (excluding ants) were slightly more abundant in native grasses early in the growing season, which again may be the result of increased presence of certain families. For some arthropods, invasive grasses may be more detrimental during certain parts of growing season (Herrera & Dudley 2003; Simao et al. 2010), coinciding with important periods in their life cycles.

CONCLUSIONS

I observed substantial changes in the arthropod community related to increases in both Kleberg bluestem and tanglehead, including decreases in overall abundance and diversity at the order and family level, which are relatively coarse levels of classification. I quantified these changes in presence and abundance within 1-m^2 plots; when extrapolating reduced abundance or complete loss of entire orders and families of arthropods across the landscape, alterations in various ecological processes and potential decrease in reproductive success, presence, or abundance of other wildlife species could be considerable (Wiens & Rotenberry 1979; Wilson 1987; Flanders et al. 2006; Litt & Steidl 2011). Although some studies have documented a shift in food web dynamics – from a system driven by herbivorous arthropods in areas dominated by native vegetation to one dependent on detritivores in areas dominated by invasive plants (Gratton & Denno 2005), this increase in dead vegetation and detritivores was not apparent during our study. I did document decreases in the presence and abundance of many arthropod herbivores, including some pollinators, and predators, suggesting a potential shift in trophic structure within the arthropod community; these changes in abundance and composition may have cascading effects.

Invasive grasses, including tanglehead and Kleberg bluestem, alter arthropod communities in notable ways and as a result can modify entire ecosystems (Vitousek et al. 1996). Because many species of birds, small mammals, and reptiles rely on arthropods as their primary food resource (Wilson 1987), the overall decreases in arthropod abundance I observed in areas dominated by tanglehead and Kleberg bluestem will likely have a negative effect on certain species of wildlife that depend on arthropods as a primary food resource, including certain species of reptiles, grassland birds, and small mammals (Wiens & Rotenberry 1979; Abell 1999; Flanders et al. 2006; Litt & Steidl 2011). Reduced arthropod abundance and diversity may indicate that important ecosystem processes such as pollination, decomposition, and seed dispersal will be similarly modified in areas dominated by invasive grasses, emphasizing the importance of conserving arthropods to maintain biodiversity and ecosystem structure and function (Wilson 1987). Although complete eradication of invasive grasses is unlikely, conservationists can focus on maintaining or increasing vegetation heterogeneity to sustain diverse and abundant arthropod communities and essential ecosystem processes.

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APPENDIX A: Plant species and the percentage of samples (*n* = 360 patch samples) where observed during 4 sampling seasons, 2009-2010, Kleberg County, Texas, USA.

Category	Common name	Scientific name	% of total samples
Native grasses	Common sandbur	*Cenchrus spinifex*	29.17
	Common witchgrass	*Panicum capillare*	8.06
	Hooded windmillgrass	*Chloris cucullata*	3.89
	Knotroot bristlegrass	*Setaria parviflora*	3.89
	Little bluestem	*Schizachyrium scoparium* var. *scoparium*	3.61
	Multiflower false Rhodesgrass	*Chloris pluriflora*	0.56
	Purple threeawn	*Aristida purpurea*	26.94
	Red lovegrass	*Eragrostis secundiflora*	4.17
	Seacoast bluestem	*Schizachyrium scoparium* var. *littoralis*	21.68
	Shortspike windmillgrass	*Chloris subdolichostachya*	0.28
	Silver bluestem	*Bothriochloa laguroides* ssp. *torreyana*	9.44
	Tanglehead	*Heteropogon contortus*	51.11
	Thin paspalum	*Paspalum setaceum*	5.00
	Tumble lovegrass	*Eragrostis sessilispica*	3.06
Non-native grasses	Buffelgrass	*Cenchrus ciliaris*	0.56
	Dallisgrass	*Paspalum dilatatum*	1.11
	Hairy crabgrass	*Digitaria sanguinalis*	2.50
	Kleberg bluestem	*Dichanthium annulatum*	61.11
	Plains lovegrass	*Eragrostis intermedia*	0.28
Forbs	American snoutbean	*Rhynchosia americana*	41.67

Appendix A. Continued

Category	Common name	Scientific name	% of total samples
Forbs	Arkansas lazy daisy	*Aphanostephus skirrhobasis*	7.78
	Bracted sida	*Sida ciliaris* var. *mexicana*	3.61
	Brazos milkvetch	*Astragalus brazoensis*	0.28
	Brown-eyed susan	*Rudbeckia hirta*	9.72
	Coreopsis	*Coreopsis nuecensoides*	0.83
	Drummonds goldenweed	*Iscoma drummondii*	3.06
	Frostweed	*Verbesina microptera*	5.56
	Globe berry	*Ibervillea lindheimeri*	0.56
	Ground cherry	*Physalis cinerascens*	27.50
	Heart-sepal wild buckwheat	*Eriogonum multiflorum*	3.33
	Huisache daisy	*Amblyolepis setigera*	1.39
	Indian Blanket	*Gaillardia pulchella*	0.83
	Karnes sensitive briar	*Schrankia latidens*	2.78
	Lemon beebalm	*Monarda citriodora*	22.22
	Lindheimer tephrosia	*Tephrosia lindheimeri*	1.94
	Mexican hat	*Ratibida columnifera*	4.72
	Narrowleaf dayflower	*Commelina erecta* var. *angustifolia*	6.94
	Northern croton	*Croton glandulosus* var. *septentrionalis*	0.83
	Palafoxia	*Palafoxia texana* var. *ambigua*	23.61
	Partridge pea	*Chamaecrista fasciculata*	4.44
	Perennial ragweed	*Ambrosia cumanensis*	48.06
	Phlox	*Phlox drummondii*	6.11
	Prairie clover	*Dalea nana*	0.28

APPENDIX A. Continued

Category	Common name	Scientific name	% of total samples
Forbs	Prickly sida	*Sida spinosa*	3.89
	Purple pleatleaf	*Alophila drummondii*	0.28
	Ridgeseed euphorbia	*Euphorbia glyptosperma*	2.50
	Sawtooth frog-fruit	*Phyla incisa*	2.78
	Scarlet pimpernel	*Anagallis arvensis* ssp. *arvensis*	18.89
	Silky evolvulus	*Evolvulus sericeus*	10.0
	Silverleaf nightshade	*Solanum elaeagnifolium*	6.11
	Slender evolvulus	*Evolvulus alsinoidea* var. *hirticaulis*	11.39
	Southwestern carrot	*Daucus pusillus*	6.39
	Texas croton	*Croton texensis*	2.22
	Texas lantana	*Lantana urticoides*	5.56
	Texas senna	*Chamaecrista flexuosa*	6.39
	Texas sleep-daisy	*Xanthisma texanum*	0.56
	Texas thistle	*Cirsium texanum*	0.56
	Texas vervain	*Verbena officinale* spp. *halei*	0.28
	Texas virgin's-bower	*Clematis drummondii*	13.33
	Tropical neptunia	*Neptunia pubescens*	2.78
	Western indigo	*Indigofera miniata* var. *leptosepala*	0.28
	Wild mercury	*Argythamnia humilis*	5.56
	Wooly croton	*Croton capitatus* var. *lindheimeri*	48.61
Succulents	Prickly pear	*Opuntia engalmannii*	2.50

APPENDIX A. Continued

Category	Common name	Scientific name	% of total samples
Succulents	Tasajillo	*Cylindropuntia leptocaulis*	1.94
Woody plants	Honey mesquite	*Prosopis glandulosa* var. *glandulosa*	3.01
	Huisache	*Acacia minuata*	8.89

APPENDIX B. Relative presence (% of *n* = 360 patch samples) and abundance (% of *n* = 68,450 total individuals) of arthropod orders and insect families captured during 4 sampling seasons, 2009-2010, Kleberg County, Texas, USA.

		Order		Family	
Order	Family	% of total samples	% of total indivs.	% of total samples	% of total indivs.
Acari		79.72	9.71		
Aranae		97.50	8.04		
Blattaria	Blatellidae	4.44	0.03	4.44	0.03
Coleoptera	Anthicidae	94.72	4.42	0.83	0.00
	Anthribidae			1.67	0.00
	Buprestidae			3.06	0.02
	Carabidae			45.28	0.55
	Cerambycidae			2.50	0.02
	Chrysomelidae			25.83	0.34
	Cleridae			0.28	0.00
	Coccinellidae			0.28	0.00
	Curculionidae			35.00	0.64
	Elateridae			14.44	0.18
	Histeridae			0.28	0.00
	Languriidae			0.28	0.00
	Latridiidae			49.17	1.51
	Meloidae			4.17	0.02
	Melyridae			2.50	0.02
	Mordellidae			19.72	0.19
	Phalacridae			16.11	0.12

APPENIX B. Continued

		Order		Family	
Order	Family	% of total samples	% of total indivs.	% of total samples	% of total indivs.
	Pselaphidae			3.61	0.02
	Scarabeidae			11.11	0.17
	Scraptiidae			12.78	0.11
	Silvaniidae			0.83	0.00
	Staphylinidae			20.00	0.17
	Tenebrionidae			26.39	0.19
	Zopheridae			0.83	0.01
Collembola	Entomobryidae	89.72	10.40	86.11	9.34
	Hypogastruridae			11.39	0.19
	Isotomidae			3.61	0.04
	Sminthuridae			28.89	0.85
Diptera	Agromyzidae	84.44	8.97	3.61	0.03
	Anthomyiidae			5.00	0.04
	Anthomyzidae			1.66	0.02
	Asilidae			2.22	0.01
	Bombyliidae			7.50	0.07
	Calliphoridae			2.78	0.02
	Cecidomyiidae			70.56	5.80
	Chironomidae			18.33	0.67
	Chloropidae			37.50	0.84
	Culicidae			9.44	0.18
	Dolichopodidae			25.28	0.34
	Drosophilidae			25.28	0.40
	Muscidae			4.44	0.02

APPENDIX B. Continued

		Order		Family	
Order	Family	% of total samples	% of total indivs.	% of total samples	% of total indivs.
	Largidae			1.11	0.01
	Lygaeidae			0.28	0.00
	Membracidae[*]			16.94	0.38
	Miridae			27.50	1.02
	Nabidae			1.39	0.01
	Pachygronthidae			16.67	0.20
	Pentatomidae			8.06	0.05
	Psyllidae[*]			1.39	0.01
	Reduviidae			7.50	0.05
	Rhopalidae			0.28	0.00
	Rhyparochromidae			13.61	0.18
	Tingidae			0.83	0.00
Hymenoptera	Agaonidae	99.72	41.35	0.83	0.00
	Aphelinidae			0.56	0.01
	Apidae			1.39	0.01
	Bethylidae			7.78	0.05
	Braconidae			22.78	0.18
	Chalcidae			1.39	0.01
	Cynipidae			0.83	0.00
	Encrytidae			0.83	0.00
	Eulophidae			5.56	0.04
	Eupelmidae			0.56	0.00
	Eurytomidae			20.00	0.29

APPENDIX B. Continued

		Order		Family	
Order	Family	% of total samples	% of total indivs.	% of total samples	% of total indivs.
Hymenoptera	Formicidae			99.44	39.86
	Halictidae			17.78	0.12
	Ichneumonidae			6.11	0.05
	Mutilidae			11.39	0.08
	Mymaridae			0.56	0.00
	Platygastridae			0.28	0.00
	Pompilidae			7.78	0.06
	Pteromalidae			36.67	0.46
	Singiphoridae			0.28	0.00
	Sphecidae			11.11	0.08
	Torymidae			1.11	0.01
	Trichogrammatidae			1.11	0.00
Isoptera	Rhinotermitidae	17.78	0.42	17.78	0.42
Lepidoptera	Geometridae	41.39	0.47	7.50	0.05
	Hesperiidae			8.33	0.09
	Noctuidae			0.28	0.00
	Nymphalidae			3.06	0.01
	Pieridae			0.28	0.00
	Pterophoridae			1.11	0.00
	Pyralidae			0.56	0.00
Mantodea	Mantidae	1.11	0.00	1.11	0.01
Microcoryphia	Machilidae	28.33	0.26	28.33	0.26
Neuroptera	Ascalaphidae	2.50	0.01	1.67	0.01
	Hemerobiidae			0.28	0.00

APPENDIX B. Continued

		Order		Family	
Order	Family	% of total samples	% of total indivs.	% of total samples	% of total indivs.
Neuroptera	Mymeliontidae			0.28	0.00
Odonata	Coenagrionidae	0.28	0.00	0.28	0.00
Orthoptera	Acrididae	94.17	3.36	49.72	0.55
	Gryllidae			86.94	2.47
	Rhaphidophoridae			3.89	0.02
	Tetrigidae			15.83	0.00
Phasmida	Heteronemiidae	2.50	0.01	2.50	0.01
Pseudoscorpiones		10.56	0.07		
Psocoptera	Psocidae	15.00	0.23	15.00	0.23
Scorpiones		6.94	0.04		
Solpugida		1.11	0.01		
Thysanoptera	Phlaeothripidae	20.83	0.24	19.44	0.23
	Thripidae			1.94	0.01
Thysanura	Lepismatidae	0.28	0.00	0.28	0.00

[*] Included in the subgrouping Homoptera (suborders Auchenorrhyncha and Sternorrhyncha combined).

APPENDIX C. Ten most common species of forbs in sites dominated by tanglehead (*Heteropogon contortus*) and Kleberg bluestem (*Dichanthium annulatum*) based on the percentage of samples (*n* =360 patch samples) where observed during 4 sampling seasons, 2009-2010, Kleberg County, Texas, USA.

	Kleberg bluestem		Tanglehead	
Rank	Scientific name	% total of samples	Scientific name	% total of samples
1	*Croton capitatus* var. *lindheimeri*	43.70	*Croton capitatus* var. *lindheimeri*	41.32
2	*Ambrosia cumanensis*	38.66	*Ambrosia cumanensis*	36.36
3	*Rhynchosia Americana*	32.77	*Rhynchosia americana*	33.06
4	*Monarda citriodora*	23.53	*Palafoxia texana* var. *ambigua*	28.10
5	*Physalis cinerascens*	20.17	*Physalis cinerascens*	27.27
6	*Palafoxia texana* var. *ambigua*	18.49	*Monarda citriodora*	22.31
7	*Anagallis arvensis* ssp. *Arvensis*	17.65	*Anagallis arvensis* ssp. *arvensis*	18.18
8	*Clematis drummondii*	13.45	*Evolvulus alsinoidea* var. *hirticaulis*	12.40
9	*Rudbeckia hirta*	10.08	*Aphanostephus skirrhobasis*	11.57
10	*Verbesina microptera*	9.24	*Rudbeckia hirta*	10.74

VITA

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