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Ground Beetle (Coleoptera: Carabidae) Assemblages in Native, Invasive, and Encroaching Grassland Habitats

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GROUND BEETLE (COLEOPTERA: CARABIDAE)

ASSEMBLAGES IN NATIVE, INVASIVE, AND ENCROACHING

GRASSLAND HABITATS

A Thesis Presented to the Graduate Faculty

of the Fort Hays State University in

Partial Fulfillment of the Requirements for

the Degree of Master of Science

by

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The Master of Science Degree

by

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ABSTRACT:

Ground beetles (Carabidae) are increasingly used as ecological indicators in studies

regarding land use because they are ubiquitous, respond quickly to environmental change, have a

well-understood taxonomy, and can be trapped with ease. While the effects of various plant

communities on ground beetle assemblages are relatively well-known, past studies have operated

within boreal and tropical forests and have not placed much emphasis on the effects of native and

nonnative species. In this study, ground beetles were investigated as indicators of invasion in a

grassland setting. Ground beetles were sampled using pitfall traps throughout the 2018 growing

season at Quivira National Wildlife Refuge, located in south central Kansas, and characterized

by the presence of inland salt marsh and prairie sand dunes, habitat types uncommon to the area.

With a sampling effort of 2 traps per array (1 sample) x 8 arrays x 3 treatments x 12 sampling

periods, 580 individuals representing 39 species were observed. Capture rates of ground beetles

more closely resembled two habitat types: encroaching and invasive habitats, with native habitats

overlapping with both. Results from pitfall traps suggest that carabids and plants were probably

responding to environmental disturbance and sandy soils rather than directly to each other. There

was a clear dominance of carabid species adapted to habitat disturbance (including *Chlaenius*

erythropus, Scarites subterraneus, and *Pterostichus permundus*). Many plant species that were

significantly associated with ground beetle assemblages, including poison ivy (*Toxicodendron*

radicans), one-seed croton (*Croton monanthogynus*), and *Panicum*, were also adapted to

disturbance. Moreover, ground beetles reacted negatively overall to areas with sandy soil. This

suggests that ground beetles might not be the best indicator species for this region, because any

effects of invasion were overshadowed by soil type or disturbance.

TABLE OF CONTENTS:

LIST OF TABLES:

LIST OF FIGURES:

LIST OF APPENDICES:

PREFACE:

This thesis is formatted in a style suitable for publication in *The Coleopterists Bulletin*.

INTRODUCTION:

The term "biodiversity" refers to the entirety of an ecosystem's plant, animal, fungal, and microbial life that interact together (Vandermeer and Perfecto 1995, Altieri 1999). Interactions between organisms are vital for most (if not all) ecological processes, including nutrient cycling, maintenance of microhabitat, and detoxification of noxious chemicals (Altieri 1999). For example, interactions between plant species form the vegetative cover present in forests and grasslands, which can reduce soil erosion and control flooding by reducing water runoff (Perry 1994, Altieri 1999). Furthermore, interactions among arthropods and plants facilitate important ecological processes such as pollination, herbivory, and nutrient cycling, both directly and indirectly. Though the collective biomass of insects and other small-bodied arthropods is relatively minor compared to groups at higher trophic levels, they may directly influence resources that enter the food web (Yang and Gratton 2014). In addition, arthropod herbivores may exert control of plant communities through selective seed consumption (Ebeling et al. 2018).

Declining global biodiversity and accelerating extinction rates have become focal topics in modern ecology and politics, but these are not new phenomena. For instance, Butchart et al. (2010) trace decreases in global biodiversity back at least 40 years. Much of this loss is attributed to habitat destruction as land is transformed from its natural state through urbanization or intensive agriculture. Though no single solution exists to solve this problem, one remedy is establishing effective land management policies (Jacobs et al. 1999, Butchart et al. 2010). Often, the first steps in implementing these procedures is gathering habitat data and conducting biodiversity surveys to discover functional groups whose protection will fuel the conservation of other species (Walker 1992, Magurran 2004). Because conservation and land management efforts are often heavily reliant on biological diversity data (Magurran 2004), biodiversity

1

surveys are often conducted with the overall goal of informing a management plan. Management

plans often involve the control of invasive species, as the introduction and establishment of

invader species can promote ecosystem disturbance (Walker and Smith 1997). Magurran (2004)

further explains that, for these diversity surveys to prove effective, they should be conducted

both at multiple taxonomic levels and at a variety of scales. However, invertebrate groups,

though a significant and ecologically critical constituent of many habitats, are often not well

represented in biodiversity studies (Refseth 1980, McGeoch 1998).

Goals of biodiversity studies are usually more complex than merely cataloging all species

within a habitat. Sometimes an indicator species is discovered that future management plans are

structured around. Indicator species can be classified in various manners: McGeoch (1998)

describes three categories of indicators (environmental, ecological, and biodiversity), whereas

Lindenmayer et al. (2000) present seven categories. A few of these categories are similar to

McGeoch's, but several are more specific, such as keystone species (species whose presence or

absence have important consequences for their ecosystems), dominant species (species whose

large biomasses have powerful influences on their environments), and management indicator

species (species whose responses are reflective of environmental disturbance or attempts to

mitigate disturbances) (Lindenmayer et al. 2000). Regardless of organization, the primary goals

of indicators remain largely the same: to reveal abiotic or biotic conditions of habitat, to illustrate

the effects of environmental change, or to provide a snapshot of overall species diversity in a

habitat, community, or ecosystem (McGeoch 1998, Lindenmayer et al. 2000, Rainio and

Niemela 2003). Management indicator species are especially useful given the unrealistic nature

of surveying all species within an area. Some key criteria for good bioindicators are a wide

distribution, inexpensive methods of study, a well understood taxonomy and ecology, quick

reaction to environmental change, and adherence to strict microhabitats (Rainio and Niemela 2003).

Ground beetles (family Carabidae) are good candidates as indicator species and are therefore becoming an integral aspect of land management (Rainio and Niemela 2003, Cajaiba et al. 2018). Not only do they fulfill important ecological roles in many environments as generalist predators, decomposers, and food sources for higher trophic levels (Didham et al. 1996, Marshall 2018), but they are easily captured with pitfall traps, which are inexpensive and simple to install. Furthermore, because every habitat contains its own collection of generalist and specialist species, ground beetle assemblages or individual ground beetle species can serve as bioindicators (Rainio and Niemela 2003).

The convenience of pitfall trapping has led to a noticeable increase in studies using pitfall traps to sample ground-dwelling arthropods (Greenslade 1964, Rainio and Niemela 2003, Boetzl et al. 2018). Though the various methods of pitfall trapping and issues of interpreting pitfall data have been decried for decades, they are often the most practical option for researchers and landowners wishing to sample such creatures (Greenslade 1964, Topping and Sunderland 1992), and great strides have been taken recently to refine and standardize trapping methods and interpret results more effectively (Spence and Niemela 1994, Brown and Matthews 2016, Hohbein and Conway 2018). Ground beetles have proved practical bioindicators in studies regarding habitat fragmentation, though their responses have varied substantially, including changes in species evenness (Davies and Margules 2002), increases in species richness (Burke and Goulet 1998), or decreases in species richness (Halme and Niemela 1993). The responses of these ground beetle groups may have varied, but they were certainly detectable. Therefore, monitoring ground beetle assemblages or community structure (which may include species

richness, species evenness, or species diversity) in an area throughout a given period may serve as a cost effective method of observing how the land reacts to disturbance or document how the habitat changes over time.

Studies involving sampling of ground beetles within North American grasslands are noticeably lacking compared to habitats on other continents. Most of the literature exploring the environmental influences on ground beetle assemblages within grassland systems describes studies occurring overseas in European systems (Thorbek and Bilde 2004, Pakeman and Stockan 2014, Brygadyrenko 2015, Twardowski et al. 2017, Teofilova 2018). Additionally, the bulk of studies focusing on environmental influences on ground beetle assemblages have occurred in boreal and tropical forests (Holliday 1984, Halme and Niemela 1993, Burke and Goulet 1998, McCollough et al. 1998, Davies and Margules 2002, Brose 2003, Gonglasky et al. 2006, Cajaiba et al. 2018). The typical vegetation structure of forest ecosystems differs from that of grassland ecosystems; grasslands are characterized by dominant grasses and forbs with few trees (Teofilova 2018), whereas forests are known for their abundant tall trees and conifers (Kuuluvanien 2009). Perhaps these differences in habitat and climate lead to differences in selective pressures imposed on ground beetle assemblages. In addition, considerable research has been conducted regarding ground beetle assemblages in different biomes and particularly in riparian zones (Bagstad et al. 2006), but the effect of invasive plants specifically on ground beetle assemblages has not been investigated previously.

Using ground beetles as indicator species might be a method to assess changes in plant communities. Ground beetle community structure is influenced by species diversity and structural heterogeneity of plants within their habitats. Brose (2003) summarizes these ideas as follows: according to the taxonomic diversity hypothesis, plant diversity and herbivore diversity

4

are positively correlated, because additional plant species might support specialized consumers. Contrastingly, the structural heterogeneity hypothesis states that a greater diversity in plant structure and form will result in increased species diversity, as herbivores, and by extension predators, have more variety in food choices. Both hypotheses have empirical support, but usually not simultaneously (Erwin 1982, Siemann et al. 1998, Dennis et al. 2002, Brose 2003, Pakeman and Stockan 2014). Some long-term studies suggest that the two hypotheses may work cooperatively (Southwood et al. 1979), especially because both factors seem heavily influenced by disturbance.

Because plant species diversity and arthropod species diversity are often correlated (Southwood et al. 1979, Siemann et al. 1998, Davidowitz and Rosenzweig 2003, Heleno et al. 2009, Cajaiba et al. 2018, Ebeling et al. 2018), we might expect to see more ground beetle species within habitats supporting more diverse plant species. In addition, invaded habitats sometimes exhibit decreased species diversity compared to uninvaded habitats (Walker and Smith 1997, Haddock et al. 2015). Simberloff and Von Holle (1999) introduced the term "invasional meltdown" to describe the interactions between nonnative species that enable each other to dominate habitats, especially the formation of monocultures. However, Siemann et al. (1998) and Heleno et al. (2009) note that, while arthropod species richness is influenced by plant species diversity, arthropod assemblages are not significantly affected. Despite this, invasive plant species can still impact arthropod communities by reducing their biomass (Heleno et al. 2009), which can have consequences for higher trophic levels, because insects are a major food source for many reptile, bird, and mammal species, and play critical ecological roles in important biological processes like nutrient cycling (McCollough et al. 1998, Cajaiba et al. 2018). Though plant diversity may act as an important influencer of ground beetle community structure, it is

probably not the only determining factor. Soil type, moisture, predator density, and plant functional traits are likely key aspects as well, particularly in grassland systems (Siemann et al. 1998, Thorbek and Bilde 2004, Pakeman and Stockan 2014, Brygadyrenko 2015, Teofilova 2018).

The primary objective of this study was to examine how habitat influences grassland ground beetle assemblages. The secondary objective was to create a catalogue of dominant ground beetle species within the study area. There are no published ground beetle studies in south central Kansas or at Quivira National Wildlife Refuge (U.S. Fish and Wildlife Service 2019). Ground beetle community structure might provide meaningful insight during the development of management plans. The lack of certainty regarding the principal selective pressures impacting ground beetle assemblages as well as the relative absence of published data about ground beetles in American grasslands signifies the value of this study. Three hypotheses were tested during this study. 1.) I hypothesized that ground beetle assemblages in native and encroaching habitats would be more similar to each other than to ground beetle assemblages in invasive habitats. Associated with this is the notion that native and encroaching habitats would support more plant species based on the phenomena that plant diversity and arthropod diversity are correlated and that ground beetle assemblages are heavily influenced by the species diversity and structural complexity of their habitats (Southwood et al. 1979, Siemann et al. 1998, Heleno et al. 2009, Davidowitz and Rosenzweig 2003, Cajaiba et al. 2018, Ebeling et al. 2018). 2.) I also hypothesized that invasive plant communities would support more ground beetles not native to the Great Plains region based partly on the invasional meltdown described by Simberloff and Von Holle (1999). According to this idea, positive interactions between nonnative species can increase survival and establishment of invasive species. In addition, saltcedar invasion is a

massive problem in Kansas and is associated with displacement of native vegetation, deterioration of wildlife habitat, and increased soil salinity (Yang and Steward 2012). 3.) I hypothesized that habitats with more bare ground would be negatively associated with ground beetle assemblages, because a greater degree of aerial cover may provide better concealment and protection from predators (Berdegue et al. 1996, Thorbek and Bilde 2004).

MATERIALS AND METHODS:

Study site:

Pitfall trapping for ground beetles occurred at Quivira National Wildlife Refuge (38.0745° N, 98.4912° W), located in south central Kansas, USA, from May - August 2018. Quivira National Wildlife Refuge is characterized by habitat types uncommon to the area: prairie sand dunes and inland salt marshes (U.S. Fish and Wildlife Service 2019). These unique habitats attract many species that are not often observed in the area, including Graham's crayfish snake [(*Regina grahamii*) Baird and Girard)] and the American Bittern [(*Botaurus lentiginosus* (Rackett)] (Skagan and Knopf 1994). The refuge is also unique because of its position on the central flyway, which places Quivira National Wildlife Refuge directly in the path of many migrating shorebirds (U.S. Fish and Wildlife Service 2019).

Pitfall trapping:

Pitfall traps were modeled after and used many of the same materials as those described by Dunn (2007). Arrays were modified nested arrays (Perner and Schueler 2004, Dunn 2007), with each array consisting of two pitfall traps organized in a linear fashion with 300 cm of plastic drift fence running between each trap. Invasive plants often lined creeks, which necessitated modification of the nested-cross pitfall trap arrays into linear designs. A white, plastic cup (13 cm tall and 11.7 cm in diameter) was buried so it was flush with ground level and remained in place throughout the field season (Figure 1). Another cup of similar size was placed within this cup and was removed to empty traps and was promptly replaced. Insertion of two of the same containers together in this manner is called "nesting" (Brown and Matthews 2016, Hohbein and Conway 2018). Nested traps are much more easily established and serviced than non-nested traps and are also recommended as a standard aspect of pitfall trap design (Brown and Matthews 2016,

Hohbein and Conway 2018). Additionally, a small funnel (13 cm deep and 13 cm in diameter) was placed over the top of the removable cup. Funnels are a suggested component of pitfall trap design because they increase capture rates of arthropods and reduce potential vertebrate bycatch (Brown and Matthews 2016, Hohbein and Conway 2018). Finally, plastic plates (22.8 cm in diameter) were inverted and staked into the ground so they were situated over the tops of the funnels to act as roofs to decrease rainwater in the traps (Figure 1). Rain guards are not associated with increased capture rates, but they do aid in inhibiting flooding of traps (Brown and Matthews 2016, Hohbein and Conway 2018), which could result in loss of samples.

Plastic containers are recommended for use in pitfall traps for several reasons. First, plastic traps are convenient to use in the field because they are much less expensive to acquire and replace than other materials like glass or metal (Brown and Matthews 2016). Second, though glass traps are credited with the lowest escape rate, arthropods are less likely to escape from plastic traps than from metal traps. Third, most researchers employing pitfall traps to sample ground-dwelling arthropods already use plastic containers for their traps, so the standardization of plastic traps increases comparability among studies (Brown and Matthews 2016, Hohbein and Conway 2018).

Cattle ear tags (GardStar®plus, Y-Tex® Corporation, Cody, WY) coated with permethrin were cut in half and placed inside the removable cup. Permethrin was the selected killing agent because it is not known to attract or repel any arthropod species (French 1998). Liquid storage of specimens was not used, as some ground beetle species (e.g., members of *Anisodactylus* and *Brachinus*) are primarily differentiated from one another by hair counts on various structures (Lindroth 1969, Erwin 1970), and storage in liquid such as ethanol can cause these hairs to

detach over time. Instead, specimens were stored in a freezer (-4°C).

Habitats:

Pitfall trap arrays were placed in three habitat types. Three woody plant species were selected to represent each habitat: native was represented by cottonwood [(*Populus deltoides*) (W. Bartram ex. Marshall)], encroaching was represented by sand plum [(*Prunus angustifolia*) Marshall)], and invasive was represented by saltcedar [(*Tamarix ramosissima*) Ledeb.)]. Locations for pitfall trap arrays in encroaching and invasive plant communities were determined by complete (or almost complete) canopy coverage of sand plum and saltcedar. In native habitats, traps were established under small groups of cottonwood trees. Each habitat was distinctive and there was no overlap among representative plant species.

Populus deltoides (Figure 2) was selected to represent a native habitat because this species is indigenous to and widespread throughout the study area (Haddock et al. 2015). Carabid sampling occurred in areas with savanna cottonwood trees. Unlike in the encroaching and invasive plant communities, trapping took place within relatively isolated trees (groups of two to three trees) because most cottonwood trees in the study area were distributed in this manner.

Prunus angustifolia (Figure 3) was selected to represent an encroaching habitat because, though native to the study area, it is becoming overabundant (Gilman and Watson 2014). Fields dominated by sand plum are common at Quivira National Wildlife Refuge. As such, all pitfall trap arrays in the encroaching plant communities were placed within dense thickets of sand plum. Habitats were considered encroached if thickets covered at least half of each pitfall trap array from above.

Tamarix ramosissima (Figure 4) was selected to represent an invasive habitat because it is not native to the study area and has invaded many habitats throughout the United States (Haddock et al. 2015). Much of the saltcedar within the refuge occurred near the edge of creeks, so pitfall trap arrays were established within these lines as well as underneath canopies formed by tall, mature saltcedar. Most management efforts at Quivira National Wildlife Refuge center around the removal of saltcedar (U.S. Fish and Wildlife Service 2019). Saltcedar, native to Eurasia and Africa, was originally introduced to the United States in the early 19th century for ornamental purposes (Haddock et al. 2015). Later, it was used as windbreaks and to prevent soil erosion. Now, however, it is invading the Great Plains by crowding out native species, especially along streams (Haddock et al. 2015). Saltcedar disrupts nutrient cycling (Walker and Smith 1997), and soil found within saltcedar communities sometimes exhibits greater salinity than normal (Shafroth et al. 1995, Walker and Smith 1997, Haddock et al. 2015). Furthermore, exotic *Tamarix* species have displaced native *Populus* species in some environments (Shafroth et al. 1995).

After representative sites were selected, 48 pitfall traps were paired within 24 arrays divided equally among each habitat type. Arrays were placed throughout the refuge, and some arrays (even those within the same treatment) were a few kilometers apart (Figure 5). The traps were open throughout the field season and were emptied weekly from May 28 to August 13, 2018, for a total of 12 sample periods (one week equaled one sample period). Many saltcedar trees were removed in winter 2018, so further sampling was not possible. Capture from the two pitfalls in each array were combined as a single sample, therefore sampling in 3 communities x 8 replicates x 12 sample periods resulted in 288 samples.

Vegetation sampling:

Vegetation surveys were conducted midway through the field season (19 July and 6 August 2018) to characterize the habitat at each pitfall trap array. Habitat structure, aerial cover, and species composition measurements were taken at two meters from each array and in all four cardinal directions, resulting in 4 plots measured for each of the arrays. Aerial cover and habitat structure were estimated using a 1-m^2 frame (Daubenmire 1959). Aerial cover was determined within the frame by assigning relative percentages in nine categories of cover class: total grass, bare ground, total forb, total shrub, litter, standing dead grass, standing dead forb, standing dead shrub, and other (usually dried cattle excrement). Percentages were determined by the midpoints of each coverage class as follows: 1.) 0-5% coverage, midpoint = 2.5. 2.) 2-25% coverage, midpoint = 15. 3.) 25-20% coverage, midpoint = 37.5. 4.) 50-75% coverage, midpoint = 62.5. 5.) 75-95% coverage, midpoint = 85. 6.) 95-100% coverage, midpoint = 97.5. Aerial cover only included grasses, forbs, and shrubs and did not include trees. Species composition was determined by identifying all plants located within the frame to species (if possible) or morphospecies (i.e., genus) level (e.g., *Panicum* species 1, *Panicum* species 2).

Statistical analysis:

Following conclusion of the field season, contents of the pitfall traps were examined, and beetle specimens were separated from bycatch. Ground beetles were identified to species level or as a morphospecies (e.g., *Harpalus* species 1, *Harpalus* species 2) if identification to species level was especially difficult, as in the *Harpalus* subgenus *Psuedoophonus*. One pitfall trap array within the encroaching plant community (E 08) never caught any ground beetles, so this array was excluded from analysis. Species were identified using several dichotomous keys (Casey

1914, Banniger 1950, Lindroth 1969, Willis 1972, Gidaspow 1973) and through comparisons

with museum specimens and entomology collections at the Sternberg Museum of Natural

History (Hays, KS), Fort Hays State University (Hays, KS), the Department of Entomology at

Kansas State University (Manhattan, KS), and the Biodiversity Institute and Natural History

Museum at the University of Kansas (Lawrence, KS). Habitat preferences were assessed for

ground beetle genera that had least 15 individuals sampled and for plant species that were

represented by at least 4 individuals.

Differences between sites concerning habitat structure, aerial cover, and plant species

composition were assessed via analysis of variance (ANOVA) tests. Ground beetle assembly

structure and environmental variables were assessed using nonmetric multidimensional scaling

methods (NMDS). All analyses were carried out in R version 3.6.1 (R Core Team 2019; Vienna,

Austria). In addition, the package vegan 2.5-6 (Oksanen et al. 2019) was used to perform NMDS.

NMDS was the chosen ordination method because it does not assume normality or

linearity between environmental variables (McCune et al. 2002, Holland 2008), and thus

provides a robust and useful method for analyzing most ecological data. Analyses were carried

out in three dimensions to assess patterns between ground beetle assemblages and habitats.

Environmental data for each site were averaged before performing the NMDS to maintain

consistency among matrices. Nonmetric multidimensional scaling was used with the Bray-Curtis

dissimilarity matrix. The Bray-Curtis method is largely unaffected by rare species and is

frequently used in community ecology (McCune et al. 2002, Hill et al. 2008, Holland 2008).

With random starting coordinates, 20 iterations were used for each run. To ensure stable results,

numerous NMDS runs were used for each analysis (McCune et al. 1997, Riley and Browne

2011). Pearson correlation tests were executed between NMDS values in each dimension with

each environmental variable and included habitat structure, aerial cover, and plant species composition at each pitfall trap array. Any p-value less than 0.05 was considered significant regardless of the dimension at which the significant value was observed. Additional Pearson correlations were conducted between environmental variables that were significant on the same axis.

RESULTS:

Carabid abundances:

Five-hundred-eighty ground beetles representing 39 species were captured in the pitfall traps (Table 1). Sampling effort consisted of 2 traps per array (1 sample) x 8 arrays x 3 treatments x 12 sampling periods for a total of 288 samples. All sampled ground beetle species were native to the Great Plains region, but two (*Anisodactylus haplomus* Chaudoir and *Harpalus katiae* Battoni) had not been published as occurring in Kansas previously (Bousquet 2012).

A few patterns were readily apparent. For example, some ground beetles, like *Pasimachus elongatus* LeConte and *Harpalus caliginosus* (Fabricius), were sampled more frequently in invasive habitats than in native or encroaching habitats (Table 1). Twenty-five *P. elongatus* individuals were sampled in invasive habitats as opposed to eight individuals in encroaching habitats and six individuals in native habitats. Similarly, I caught 19 *H. caliginosus* individuals in invasive habitats compared to eight *H. caliginousus* individuals in native habitats and only one *H. caliginosus* in encroaching habitats. In other cases, species such as *Pterostichus permundus* (Say) and *Calathus opaculus* LeConte were sampled more often in native habitats than in invasive habitats (Table 1). Fifty-four *P. permundus* individuals were trapped in native habitats compared to three *P. permundus* individuals in encroaching habitats and 16 individuals of *P. permundus* in invasive habitats. Meanwhile, seven *C. opaculus* individuals were observed in native habitats compared to encroaching and invasive plant habitats, in which three and one individual were sampled, respectively.

Within encroaching and invasive habitats, ground beetle assemblages were most closely related to assemblages within the same treatment, but overlap of assemblages was observed within the native habitats (Figure 7). This suggests that ground beetle assemblages within

encroaching and invasive habitats were dissimilar while ground beetle assemblages within native habitats shared similarities with both habitat types. This is exemplified by capture rates of *Brachinus alternans* Dejean and *Chlaenius erythropus* Germar (Table 1). Both species were trapped consistently in native (26 *B. alternans* individuals and 40 *C. erythropus* individuals) and invasive habitats (17 *B. alternans* individuals and 106 *C. erythropus* individuals) but were not observed in encroaching habitats as often (or at all in the case of *B. alternans*). Additionally, *Selenophorus opalinus* (LeConte) was only observed in native and encroaching habitats (Table 1).

Environmental variables explained much of the observed dissimilarities in ground beetle assemblages among sites ($R^2= 0.898$). Ground beetle assemblages were positively correlated with litter and negatively correlated with grass cover and standing dead shrubs (Table 3). Additionally, ground beetle assemblages were positively correlated to the presence of poison ivy [(*Toxicodendron radicans*) (L.)] though rarely encountered, croton [(*Croton monanthogynus*) (Michx) and (*C. texensis*) (Klotzsch Müll. Arg)], and sand plum (*Prunus angustifolia*), and negatively correlated with erect dayflower [(*Commelina erecta*) (L.)], Louisiana sage [(*Artemisia ludoviciana*) (Nutt)], groundcherry [(*Physalis* sp.) (L.)], sand dropseed [(*Sporobolus cryptandrus*) (Torr. A. Gray)], ashy goldenrod [(*Solidago mollis*) (Bartlett)], and *Panicum* [(*P. capillare*) (L.) and (*P. virgatum*) (L.)] (Table 3). Statistically significant correlations between ground beetle assemblages and environmental variables were (except for the weakly negative association with standing dead shrubs) moderate, as correlation coefficients ranged between 0.40 and 0.50 and between -0.40 and -0.50 (Table 3).

ANOVA and post hoc comparisons with Tukey's test revealed several differences among sites relative to habitat structure, aerial cover, and plant species composition. Significant

16

differences were observed among native and encroaching habitats concerning grass and litter coverage (Table 2). Differences among habitats concerning specific plant species were also observed but are probably unimportant to ground beetle assemblages. The only plant species significantly correlated with ground beetle assemblages and exhibiting significant differences among habitats was sand plum (p= 1.7×10^{-5}), and this difference was already assumed from the selection of sand plum as the representative species for the encroaching habitat.

Vegetative structure:

Only a few variables of habitat structure and aerial cover were significantly correlated with ground beetle assemblages. No significant correlations were observed between ground beetle assemblages and bare ground, total forb coverage, total shrub coverage, standing dead grass, or standing dead shrubs (Table 3). Likewise, there were no statistically significant correlations between ground beetle assemblages and the miscellaneous "other" category of cover class (Table 3). However, significant differences were observed among ground beetle assemblages and habitats with grass (p = 0.02, r = -0.50 on the first axis), litter (p = 0.03, r = 0.45 on the third axis), and standing dead shrubs (p = 0.03, r = -0.25 on the third axis) (Table 3; Figure 8). Native and encroaching habitats also exhibited significant differences in grass and litter coverage (p=0.03, p=0.02).

Plant species composition:

Though a few significant differences concerning specific plant species were observed among habitats, these differences probably did not influence ground beetle assemblages. Furthermore, the most numerous plant species within the study area were not significantly correlated with ground beetle assemblages (Tables 3 and 4).

17

Significant differences in ground beetle assemblages were observed between habitats containing crotons (p = 0.04, r = 0.44 on the first axis), ashy goldenrod (p = 0.03, r = -0.46 on the first axis), *Panicum* species (p = 0.03, r = -0.44 on the first axis), sand plum (p = 0.04, r = 0.44 on the first axis), erect dayflower (p = 0.04, r = -0.42 on the second axis), Louisiana sage (p = 0.01, r = -0.53 on the third axis), ground cherries (p = 0.03, r = -0.44 on the third axis), poison ivy (p = 0.03, r = 0.45 on the third axis), and sand dropseed (p = 0.05, r = -0.42 on the third axis) (Table 3; Figure 8).

Furthermore, none of the plant species significantly correlated with ground beetle assemblages occurred in all habitats. Croton, ashy goldenrod, poison ivy, and erect dayflower were only observed in native and encroaching habitats, while ground cherries were observed only in encroaching and invasive habitats (Table 4). In addition, Louisiana sage, sand dropseed, and sand plum were only observed in encroaching habitats, and *Panicum* was only observed in native habitats (Table 4). Pearson correlations between environmental variables that were significant on the same axis in NMDS (Table 5) indicated a strong association between ashy goldenrod and *Panicum* (r = 0.97), probably because these species are found in very similar habitat types: disturbed areas with dry, sandy soil (Haddock 2005, Haddock et al. 2015). *Panicum* probably included both switchgrass (*Panicum virgatum*) and witchgrass (*Panicum capillare*), but because the two species are quite similar in appearance, they are sometimes difficult to distinguish from one another. In other cases, I was able to positively identify either switchgrass or witchgrass (Table 4). However, it is unlikely that ground beetles displayed a preference for one *Panicum* species over the other.

DISCUSSION:

Ground beetle sampling occurred within grassland habitats in south central Kansas in a region characterized by inland salt marshes and prairie sand dunes, habitat types uncommon to the surrounding area. Study objectives included assessing the influences of native, invasive, and encroaching habitats on ground beetle assemblages.

Ground beetle assemblages in different habitats:

I did not identify any ground beetle species nonnative to the Great Plains region, and ground beetle assemblages within native habitats were similar to those observed within invasive habitats. Therefore, neither my hypothesis of native and encroaching habitats sharing similar ground beetle assemblages nor my hypothesis of invasive habitats including more nonnative ground beetles were supported. Furthermore, little evidence was found in support of the invasional meltdown hypothesis. Invasive habitats supported many more ground beetles than native or encroaching habitats (Table 1), but all plant species that displayed significant correlations with ground beetle assemblages were native to the area. A few nonnative *Physalis* (groundcherry) species occur in the area, but because I was only able to identify these plants to genus level, I could not draw any conclusions regarding the effects of invasive species on ground beetle assemblages. Additionally, my hypothesis that bare ground would be negatively correlated with ground beetle assemblages was also not supported. Bare ground was not significantly correlated with ground beetle assemblages (Table 3).

The most commonly collected ground beetle genus was *Chlaenius*. Two species of *Chlaenius* were caught: 151 individuals of *Chlaenius erythropus*, the largest of the genus (Lindroth 1969), and one individual of *Chlaenius sericeus* (Forster). *Chlaenius* species are characterized by their large size, their often metallic luster, their dense dorsal pubescence, and

their release of odorous defensive chemicals when disturbed (Lindroth 1969, Marshall 2018). Members of this genus are often active near water (Lindroth 1969). This is consistent with my data, as most individuals were found in the invasive habitats, and all pitfall trap arrays within this treatment were located along creek beds, because saltcedar often invades habitats near surface water (Haddock et al. 2015). Individuals of *Chlaenius* also are often encountered in disturbed areas (Marshall 2018).

The second most commonly collected genus was *Scarites*. One-hundred and one individuals of *Scarites subterraneus* Fabricius and two individuals of *Scarites lissopterus* Chaudoir were documented. *Scarites subterraneus* was observed primarily in native and invasive habitats, and *Scarites lissopterus* was only captured in invasive plant habitats. *Scarites* species are usually encountered under stones and within leaf litter. They are also associated with dry, sandy soil (Lindroth 1969).

The third most captured genus was *Pterostichus*. *Pterostichus* species represent a large genus with a worldwide distribution (Bousquet 1999). Despite such a wide diversity, the only species caught within this genus was *Pterostichus permundus* (n=73). This species is often found in damp areas, including open fields (Lindroth 1969). Individuals were sampled almost entirely in native (54) and invasive habitats (16). By contrast, only three individuals of *P. permundus* were observed in encroaching habitats. The invasive habitat pitfall trap arrays were all located around water, and the soil surrounding many of the native habitat pitfall trap arrays was quite moist. Two pitfall trap arrays from the native habitat were located in particularly wet areas (N 04 and 06; Appendix A), and standing water was frequently observed around the pitfall traps.

The fourth most trapped genus was *Anisodactylus,* with 53 representatives. Five *Anisodactylus* species were sampled: *A. haplomus, A. merula* (Germar)*, A. rusticus* (Say)*, A.*

ovularius (Casey)*,* and *A. dulcicollis* (LaFerté-Sénectère)*.* These species are closely related; they are classified within the subgenus *Gynandrotarsus* and in the *rusticus* group (Lindroth 1969). *Anisodactylus haplomus* has not been recorded in Kansas previously, but it has been observed in Missouri and in northeastern Oklahoma (Bousquet 2012). Furthermore, members of the *rusticus* group have similar habitat preferences: they are often found in dry, sandy areas, with sparse yet tall vegetation (Lindroth 1969). *Anisodactylus* species were found consistently among all habitats, but they were slightly more numerous in invasive habitats (Table 1), which is unsurprising considering that many of the study sites were characterized by open ground (Table 6).

The genus *Harpalus* was represented by three defined species (*H. caliginosus, H. katiae, H. herbivagus* Say) and four morphospecies. Altogether, 74 individuals of *Harpalus* were sampled. The morphospecies all belonged to subgenus *Pseudoophonus*, a group in which distinguishing among species is notoriously difficult (Ball and Anderson 1962, Lindroth 1969). To reduce the risk of misidentification, morphospecies titles were applied. Carabids classified within *Pseudoophonus* are usually associated with open areas, tall, meadow-type vegetation, and cultivated fields (Lindroth 1969). Most *Pseudoophonus* species were observed in native habitats. Similarly, subgenus *Megapangus*, which includes *H. caliginosus* and *H. katiae*, are often found in dry, sandy fields supporting thin, tall vegetation (Lindroth 1969). *Harpalus katiae* has not been published as occurring in Kansas, but it does occur in all neighboring states (Bousquet 2012), and there are museum specimens from Kansas. *Harpalus katiae* is also morphologically very similar to *H. caliginosus* and was not described as a separate species until 1985 (Will 1997), so it is possible that some Kansas specimens of *H. katiae* (especially those collected before 1985) are mislabeled as *H. caliginosus.* In addition, range maps of *H. katiae* produced by Will (1997)

21

suggest that *H. katiae* probably exists in Kansas. The *somnulentus* group, which includes *H. herbivagus*, are often collected in open meadows with sandy soil (Lindroth 1969). *Harpalus* species were collected primarily within native habitats, except for the large-bodied *H. caliginosus*, which was most numerous in invasive habitats. This could be due to the preferred diet of *H. caliginosus*; in contrast to *H. herbivagus* and the *Pseudoophonus* morphospecies, *H. caliginosus* is largely predatory, especially on larvae (Lindroth 1969). Large, predatory ground beetles are most often associated with open ground, while smaller omnivorous or granivorous ground beetles are more likely to be observed on or near weedy vegetation (Luff 1987).

Forty-three *Brachinus* ground beetles were captured. These all belonged to a single species, *Brachinus alternans. Brachinus* species, also known as bombardier beetles, are well known for their ability to excrete boiling, caustic chemicals from their abdomens to ward off predators, an exceedingly rare characteristic within the Carabidae (Marshall 2018). This species was collected in native and invasive habitats fairly evenly, though it was slightly more numerous within the native habitats. Steury and Messer (2017) also collected specimens of this species under leaf litter.

Thirty-nine *Pasimachus elongatus* were collected. *Pasimachus elongatus* was most often observed within invasive habitats. This species is characterized by its preference for dry, sandy, open prairies with short vegetative cover, and is often found beneath stones (Lindroth 1969). This is consistent with my data. Because pitfall trap arrays within the invasive habitats were placed near standing water, vegetative cover was scarce.

Finally, *Tetracha virginica* (L.) was represented by 23 individuals. *Tetracha* species are classified within the Cicindelinae (tiger beetles). Tiger beetles are distinguished from other coleopteran groups by their large, bulging eyes and their sickle-shaped mouthparts (Willis 1972).

Their bodies are also usually somewhat shiny and metallic. *Tetracha virginica*, for example, is easily identifiable by its shiny, dark green coloration and its long, tan legs. *Tetracha virginica* was represented relatively equally in all habitats. It is flightless and nocturnal; as such, it is usually found in open, grassy areas with sparse vegetation (Willis 1972).

Plant species composition and structure:

The first and third axes most completely explained the observed variation within ground beetle assemblages, as all but one of the environmental variables significantly correlated with ground beetle assemblages that occurred on the first or third axis. However, relationships appear complex or even subtle among environmental variables. For instance, concerning habitat structure and aerial cover, both standing dead shrubs and total grass were negatively correlated with ground beetle assemblages, but while standing dead shrubs was significant on the third axis, total grass was significant on the first axis (Figure 8). Concerning plant species composition, correlations between ground beetle assemblages and plant species seem heavily driven by environmental disturbance and sandy soil. For example, ground cherries, Louisiana sage, and sand dropseed, all of which were negatively correlated with ground beetle assemblages on the third axis, are frequently encountered in disturbed sites with sandy soil (Haddock 2005, Haddock et al. 2015). Similarly, croton and sand plum were positively correlated with ground beetle assemblages on the first axis and are associated with habitat disturbance (Haddock et al. 2015). However, poison ivy, while also associated with habitat disturbance and positively correlated with ground beetle assemblages, was significant on the third axis (Figure 8).

Relationships between ground beetle assemblages and their environments are probably determined by several factors in addition to plant taxonomic diversity and habitat structural heterogeneity. If ground beetle assemblages were entirely dependent on either habitat structure,

23

aerial cover, or the plant species composition of their habitats, then ordination results would depict direct relationships between ground beetle assemblages and environmental variables or treatment types. However, patterns displayed are not as simple. For instance, the clusters on Figure 8 do not reveal clear patterns relative to ground beetle assemblages and environmental variables. Each cluster represents groupings of similar ground beetle assemblages among habitats. The relatively obscure cluster associations suggests that, while habitat structure, aerial cover, and plant species composition influenced ground beetle assemblages, other environmental factors probably contributed as well.

Disturbance:

Though I did not specifically measure habitat disturbance, it can be inferred from the large numbers of disturbance adapted ground beetle and plant species observed that all habitats exhibited some degree of environmental disturbance. In general, ground beetles are attracted to early succession, disturbed environments (Lovei and Sunderland 1996). A clear dominance of large-bodied, habitat generalist ground beetle species was observed. Members of the three most commonly collected genera, *Chlaenius*, *Scarites*, and *Pterostichus* are described as habitat generalists (Lovei and Sunderland 1996, Riley and Browne 2011); that is, they can be found in multiple habitat types. Large-bodied, ground-dwelling, generalist ground beetle species are typically found in pitfall samples more often than smaller species, because they are more associated with ground cover than with above ground vegetation (Ulyshen et al. 2005). Additionally, most of the plant species that exhibited significant correlations with ground beetle assemblages, including one seed croton, poison ivy, Louisiana sage, sand dropseed, goldenrod, and *Panicum* spp. are common within disturbed areas. In turn, disturbed sites are usually

characterized by the presence of many generalist ground beetle species (Halme and Niemela 1993, Rainio and Niemela 2003, Riley and Browne 2011, Marshall 2018).

Both native and encroaching habitats contained almost all the plant species significantly correlated with ground beetle assemblages and characteristic of disturbance (Table 4). Native habitats also supported many individuals of ground beetle species whose habitat preferences include environmental disturbance (including 40 *C. erythropus,* 55 *S. subterraneus,* and 54 *P. permundus*) (Table 1). Interestingly, though encroaching habitats exhibited many individuals of plant species adapted to disturbed environments (including 13 croton plants; Table 4), ground beetles, even those adapted to disturbed habitats, were scarce (Table 1). This can probably be attributed to the large areas of sandy soil found in encroaching habitats. Ground beetles were markedly less prevalent in areas with sandy soil.

Contrastingly, while invasive habitats contained none of the plant species significantly correlated with ground beetle assemblages and associated with habitat disturbance (Table 4), they supported not only the most ground beetles linked with disturbed areas (106 *C. erythropus,* 42 *S. subterraneus*, 25 *P. permundus*), but the greatest number of ground beetles overall (Table 1). This is possibly indicative of invasional meltdown. Ground beetles were clearly reacting to environmental disturbance, but these disturbances were probably unrelated to habitat structure, aerial cover, and plant species composition. Instead, disturbance may have resulted from saline water and soil in invasive habitats. Not only is saltcedar sometimes associated with increased soil salinity (Shafroth et al. 1995, Walker and Smith 1997, Haddock et al. 2015), but saltgrass [(*Distichlis spicata*) (L.)] was also prevalent in invasive habitats (Table 4). Saltgrass is linked with saline water (Skaradek and Miller 2010).

Also compelling is the lack of overlap between encroaching and invasive habitats on Figure 7 concerning ground beetle assemblages despite native habitats clustering within both. This suggests that native habitats were affected by environmental changes facilitated by encroaching and invasive species.

Soil:

Though I did not measure soil conditions within sites, most of the correlations between ground beetle assemblages and habitat characteristics seem heavily driven by soil type and moisture. Ashy goldenrod, erect dayflower, Texas croton, sand dropseed, and *Panicum* spp. are plant species significantly correlated with ground beetle assemblages and whose habitat preferences include sandy areas (Haddock 2005, Haddock et al. 2015). Interestingly, croton was the only plant species from those adapted to sandy soil to exhibit a positive correlation with ground beetle assemblages. This probably resulted from presence of croton in the native habitats (Table 4). In general, the native habitats were notable for having much wetter soil than the other sites. This was also reflected with the increased prevalence of *Pterostichus permundus*. Of the 73 *P. permundus* captured, 54 were observed in native habitats.

Overall, ground beetles seemed to respond negatively to dry, sandy soil. Though several of the most commonly observed ground beetle species, such as *Scarites subterraneus, Harpalus caliginosus,* and *Pasimachus elongatus* prefer sandy soil, correlations between ground beetle assemblages and plant species characteristic of sandy soil were almost all negative, except for croton (Table 3), several of which were observed in much wetter areas of the study site (Table 4). These findings support the notion of soil type and moisture as important contributions of ground beetle assemblages. Observances of both ground beetle and plant species whose habitat preferences include dry, sandy soil in the same areas indicate that ground beetles and plants were

responding to the soil conditions of their environments.

Management Implications:

Ground beetles were probably not responding to plant communities directly. Most likely, ground beetles and plants were responding to similar environmental conditions. Many of the most numerous ground beetle species and plant species significantly correlated with ground beetle assemblages are common to disturbed habitats and areas with sandy soil. Because land management efforts often paradoxically involve introducing new disturbance regimes to control those already active (Dale et al. 2005), the presence of many species typical of disturbance could indicate either disturbance mitigation efforts are necessary, or that ongoing management activities are not proving effective. Furthermore, ground beetles seemed to respond negatively to sandy environments, which could disqualify them for use as bioindicators at Quivira National Wildlife Refuge, because a sizeable portion of the refuge consists of prairie sand dunes. Alternative bioindicator species might include ants or spiders. Because sandy soils tend to provide good nesting sites for ants (Hill et al. 2008), it is possible that ants are more abundant within the study site than ground beetles. If so, then studying the ecological preferences of ants may prove more useful to land managers seeking to mitigate habitat disturbance. Indeed, many of my samples included ants, but I did not identify them, so I cannot currently form any predictions regarding ants as bioindicators. Similarly, spiders have been proposed as possible indicator species as well, and for some of the same reasons as ground beetles: they are widely distributed, promptly respond to environmental change, and can be conveniently sampled in the field (Schwert et al. 2018). Spiders have been shown to act as indicators of soil quality and pollution, particularly metal pollution (Ghione et al. 2013). Like ants, many spiders were present in the bycatch, but these were also not identified. However, both these potential indicator species

warrant investigating at Quivira National Wildlife Refuge because, like ground beetles, ants and spiders can be sampled easily and inexpensively with pitfall traps and may respond to the refuge's unique habitat types more meaningfully than ground beetles.

Overall, ground beetle assemblages were not obviously influenced by either plant taxonomic diversity or the structural heterogeneity of their habitats. Pitfall trap data indicate a poor relationship between ground beetle assemblages and habitats, as both seemed more sensitive to environmental disturbance and soil type rather than directly influencing each other. The most numerous ground beetle species sampled (e.g., *Chlaenius erythropus, Scarites suberraneus*) and several plant species significantly correlated with ground beetle assemblages (e.g., poison ivy, ashy goldenrod, *Panicum*, sand dropseed) are characteristic of disturbed areas. Likewise, many of the dominant ground beetle species captured (e.g., *Harpalus caliginosus, Pasimachus elongatus,* and members of the rusticus group of *Anisodactylus*) and correlated plant species (e.g., ashy goldenrod, *Panicum,* erect dayflower, croton, and sand dropseed) are adapted to sandy soil. Despite this, ground beetles responded negatively to sandy soil. The only plant species exhibiting a significant positive correlation with ground beetle assemblages was croton, and a few of these plants were found in the wettest areas of the study site. This supports claims that soil type and moisture are key influencers of ground beetle community structure (Brygadyrenko 2015, Teofilova 2018). Encroaching habitats occurred in the most extreme sandy soil and captures were the fewest compared to native and invasive habitats (Table 1). Teofilova (2018) also cites humidity as an important determining factor of ground beetle assemblages, which is likely influenced by soil moisture.

The only plant cover class positively correlated with ground beetle assemblages was litter, which is likely more indicative of ground beetle natural history than of the influence of

habitat structure. While ground beetles could serve as useful indicators of habitat disturbance at Quivira National Wildlife Refuge, their relative aversion to sandy areas could be problematic, because the region is characterized by dry, sandy soil. These findings support the assertion by Rainio and Niemela (2003) that the practicality of ground beetles as bioindicators depends on the characteristics of the habitat and the goals of the study.

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Table 1. Number of individuals of ground beetle species sampled within encroaching, invasive, and native grassland habitats at Quivira National Wildlife Refuge, Kansas.

Species:	Habitat: Encroaching	Invasive	Native	Total
Chlaenius erythropus Germar	5	106	40	151
Scarites subterraneus Fabricius	4	42	55	101
Pterostichus permundus (Say)	3	16	54	73
Brachinus alternans Dejean		17	26	43
Pasimachus elongatus LeConte	8	25	6	39
Harpalus caliginosus (Fabricius)	1	19	8	28
Tetracha virginica (L.)	6	8	9	23
Anisodactylus rusticus (Say)	5	13	3	21
Anisodactylus merula (Germar)	2	11	3	16
Anisodactylus haplomus Chaudoir	7	2	2	11
Calathus opaculus LeConte	3	1	7	11
Cyclotrachelus torvus (LeConte)		7	3	10
Harpalus Latreille sp. 3		1	6	7
Scaphinotus elevatus (Fabricius)		3	2	5
Anisodactylus ovularis (Casey)		3		3
Harpalus katiae Battoni		3		3
Harpalus (Latreille) sp. 1		1	2	3
Selenophorus opalinus (LeConte)	1		2	3
Agonum punctiforme (Say)			2	2
Anisodactylus dulcicollis (LaFerté-Sénectère)	1		1	2
Cicindela punctulata Olivier	1	1		2
Cyclotrachelus substriatus (LeConte)		2		2
Galerita janus (Fabricius)			2	2
Harpalus herbivagus Say			2	2
Helluomorphoides praeustus bicolor (Harris)	1	1		2
Scarites lissopterus Chaudoir		2		2
Agonum decorum (Say)		1		1
Amara musculis (Say)			1	1
Amara pennsylvanica Hayward	1			1
Calosoma scrutator (Fabricius)			1	1
Chlaenius sericeus (Forster)		1		1
Cicindela formosa Say	1			1
Cicindela scutellaris Say	1			1
Cymindis laticollis Say			1	1
Euryderus grossus (Say)	1			1
Harpalus Latreille sp. 2			1	1
Harpalus Latreille sp. 4			1	1
Selenophorus ellipticus Dejean	1			1
Xestonotus lugubris (Dejean)		1		1
Total	53	287	240	580

Table 2. Results from analysis of variance (ANOVA) tests and Tukey's tests on variables of habitat structure and aerial cover within native, invasive, and encroaching grasslands. Significant differences were present between native and encroaching habitats regarding grass and litter coverage. Encroaching habitats had significantly less grass and litter coverage than native habitats.

Variable:	df:	Sum sq:	Mean sq:	f-value:	p-value:
Total Grass	2	1695	847.7	3.75	0.04
Litter	2	1777	888.5	4.81	0.02

Total Grass		
Habitat Comparisons:	**Mean:**	**Tukey:**
Native	41.41	A
Invasive	28.75	AB
Encroaching	21.02	B
Litter		
Habitat Comparisons:	**Mean:**	**Tukey:**
Encroaching	19.14	A
Invasive	32.58	AB
Native	39.92	B

Table 3. Results from Pearson correlations between ground beetle assemblages and NMDS scores representing vegetation characteristics and composition in 1-m^2 frames.

Variable:	Axis:	p-value:	df:	r value:	t-value:
Total Grass	1	0.01	21	-0.50	2.62
Ashy Goldenrod (Bartlett)	1	0.03	21	-0.46	2.40
Panicum sp. (L.)	1	0.03	21	-0.44	2.27
Sand Plum (Marshall)	1	0.04	21	0.44	2.24
Croton sp. (L.)	1	0.04	21	0.44	2.24
Erect Dayflower (L.)	2	0.04	21	-0.42	2.14
Standing Dead Shrub	3	0.03	21	-0.25	2.29
Lousiana Sage (Nutt)	3	0.01	21	-0.53	2.87
Physalis sp. (L.)	3	0.04	21	-0.44	2.26
Sand Dropseed (Torr.) A. Gray	3	0.05	21	-0.42	2.12
Poison Ivy (L.)	3	0.03	21	0.45	2.30
Litter	3	0.03	21	0.45	2.34

Table 4. Number of plant species observations in four 1-m^2 frames at each pitfall trap array.

Species significantly correlated with ground beetle assemblages are bolded.

Species:	Habitat:			
	Encroaching	Invasive	Native	Total
Ragweed (L)	16	12	14	42
Prairie Cordgrass (Bosc ex Link)	1	22	16	39
Sand Plum (Marshall)	24			24
Little Bluestem (Michx.) Nash	21	1	1	23
Unknown Sedge	3	5	12	20
Switchgrass (L)	5	5	10	20
Croton sp. (L)	13		2	15
Canada Wildrye (L)		5	8	13
Erect Dayflower (L)	12		1	13
Downy Brome (L)		11	2	13
Western Ragweed (DC.)	8	2	3	13
***Physalis* sp. (L)**	7	5		12
Saltgrass (Raf.)		12		12
Unknown Willow		3	8	11
Unknown Forb	3		7	10
Ashy Goldenrod (Bartlett)	2		7	9
Witchgrass (L)	6		3	9
Scribner's Rosette Grass (Schult.)	6		2	8
Composite Dropseed (Poir.) Merr.	5	1	2	8
Japanese Brome (Thunb.)			7	7
Sand Dropseed (Torr.) A. Gray	5		2	7
Missouri Goldenrod (Nutt)	1		5	6
Unknown Rush			6	6
***Panicum* sp. (L)**			6	6
Common Sunflower (L)	3	2		5
Louisiana Sage (Nutt)	4			4
Poison Ivy (L)	1		3	4
Prairie Spiderwort (Britton) Smyth	3		1	4
Unknown Clover	2		2	4
Unknown Grass	2		2	4
Western Wheatgrass (Rydb.) Á. Löve	1	2	1	4
Total	154	88	133	333

Table 5. Results from Pearson correlations between variables that were significant on the same axis following the NMDS and Pearson correlations between ground beetle assemblages and environmental variables (habitat structure, aerial cover, and plant species composition) at Quivira National Wildlife Refuge, a south central Kansas grassland.

Correlation:	Axis:	r-value:	p-value:	df:	t-value:
Litter and Standing Dead Shrubs	3	-0.21	0.33	21	1
Croton sp. (L) and ashy goldenrod (Bartlett)	1	-0.1	0.65	21	0.46
Croton sp. (L) and *Panicum* sp. (L)	1	-0.16	0.47	21	0.74
Croton sp. (L) and sand plum (Marshall)	1	0.65	0	21	3.89
Ashy goldenrod (Bartlett) and *Panicum* sp. (L)	1	0.97	4.01E-14	21	17.74
Ashy goldenrod (Bartlett) and sand plum (Marshall)	1	-0.18	0.42	21	0.83
Panicum sp. (L) and sand plum (Marshall)	1	-0.18	0.4	21	0.86
Louisiana sage (Nutt) and ground cherry (L)	3	0.39	0.07	21	1.9
Louisiana sage (Nutt) and poison ivy (L)	3	-0.01	0.65	21	0.46
Louisiana sage (Nutt) and sand dropseed (Torr.) A. Gray	3	0.22	0.31	21	1.04
Ground cherry (L) and poison ivy (L)	3	-0.22	0.32	21	1.01
Ground cherry (L) and sand dropseed (Torr.) A. Gray	3	0.34	0.06	21	1.2
Poison ivy (L) and sand dropseed (Torr.) A. Gray	3	-0.12	0.48	21	0.72

Table 6. Average assigned percentages of cover classes among sites. N= native habitat, E= encroaching habitat, I= invasive habitat. Measurements were taken in the four cardinal directions 2 m around each pitfall trap array and averaged.

	Total Grass	Bare Ground	Total Forb	Total Shrub	Litter	Standing Dead Grass	Standing Dead Forb	Standing Dead Shrub	Other
N 01	85.625	0	11.875	0.625	14.375	0.625	0.625	0	0
N 02	61.875	0	15	0	17.5	2.5	0	0	0.625
N 03	37.5	0.625	11.875	0	50	5.625	0	0	0
N 04	31.875	3.75	5	0	49.375	2.5	0	0	1.25
N 05	44.375	13.75	2.5	0	38.125	15	0	0	20.625
N 06	11.875	5	43.75	0	43.75	14.375	0.625	0.625	0
N 07	31.875	0	17.5	0.625	50	11.875	0.625	0	0
N 08	26.25	7.5	11.25	0	56.25	5.625	2.5	0	0
E 01	20.625	1.25	37.5	0.625	31.875	5.625	1.25	0	0
E 02	8.75	0.625	37.5	62.5	15	0.625	0	8.75	0
E 03	26.25	17.5	13.75	38.125	17.5	8.75	0	0.625	0
E 04	28.75	34.375	33.125	28.75	1.25	1.875	0	0	0
E 05	34.375	5	5	18.75	34.375	5	0	0	0
E 06	8.75	28.75	26.25	25.625	15	15	2.5	0	0
E 07	20.625	20.625	20.625	41.25	26.25	15	0	0	0
E 08	20	5	5.625	32.5	11.875	14.375	0	0	0.625
I 01	20.625	79.375	0	0	8.125	1.25	0	0	0.625
I 02	28.75	0.625	10	0	34.375	8.125	0	0	0
I 03	40.625	0	3.75	0	34.375	16.875	0.625	0	0
I 04	20.625	28.75	35	0	29.375	11.875	0	0	0
I 05	31.875	25.625	11.25	4.375	20	11.875	0	0	0
I 06	40.625	1.25	0	0	46.25	20	0	0	0
I 07	20.625	40.625	11.25	0	38.125	17.5	0	0	0.625
I 08	26.25	14.375	8.75	0	50	5	0	0.625	0

FIGURES:

Figure 1. Closeup view of a pitfall trap for carabid trapping. Pitfall trap arrays consisted of two traps separated by 300 cm of plastic drift fence. Sampling occurred in a grassland characterized by prairie sand dunes. Each trap consisted of a plastic cup dug in the ground. A second cup was placed within and was removed to empty traps. A cattle ear tag impregnated with permethrin was used as a killing agent. Each trap was equipped with a funnel to increase capture rates of invertebrates and decrease vertebrate bycatch. An inverted plastic plate was used as a rain guard to prevent flooding of traps.

Figure 2. Typical placement of a pitfall trap array for trapping carabid beetles in the native grassland habitat associated with cottonwood (*Populus deltoides* Bartram ex. Marshall). Savanna cottonwood was selected to represent a native habitat because it is indigenous and widespread throughout the area. Eight pitfall trap arrays were established within native habitats throughout the area.

Figure 3. Typical placement of a pitfall trap array for carabid sampling at a grassland in the encroaching grassland community associated with sand plum (*Prunus angustifolia* Marshall). Sand plum was selected to represent an encroaching plant community because, though native to the area, it is overabundant. Eight pitfall trap arrays were established in dense plum thickets throughout the study area.

Figure 4. Typical placement of a pitfall trap array for carabid sampling in the invasive grassland habitat associated with saltcedar (*Tamarix ramosissima* Ledeb.). This species was selected to represent an invasive habitat because it is nonnative and causing many management problems in the Great Plains region. Eight pitfall trap arrays were placed within invasive habitats throughout the study site. Invasive habitats were characterized by tall saltcedar shrubs occurring along a creek.
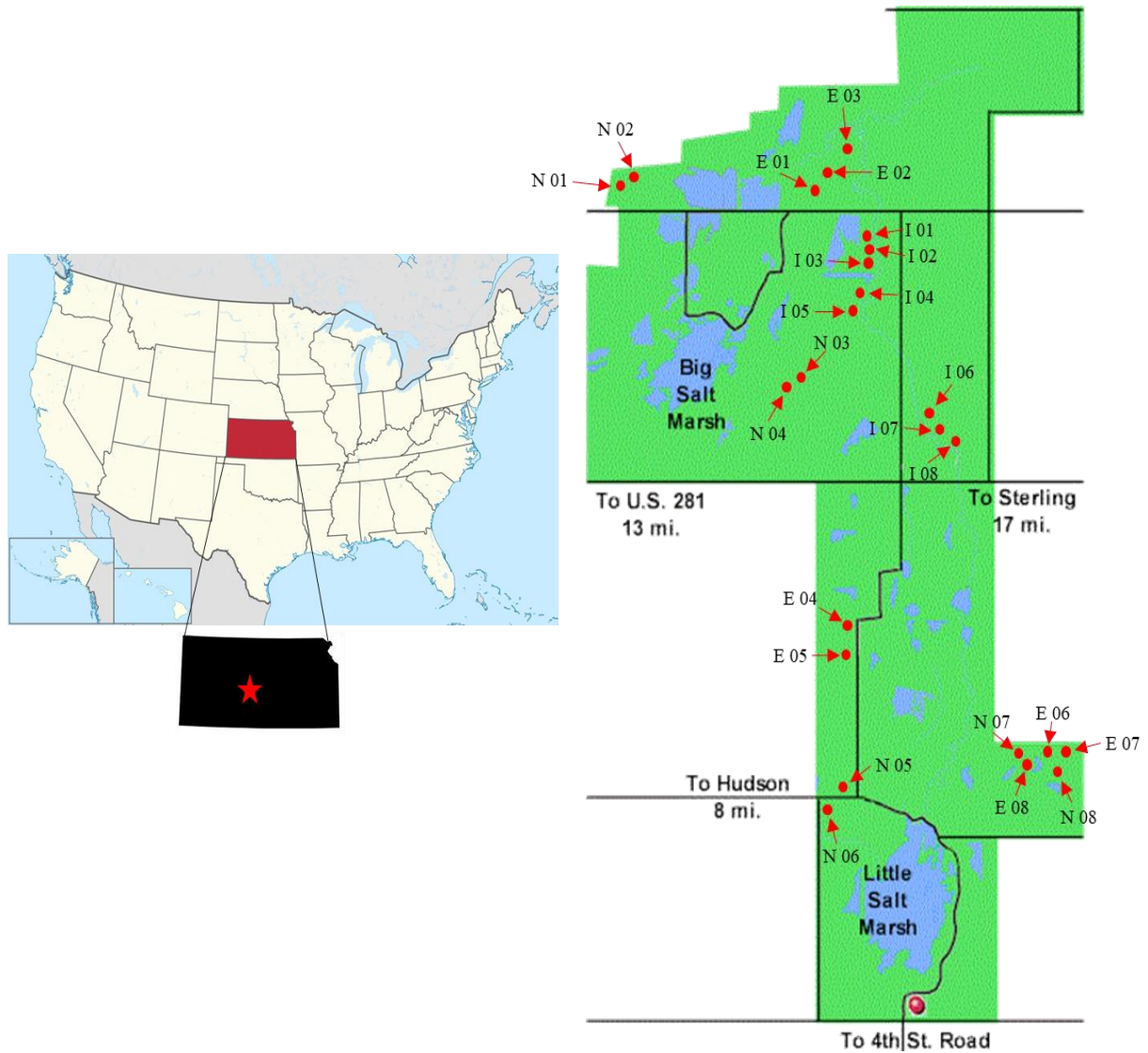
Figure 5. Map of study site. Pitfall trapping of carabids occurred in native, invasive, and encroaching habitats within a south central Kansas grassland characterized by prairie sand dune habitats. N= native habitat, E= encroaching habitat, I= invasive habitat.
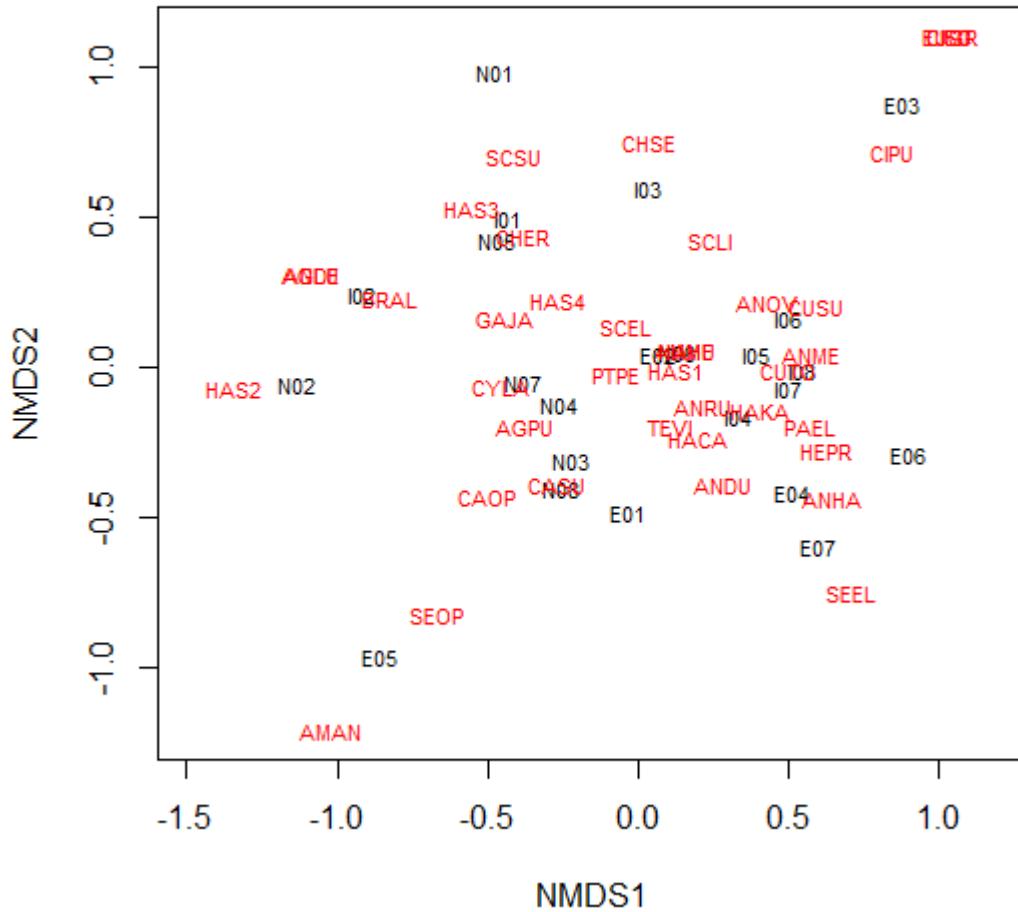
Figure 6. NMDS ordination plot showing ground beetle assemblages in native, invasive, and encroaching grassland habitats in two dimensions. A stress level of 0.12 indicates a good model that decently shows natural relationships in reduced dimensional space. N= native habitat, E= encroaching habitat, and I= invasive habitat. AGDE= *Agonum decorum*, AGPU= *Agonum punctiforme,* AMAN= *Amara pennsylvanica*, ANDU= *Anisodactylus dulcicollis*, ANHA= *Anisodactylus haplomus*, ANOV= *Anisodactylus ovularis*, ANRU= *Anisodactylus rusticus*, BRAL= *Brachinus alternans*, CAOP= *Calathus opaculus*, CHER= *Chlaenius erythropus*, CHSE= *Chlaenius sericeus*, CIPU= *Cicindela punctulata*, CUSU= *Cyclotrachelus substriatus*, CUTO= *Cyclotrachelus torvus*, CYLA= *Cymindis laticollis*, GAJA= *Galerita janus*, HACA= *Harpalus caliginosus*, HAS1= *Harpalus* species 1, HAS2= *Harpalus* species 2, HAS3= *Harpalus* species 3, HAS4= *Harpalus* species 4, HEPR= *Helluomorphoides praeustus bicolor*, PAEL= *Pasimachus elongatus*, PTPE= *Pterostichus permundus*, SCEL= *Scaphinotus elevatus*, SCLI= *Scarites lissopterus*, SCSU= *Scarites subterraneus*, SEEL= *Selenophorus ellipticus*, SEOP= *Selenophorus opalinus*, TEVI= *Tetracha virginica*

Cluster Dendrogram

species.bray
hclust (*, "complete")
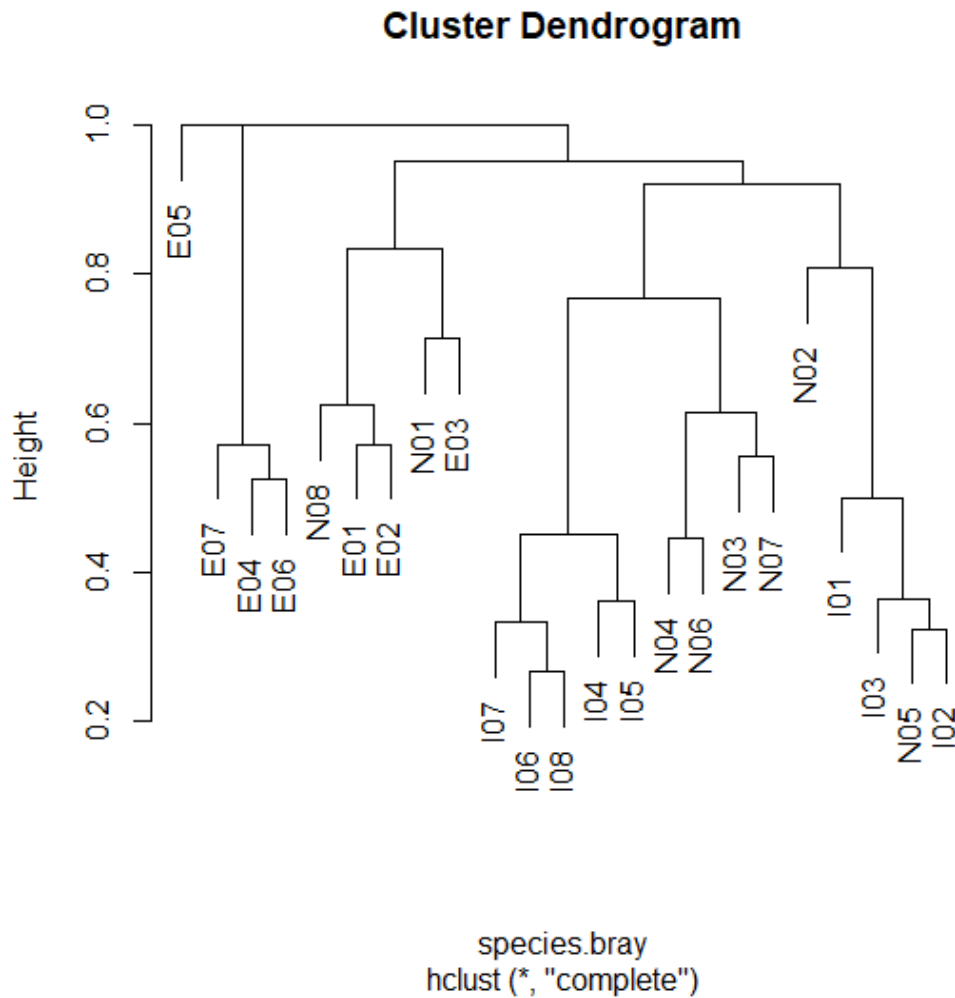
Figure 7. Dendrogram showing relationships among ground beetle assemblages between grassland habitats. N= native habitat, E= encroaching habitat, I= invasive habitat. Branching at greater heights indicates more distant relationships among variables than branching at lower heights. Complete linkage clustering was used to create the dendrogram because separation of clusters is more balanced as the maximum distance between individuals is used as the distance between clusters and tends to produce more compact clusters. Encroaching and invasive habitats form distinct groups and do not overlap. However, native habitats only appear within groups formed by encroaching and invasive habitats. Therefore, it is evident that ground beetle assemblages in native habitats were influenced by encroaching and native plant species.
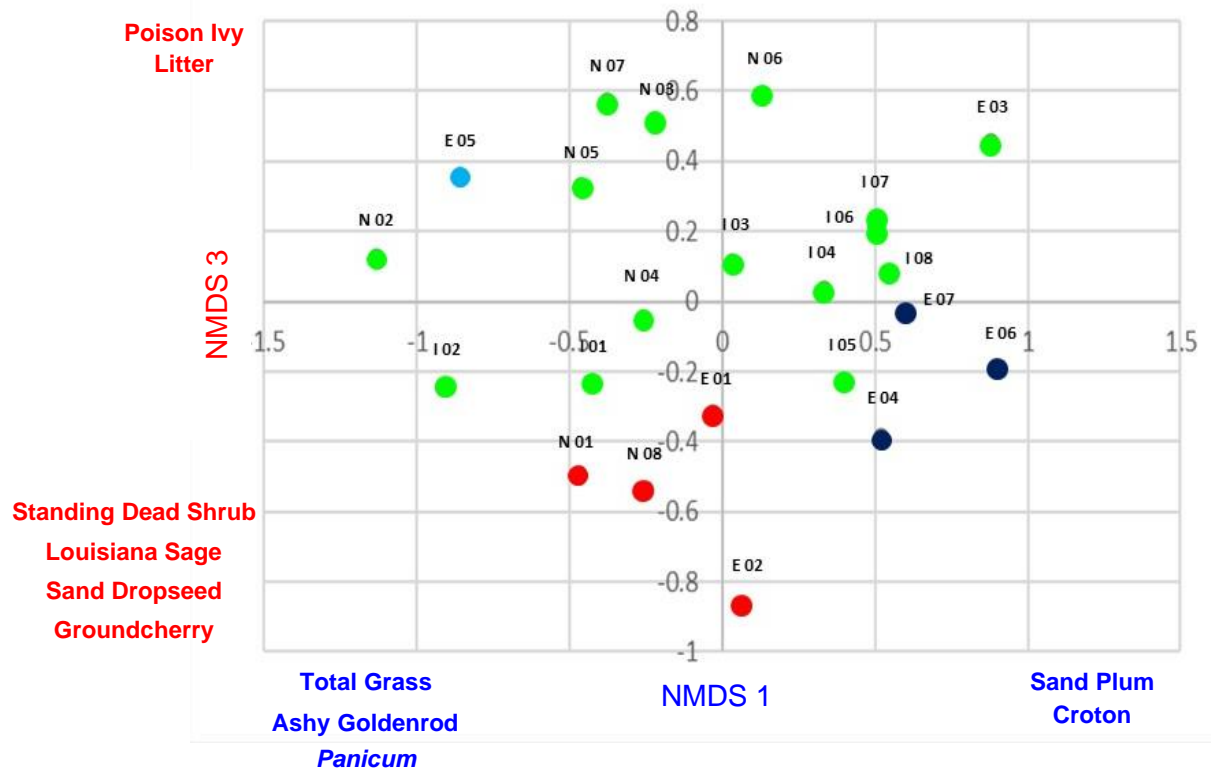
Figure 8. Four clusters were extracted from the dendrogram produced via NMDS ordination of ground beetle assemblages from native (N), invasive (I), and encroaching (E) grassland habitats. These clusters assess patterns of ground beetle captures relative to their environment, including habitat structure, aerial cover, and plant species composition. Axis 1 and axis 3 are graphed because almost all significant differences observed between ground beetle assemblages and environmental variables occurred on either the first or the third axis. Significantly correlated variables of habitat structure and aerial cover are listed on the axis they are significantly correlated with and on the positive or negative end according to the direction of correlation.

Appendix A. Total number of carabid individuals captured at each pitfall trap array deployed in the native grassland habitats at Quivira National Wildlife Refuge in 2018.

Species	N 01	N 02	N 03	N 04	N 05	N 06	N 07	N 08	Total
Agonum decorum (Say)	0	0	0	0	0	0	0	0	0
Agonum punctiforme (Say)	0	0	1	0	0	0	1	0	2
Amara musculis (Say)	0	0	0	0	0	1	0	0	1
Amara pennsylvanica Hayward	0	0	0	0	0	0	0	0	0
Anisodactylus dulcicollis (LaFerté-Sénectère)	0	0	0	1	0	0	0	0	1
Anisodactylus haplomus Chaudoir	0	0	1	1	0	0	0	0	2
Anisodactylus merula (Germar)	0	0	1	0	0	2	0	0	3
Anisodactylus ovularis (Casey)	0	0	0	0	0	0	0	0	0
Anisodactylus rusticus (Say)	0	0	0	2	0	0	1	0	3
Brachinus alternans Dejean	0	12	1	2	8	2	1	0	26
Calathus opaculus LeConte	0	1	1	3	0	0	1	1	7
Calosoma scrutator (Fabricius)	0	0	1	0	0	0	0	0	1
Chlaenius erythropus Germar	1	1	4	10	16	6	0	2	40
Chlaenius sericeus (Forster)	0	0	0	0	0	0	0	0	0
Cicindela formosa Say	0	0	0	0	0	0	0	0	0
Cicindela punctulata Olivier	0	0	0	0	0	0	0	0	0
Cicindela scutellaris Say	0	0	0	0	0	0	0	0	0
Cyclotrachelus substriatus (LeConte)	0	0	0	0	0	0	0	0	0
Cyclotrachelus torvus (LeConte)	0	0	0	0	0	3	0	0	3
Cymindis laticollis Say	0	0	0	0	0	0	1	0	1
Euryderus grossus (Say)	0	0	0	0	0	0	0	0	0
Galerita janus (Fabricius)	0	0	1	0	1	0	0	0	2
Harpalus caliginosus (Fabricius)	0	0	0	0	1	3	0	4	8
Harpalus herbivagus Say	0	0	0	0	0	2	0	0	2
Harpalus katiae Battoni	0	0	0	0	0	0	0	0	0
Harpalus Latreille sp. 1	0	0	0	1	0	1	0	0	2
Harpalus Latreille sp. 2	0	1	0	0	0	0	0	0	1
Harpalus Latreille sp. 3	0	0	0	0	1	2	2	0	5
Harpaus Latreille sp. 4	0	0	0	0	1	0	0	0	1
Helluomorphoides praeustus bicolor (Harris)	0	0	0	0	0	0	0	0	0
Pasimachus elongatus LeConte	0	0	0	0	0	4	2	0	6
Pterostichus permundus (Say)	0	0	5	17	7	21	4	0	54
Scaphinotus elevatus (Fabricius)	0	0	1	1	0	0	0	0	2
Scarites lissopterus Chaudoir	0	0	0	0	0	0	0	0	0
Scarites subterraneus Fabricius	6	1	3	23	5	6	10	1	55
Selenophorus ellipticus Dejean	0	0	0	0	0	0	0	0	0
Selenophorus opalinus (LeConte)	0	0	1	0	0	1	0	0	2
Tetracha virginica (L.)	0	0	1	3	1	1	0	3	9
Xestonotus lugubris (Dejean)	0	0	0	0	0	0	0	0	0
Total	7	16	22	64	41	55	23	11	239

Appendix B. Total number of carabid individuals captured at each pitfall trap array deployed in the encroaching grassland habitats at Quivira National Wildlife Refuge in 2018.

Species	E 01	E 02	E 03	E 04	E 05	E 06	E 07	E 08	Total
Agonum decorum (Say)	0	0	0	0	0	0	0	0	0
Agonum punctiforme (Say)	0	0	0	0	0	0	0	0	0
Amara musculis (Say)	0	0	0	0	0	0	0	0	0
Amara pennsylvanica Hayward	0	0	0	0	1	0	0	0	1
Anisodactylus dulcicollis (LaFerté-Sénectère)	0	0	0	1	0	0	0	0	1
Anisodactylus haplomus Chaudoir	1	0	0	2	0	3	1	0	7
Anisodactylus merula (Germar)	0	0	1	0	0	1	0	0	2
Anisodactylus ovularis (Casey)	0	0	0	0	0	0	0	0	0
Anisodactylus rusticus (Say)	2	1	0	1	0	0	1	0	5
Brachinus alternans Dejean	0	0	0	0	0	0	0	0	0
Calathus opaculus LeConte	2	0	0	0	1	0	0	0	3
Calosoma scrutator (Fabricius)	0	0	0	0	0	0	0	0	0
Chlaenius erythropus Germar	1	3	1	0	0	0	0	0	5
Chlaenius sericeus (Forster)	0	0	0	0	0	0	0	0	0
Cicindela formosa Say	0	0	1	0	0	0	0	0	1
Cicindela punctulata Olivier	0	0	1	0	0	0	0	0	1
Cicindela scutellaris Say	0	0	1	0	0	0	0	0	1
Cyclotrachelus substriatus (LeConte)	0	0	0	0	0	0	0	0	0
Cyclotrachelus torvus (LeConte)	0	0	0	0	0	0	0	0	0
Cymindis laticollis Say	0	0	0	0	0	0	0	0	0
Euryderus grossus (Say)	0	0	1	0	0	0	0	0	1
Galerita janus (Fabricius)	0	0	0	0	0	0	0	0	0
Harpalus caliginosus (Fabricius)	0	0	0	0	0	0	1	0	1
Harpalus herbivagus Say	0	0	0	0	0	0	0	0	0
Harpalus katiae Battoni	0	0	0	0	0	0	0	0	0
Harpalus Latreille sp. 1	0	0	0	0	0	0	0	0	0
Harpalus Latreille sp. 2	0	0	0	0	0	0	0	0	0
Harpalus Latreille sp. 3	0	0	0	0	0	0	0	0	0
Harpaus Latreille sp. 4	0	0	0	0	0	0	0	0	0
Helluomorphoides praeustus bicolor (Harris)	0	0	0	1	0	0	0	0	1
Pasimachus elongatus LeConte	0	0	0	4	0	2	2	0	8
Pterostichus permundus (Say)	1	0	0	1	1	0	0	0	3
Scaphinotus elevatus (Fabricius)	0	0	0	0	0	0	0	0	0
Scarites lissopterus Chaudoir	0	0	0	0	0	0	0	0	0
Scarites subterraneus Fabricius	1	0	1	1	0	0	1	0	4
Selenophorus ellipticus Dejean	0	0	0	0	0	0	1	0	1
Selenophorus opalinus (LeConte)	0	0	0	0	1	0	0	0	1
Tetracha virginica (L.)	1	1	0	3	0	1	0	0	6
Xestonotus lugubris (Dejean)	0	0	0	0	0	0	0	0	0
Total	9	5	7	14	4	7	7	0	53

Appendix C. Total number of carabid individuals captured at each pitfall trap array deployed in the invasive grassland habitats at Quivira National Wildlife Refuge in 2018.

Species	I 01	I 02	I 03	I 04	I 05	I 06	I 07	I 08	Total
Agonum decorum (Say)	0	1	0	0	0	0	0	0	1
Agonum punctiforme (Say)	0	0	0	0	0	0	0	0	0
Amara musculis (Say)	0	0	0	0	0	0	0	0	0
Amara pennsylvanica Hayward	0	0	0	0	0	0	0	0	0
Anisodactylus dulcicollis (LaFerté-Sénectère)	0	0	0	0	0	0	0	0	0
Anisodactylus haplomus Chaudoir	0	0	0	1	0	0	1	0	2
Anisodactylus merula (Germar)	0	0	1	2	2	2	3	1	11
Anisodactylus ovularis (Casey)	0	0	1	0	0	0	1	1	3
Anisodactylus rusticus (Say)	0	0	2	1	4	2	3	1	13
Brachinus alternans Dejean	7	3	6	1	0	0	0	0	17
Calathus opaculus LeConte	0	1	0	0	0	0	0	0	1
Calosoma scrutator (Fabricius)	0	0	0	0	0	0	0	0	0
Chlaenius erythropus Germar	49	19	27	1	2	3	3	2	106
Chlaenius sericeus (Forster)	0	0	1	0	0	0	0	0	1
Cicindela formosa Say	0	0	0	0	0	0	0	0	0
Cicindela punctulata Olivier	0	0	0	0	0	1	0	0	1
Cicindela scutellaris Say	0	0	0	0	0	0	0	0	0
Cyclotrachelus substriatus (LeConte)	0	0	0	0	0	2	0	0	2
Cyclotrachelus torvus (LeConte)	0	0	0	0	0	1	5	1	7
Cymindis laticollis Say	0	0	0	0	0	0	0	0	0
Euryderus grossus (Say)	0	0	0	0	0	0	0	0	0
Galerita janus (Fabricius)	0	0	0	0	0	0	0	0	0
Harpalus caliginosus (Fabricius)	0	0	0	6	3	2	5	3	19
Harpalus herbivagus Say	0	0	0	0	0	0	0	0	0
Harpalus katiae Battoni	0	0	0	2	1	0	0	0	3
Harpalus Latreille sp. 1	0	0	0	0	1	0	0	0	1
Harpalus Latreille sp. 2	0	0	0	0	0	0	0	0	0
Harpalus Latreille sp. 3	0	0	1	0	0	0	0	0	1
Harpaus Latreille sp. 4	0	0	0	0	0	0	0	0	0
Helluomorphoides praeustus bicolor (Harris)	0	0	0	0	0	0	0	1	1
Pasimachus elongatus LeConte	0	0	0	3	3	6	8	5	25
Pterostichus permundus (Say)	1	0	2	2	2	3	3	3	16
Scaphinotus elevatus (Fabricius)	1	0	0	0	0	1	1	0	3
Scarites lissopterus Chaudoir	0	0	1	0	1	0	0	0	2
Scarites subterraneus Fabricius	19	5	2	4	3	4	2	3	42
Selenophorus ellipticus Dejean	0	0	0	0	0	0	0	0	0
Selenophorus opalinus (LeConte)	0	0	0	0	0	0	0	0	0
Tetracha virginica (L.)	1	0	0	1	5	0	0	1	8
Xestonotus lugubris (Dejean)	0	1	0	0	0	0	0	0	1
Total	78	30	44	24	27	27	35	22	287

Appendix D. Total number of plant individuals observed in four 1-m² frames at each pitfall trap array deployed in native habitats at Quivira National Wildlife Refuge in 2018.

Species	N 01	N 02	N 03	N 04	N 05	N 06	N 07	N 08	Total
Common Sunflower (L)	0	0	0	0	0	0	0	0	0
Canada Wildrye (L)	0	0	1	2	0	2	1	2	8
Prairie Clover (L)	0	0	0	0	2	0	0	0	2
Croton sp. (L)	0	0	0	0	0	0	1	1	2
Erect Day Flower (L)	0	0	0	0	0	0	0	1	1
Downy Brome (L)	0	0	0	0	0	0	2	0	2
Unknown Forb	0	2	1	0	1	0	1	3	8
Ashy Goldenrod (Bartlett)	3	4	0	0	0	0	0	0	7
Unknown Grass	0	0	0	0	1	0	1	0	2
Japanese Brome (Thunb.)	0	0	0	1	4	2	0	0	7
Little Bluestem (Michx.) Nash	0	0	0	0	1	0	0	0	1
Louisiana Sage (Nutt)	0	0	0	0	0	0	0	0	0
Missouri Goldenrod (Nutt)	0	0	0	0	1	4	0	0	5
Physalis sp. (L)	0	0	0	0	0	0	0	0	0
Panicum **sp. (L)**	3	3	0	0	0	0	0	0	6
Poison Ivy (L)	0	0	0	0	1	2	0	0	3
Prairie Cordgrass (Bosc ex Link)	2	4	0	0	3	3	3	1	16
Prairie Spiderwort (Britton) Smyth	0	0	0	0	0	1	0	0	1
Ragweed (L)	1	0	2	1	2	4	2	2	14
Unknown Rush	1	1	2	0	0	0	1	1	6
Saltgrass (Raf.)	0	0	0	0	0	0	0	0	0
Sand Dropseed (Torr.) A. Gray	0	0	0	0	0	0	0	2	2
Sand Plum (Marshall)	0	0	0	0	0	0	0	0	0
Scribner's Rosette Grass (Schult.)	0	0	1	0	0	0	1	0	2
Unknown Sedge	4	3	0	1	0	1	1	2	12
Switchgrass (L)	0	0	4	4	0	0	0	2	10
Composite Dropseed (Poir.) Merr.	0	0	1	0	0	0	0	1	2
Western Ragweed (DC.)	0	0	1	1	0	0	1	0	3
Western Wheatgrass (Rydb.) Á. Löve	0	1	0	0	0	0	0	0	1
Unknown Willow	4	1	1	0	0	0	2	0	8
Witchgrass (L)	0	0	0	0	0	3	0	0	3
Total	18	19	14	10	16	22	17	18	134

Appendix E. Total number of plant individuals observed in four 1-m2 frames at each pitfall trap

array deployed in encroaching habitats at Quivira National Wildlife Refuge in 2018.

Species	E 01	E 02	E 03	E 04	E 05	E 06	E 07	E 08	Total
Common Sunflower (L)	0	0	0	0	0	3	0	0	3
Canada Wildrye (L)	0	0	0	0	0	0	0	0	0
Prairie Clover (L)	0	0	0	0	0	0	1	1	2
Croton sp. (L)	2	0	2	0	0	3	4	2	13
Erect Day Flower (L)	4	1	0	0	0	2	3	2	12
Downy Brome (L)	0	0	0	0	0	0	0	0	0
Unknown Forb	0	1	0	2	0	0	0	0	3
Ashy Goldenrod (Bartlett)	1	0	0	0	0	0	0	1	2
Unknown Grass	0	0	0	0	0	0	2	0	2
Japanese Brome (Thunb.)	0	0	0	0	0	0	0	0	0
Little Bluestem (Michx.) Nash	2	2	4	0	3	4	2	4	21
Louisiana Sage (Nutt)	1	3	0	0	0	0	0	0	4
Missouri Goldenrod (Nutt)	0	0	0	1	0	0	0	0	1
Physalis sp. (L)	1	2	0	0	0	2	2	0	7
Panicum sp. (L)	0	0	0	0	0	0	0	0	0
Poison Ivy (L)	0	0	0	0	1	0	0	0	1
Prairie Cordgrass (Bosc ex Link)	0	0	0	0	1	0	0	0	1
Prairie Spiderwort (Britton) Smyth	0	0	0	3	0	0	0	0	3
Ragweed (L)	2	2	1	0	3	3	2	3	16
Unknown Rush	0	0	0	0	0	0	0	0	0
Saltgrass (Raf.)	0	0	0	0	0	0	0	0	0
Sand Dropseed (Torr.) A. Gray	0	1	0	0	0	1	2	1	5
Sand Plum (Marshall)	1	4	4	2	2	3	4	4	24
Scribner's Rosette Grass (Schult.)	2	1	0	0	0	3	0	0	6
Unknown Sedge	0	0	0	0	0	1	0	2	3
Switchgrass (L)	2	1	0	0	0	2	0	0	5
Composite Dropseed (Poir.) Merr.	0	0	1	0	0	1	3	0	5
Western Ragweed (DC.)	2	2	1	0	0	1	2	0	8
Western Wheatgrass (Rydb.) Á. Löve	0	0	0	0	0	0	0	1	1
Unknown Willow	0	0	0	0	0	0	0	0	0
Witchgrass (L)	0	1	2	0	0	1	0	2	6
Total	20	21	15	8	10	30	27	23	154

Appendix F. Total number of plant individuals observed in four 1-m2 frames at each pitfall trap array deployed in invasive habitats at Quivira National Wildlife Refuge in 2018.

	I 01	I 02	I 03	I 04	I 05	I 06	I 07	I 08	Total
Common Sunflower (L)	0	1	0	1	0	0	0	0	2
Canada Wildrye (L)	0	1	1	1	1	0	1	0	5
Prairie Clover (L)	0	0	0	0	0	0	0	0	0
Croton sp. (L)	0	0	0	0	0	0	0	0	0
Erect Day Flower (L)	0	0	0	0	0	0	0	0	0
Downy Brome (L)	0	2	1	3	2	2	0	1	11
Unknown Forb	0	0	0	0	0	0	0	0	0
Ashy Goldenrod (Bartlett)	0	0	0	0	0	0	0	0	0
Unknown Grass	0	0	0	0	0	0	0	0	0
Japanese Brome (Thunb.)	0	0	0	0	0	0	0	0	0
Little Bluestem (Michx.) Nash	0	0	1	0	0	0	0	0	1
Louisiana Sage (Nutt)	0	0	0	0	0	0	0	0	0
Missouri Goldenrod (Nutt)	0	0	0	0	0	0	0	0	0
Physalis sp. (L)	0	3	1	0	1	0	0	0	5
Panicum sp. (L)	0	0	0	0	0	0	0	0	0
Poison Ivy (L)	0	0	0	0	0	0	0	0	0
Prairie Cordgrass (Bosc ex Link)	0	4	4	2	2	3	3	4	22
Prairie Spiderwort (Britton) Smyth	0	0	0	0	0	0	0	0	0
Ragweed (L)	0	1	1	3	2	0	3	2	12
Unknown Rush	0	0	0	0	0	0	0	0	0
Saltgrass (Raf.)	2	0	0	1	2	4	2	1	12
Sand Dropseed (Torr.) A. Gray	0	0	0	0	0	0	0	0	0
Sand Plum (Marshall)	0	0	0	0	0	0	0	0	0
Scribner's Rosette Grass (Schult.)	0	0	0	0	0	0	0	0	0
Unknown Sedge	1	0	0	1	0	0	1	2	5
Switchgrass (L)	0	0	0	1	1	0	1	2	5
Composite Dropseed (Poir.) Merr.	0	0	0	1	0	0	0	0	1
Western Ragweed (DC.)	0	0	1	1	0	0	0	0	2
Western Wheatgrass (Rydb.) Á. Löve	0	0	0	1	1	0	0	0	2
Unknown Willow	0	0	0	0	0	0	1	2	3
Witchgrass (L)	0	0	0	0	0	0	0	0	0
Total	3	12	10	16	12	9	12	14	88

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