

EFFECTS OF BISON, CATTLE, AND ENVIRONMENTAL FACTORS
ON GRASSLAND DUNG BEETLE ABUNDANCE AND COMMUNITY STRUCTURE

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The following faculty members have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science with a major in Biological Sciences.

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“It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living”
- David Attenborough

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ABSTRACT

Dung beetles are crucial ecosystem providers in grassland ecosystems, and research suggests that diverse dung beetle communities are required for improved ecosystem functioning. However, the factors driving dung beetle community structure are poorly understood. We compared the dung beetle community structure associated with bison-grazed and cattle-grazed temperate grasslands in Barber County, Kansas, USA. Our pilot study is the first to examine dung beetle communities (guild and species composition) associated with bison-grazed and cattle-grazed sites. We deployed dung-baited pitfall traps to examine dung beetle community structure associated with grazing site (cattle versus bison) and environmental factors (above-ground plant biomass, bare ground, and bulk density) that may affect dung beetle community structure. Our sample design included two sites (a bison grazed ranch and cattle grazed ranch), sampled with 4 transects comprised of 3 sample points for each grazing site (8 total transects; 24 total sample points). Soil textural class and percent sand in the soil were examined as covariates of the grazing site. We did not find a significant difference in total dung beetle abundance between the bison-grazed and cattle-grazed sites. But, two-sample t-tests, linear regression, PerMANOVA, and NMDS ordination showed that dung beetle communities differed on bison-grazed and cattle-grazed sites. These community differences are driven by above-ground plant biomass and bare ground, factors that are likely influenced by differences in bison and cattle grazing behavior. Additionally, we found that dung beetle communities are driven by percent sand in the soil – a factor that is not affected by the differing behaviors of bison and cattle. We hope our findings stimulate future research into the ecology of ecosystem services and inspire natural resource management centered around the conservation of diverse dung beetle communities.

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CHAPTER 1

INTRODUCTION

Exploring the connections between ecological functions and biodiversity is crucial for understanding complex ecosystems. In terrestrial ecosystems, biodiverse insect communities play vital roles in ecological processes such as nutrient cycling, seed dispersal, bioturbation, and pollination (Nichols et al. 2008). Dung beetles (Coleoptera: Scarabaeidae) feed on fresh dung to obtain nutrition and moisture (Halffter and Matthews 1971; Scholtz et al. 2009); and their unique feeding and nesting behaviors (de Groot et al. 2010), including the excavation of tunnels and relocation of dung from the soil surface to the upper soil horizons, provide key ecosystem services in grassland ecosystems.

Ecosystem services are those provisioning, regulating, cultural, and supporting functions that benefit human well-being (deGroot 2002). Dung beetles provide ecosystem services through ecological and biophysical benefits relating to their intensive tunneling and dung burial behavior. Scarabaeoid dung beetles are classified into three broad functional guilds based on their nesting strategies (Doubé 1990, Floate 2011). Paracoprid (tunneler species) excavate vertical brood chambers and bury brood balls adjacent to the dung, while telecoprid (roller) species transport brood balls away from the dung site before burial beneath the soil surface, and endocoprid (dweller) species brood young in the dung pat where they will develop into adults (Hanski and Cambefort 2014). Tunneling into the soil allows dung beetles to act as effective soil engineers, mainly through bioturbation (the displacement and mixing of sediment particles by animals or plants) that occurs during burrow creation (Vidal et al. 2019). Dung beetles in the tunneling guild contribute the most to beneficial soil mixing by moving large quantities of earth to the soil surface during nesting (Mittal 1993). This tunneling strategy leads to the formation of beneficial

soil aggregates and macropores that alter air and water exchange in the soil and facilitate plant root growth (Brady & Weil 2008). Several studies link dung beetle bioturbation and nutrient mobilization to increases in both above- and below-ground plant biomass (Badenhorst 2018; Manning 2017; Bang et al., 2005; Kabir et al. 1983) and show that the effects of nutrient mobilization by dung beetles on plant growth rival that of chemical fertilizers (Miranda et al. 2000). Dung pats with no dung beetle activity quickly develop a hardened crust and remain on the soil surface for weeks or months – losing essential nutrients and reducing forage quality (Losey and Vaughan 2006) and smothering nutritious grasses. Stagnant dung pats are also breeding grounds for detrimental pests; fortunately, the beneficial feeding and nesting behaviors of dung beetles result in biological pest control by reducing livestock pest habitat (Fincher 1981; Bornemissza 1970; Nichols et al. 2008).

These ecosystem services provided by dung beetles are critically important for the management and profitability of ranchland ecosystems. A 2006 study estimated that dung beetle services had an astounding \$380 million annual impact on the U.S. cattle industry (Losey & Vaughan, 2006). This value represents the estimated avoided costs in fertilizer application and production losses from forage fouling, enteric parasites, and flies (Nichols et al. 2008). A thorough review of the ecological functions and ecosystem services provided by Scarabaeinae dung beetles called for additional research and improved understanding of the linkages between dung beetle ecological functions and ecosystem services (Nichols et al. 2008). Knowledge emerging from this research is critical to the future management of dung beetle services in agricultural systems, but the current understanding of ecosystem services is limited (Kremen 2005). Previous ecological studies fail to measure the underlying role of biodiversity in these ecosystem services.

Kremen (2005) suggested that future work should identify key approaches needed to understand valuable ecosystem service providers and ecosystem functions. Additionally, Kremen (2005) called for research investigating key species or traits that provide ecosystem functions, relationships between ecosystem function and community assembly and disassembly processes, and the environmental factors that influence the production of ecosystem functions. Filling these gaps in knowledge is key to understanding ecosystem service providers and complex ecosystem functions.

How can we understand which factors influence dung beetle community assemblage dynamics? Considering that dung beetle diversification occurred in response to the adaptive radiation of mammals in the Cenozoic Era (Hanski & Cambefort, 1991), it is unsurprising that dung beetles have a close association with mammalian fauna and may show a preference towards dung condition (Doubé 1987, Yasuda 1987), dung odor (Dormont et al., 2004) or host species (Whipple 2012). In North American grasslands, the American plains bison was once widely distributed from south-central Canada to Mexico (Gates and Aune 2008), and dung beetle species evolved a close association with these herbivores. The demise of the American bison and the introduction of cattle following European settlement has led to two hypotheses regarding the fate of bison dung-associated insects. The “extant” hypothesis proposes that these taxa now persist in the dung of cattle, while the “extinct” hypothesis proposes that a subset of these taxa were unable to make the transition to the new host and have gone extinct (Tiberg and Floate 2011).

Considering this legacy, how do dung beetle communities associated with bison-grazed grasslands and cattle-grazed grasslands differ? There is a significant gap in research on this topic, and only one study provided an experimental comparison of bison dung versus cattle dung

as food and habitat for coprophilous insects, including dung beetles (Tiberg and Floate 2011). This research compared the response of coprophilous insects to the dung of bison versus the dung of cattle, using dung based on a similar diet (cattle fed hay supplement with 10% grain and bison fed natural grass and hay) or different diets (cattle fed silage). The abundance and species richness of dung beetles associated with these sites showed that insects were more responsive to diet changes than to changes in grazer species. These results support the “extant” hypothesis: bison-associated dung beetle species persist in cattle dung. Tiberg and Floate (2011) addressed the abundance and species richness of dung beetle species associated with bison and cattle. However, they did not address the structure and assemblage of dung beetle communities and species associated with bison-grazed and cattle-grazed grasslands. There are no other studies that have examined dung beetle communities associated with bison and cattle grazed grasslands.

To understand how dung beetle communities associated with bison and cattle differ, it is vital to analyze how these communities respond to environmental factors of the soil interface. Bison and cattle differ in grazing, standing, bedding, moving behaviors (Kohl et al. 2013), and soil compaction, so it is logical to consider that these dung beetle communities may respond to environmental variations caused by differing livestock behavior.

Dung beetles are highly associated with vegetation structure (Hanski and Cambefort 1991; Nichols et al. 2007; Gardner et al. 2008; Almeida et al. 2011). Their close interactions with plants occur below the soil, with roots, as the beetles tunnel through dense plant roots to create macropores in the soil, consequently facilitating root growth. At the surface, dung beetles push through plant stems to reach dung pats, and rolling dung beetles must navigate balls of dung through the dense plant stems to bury its brood ball away from the dung pat. Above the surface,

many dung beetles utilize plant leaves or stems for perching and detecting fresh dung (Noriega and Vulinec 2021).

Differences in foraging behavior between cattle and bison could likely impact vegetation structure, and thus, dung beetle communities. Cattle and bison are predominantly graminoid feeders, and they generally show high dietary overlap. While both grazers exhibit forage selectivity, bison are less selective in foraging and show lower dietary niche breadth (number of available species/growth forms consumed) than cattle (Hartnett et al. 1996). Cattle diets are characterized by lower percentage of graminoids and a higher percentage of browse/forb than bison (Damhoureyeh and Hartnett 1997). Behavioral differences between cattle and bison, such as wallowing by bison, may also result in unique patterns of environmental patchiness and plant responses (Damhoureyeh and Hartnett 1997). Comparisons between how bison and cattle grazing affect the plant community are understood poorly because of confounding differences in how the herbivores are typically managed (Towne et al. 2005). Towne et al. (2005) compared the plant community associated with bison and cattle grazing in Kansas tallgrass prairie and found that grazing by either bison or cattle increased the canopy cover of annual forbs, perennial forbs, and cool-season graminoids. However, both annual and perennial forb cover increased at a greater rate in bison pastures than in cattle pastures. Their results also suggested species richness at both small (10 m²) and large (200 m²) spatial scales increased at a greater rate in bison pastures than in cattle pastures, but species richness did not change through time in ungrazed prairie. Differences in how these grazer species are managed might play a prominent role in their impact on prairie vegetation (Towne et al. 2005).

Dung beetles are also strongly influenced by environmental factors at the soil interface. Soil type and texture affect the moisture and temperature of dung deposited on the surface, and

these factors influence dung beetle assemblage responses (Nealis 1977), habitat preference, and reproductive success (Doubé 1983; Davis 1966). Furthermore, soils can be highly compacted in some environments due to natural processes or livestock and machine activity. Bulk density is a measure of soil compaction and could influence dung beetle communities. On a reclaimed mine with highly compacted soils in South Africa, greater bulk density on sandy soils was associated with higher dung beetle species richness (Dabrowski et al. 2019). Grazing conditions can also affect soil environments and dung beetle responses. For example, overgrazing (characterized by reduced surface cover, increased surface temperature, increased runoff, reduced soil moisture, and a change in plant community composition reduces dung beetle abundance (Hutton and Giller 2003). Unfortunately, data are lacking on how North American grassland dung beetle communities are influenced by grazing or environmental factors such as vegetation, soil texture, and bulk density.

Because of the overwhelming importance of dung beetle community assembly in rangeland ecosystems, their benefits on soil health and plant communities, and overall significance in ecosystem function, I sought to compare dung beetle community assemblages in bison-grazed versus cattle-grazed grasslands. In these managed ecosystems, differences in bison-grazing and cattle-grazing result in differences in plant biomass and bulk density, both of which may drive dung beetle community abundance, species richness, and community structure. There are no previous studies which compare the dung beetle communities associated with bison grazed and cattle grazed grasslands.

I compared the dung beetle abundance, species richness, and community assemblage (guild and species abundances) of bison-grazed and cattle-grazed grasslands, focusing specifically on the interaction of dung beetles with the habitat surface and soil interface.

Specifically, I asked two broad questions: 1) Do dung beetle community structure and composition differ on bison-grazed versus cattle-grazed grasslands? Furthermore, 2) Is dung beetle abundance associated with the interactions of grazers with their environment, including the habitat surface such as plant density (measured as plant biomass) and bare ground, and the soil interface (measured as soil texture and bulk density)?

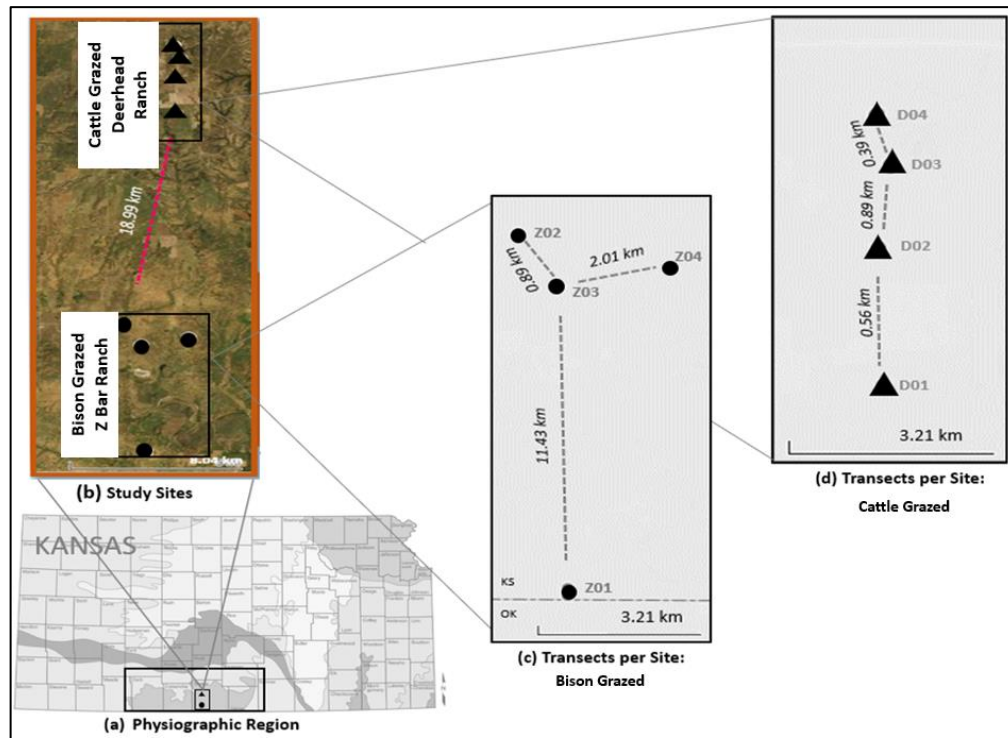
CHAPTER 2

METHODS

2.1 Study Sites: Bison-Grazed versus Cattle-Grazed

The study was conducted in Barber County, Kansas, USA, from April to December 2018. The region's climate is classified as humid subtropical (Köppen 1931), and the Red Hills ecological area is dominated by mixed-grass and sand-sage prairie communities (Egbert 1997). Rolling sandy soils and sloping to moderately steep loamy soils in the county are typically used for rangeland (USDA 1997).

Data were collected from grasslands located in Barber County: one site grazed by cattle and one site grazed by bison. Sites were separated by 18.99 kilometers at the closest point (Figure 1). Livestock on both ranches is rotationally grazed and treated with Cydectin ® (moxidectin) dewormer (personal communication [Keith Yearout, Z Bar Ranch; David Johnson, Deerhead Ranch; April 2018]). Due to the widespread use of detrimental ivermectin dewormers, we had difficulty locating suitable sites and did not have site replication (one bison grazed site and one cattle grazed site). Data were collected over nine months from four independent transects on each property (8 transects in total: 4 grazed by cattle and 4 grazed by bison).



Transects were placed under a north-south-oriented fence line to negate wind direction bias and avoid livestock disturbance and injury (Figure 1). Transects were each placed further than 100 meters apart to ensure independence. The standard of at least 100 meters between transects is based on native dung beetle dispersal rates (Stone et al., 2021). Each transect consisted of three sample points placed 40 meters apart.

2.2 Insect Collection and Analysis

To study dung beetle abundance and diversity, we collected scarabaeoid beetles using pitfall traps baited with human dung. Human omnivore dung has been shown to result in the highest capture rate of dung beetles (Whipple and Hoback, 2012). Fresh human dung was collected weekly and stored in a 1°C refrigerator. Dung was mixed with enough water to homogenize into a creamy texture. Approximately 57 ml of homogenized dung was suspended in a dish over each trap (Figure 2). Pitfall traps were refreshed every three weeks throughout the study.

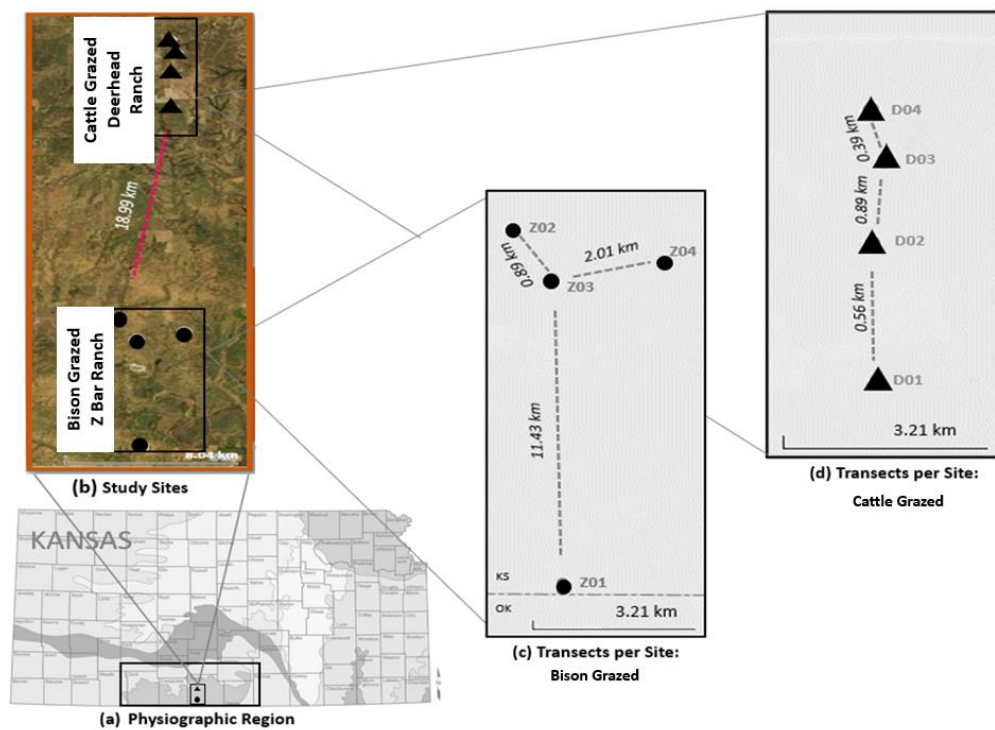


Figure 1. Experimental design showing **(a)** the Red Hills physiographic region in Kansas, **(b)** study sites (bison-grazed grassland versus cattle-grazed grassland), **(c)** transect locations and intertransect distances within the bison-grazed treatment (4 per site; each transect has 3 pitfall traps), **(d)** transects locations and intertransect distances within the cattle-grazed treatment (4 per site; each transect has 3 pitfall traps; **Figure 4**) Map modified from Kansas

The pitfall trap design consisted of two 946 ml (32 fluid ounces) plastic cups (97 mm diameter opening and 172 mm height), nested inside each other and flush to the ground, filled with a 50-50 mixture of propylene glycol and tap water (for specimen preservation). Holes drilled in the sides and bottom of the cups prevented overflow by rainwater (drain holes were placed 6.5 cm from the top of the cup). Each trap was covered by a steel cattle guard (0.635 cm thick with 2.54 x 7.62 cm openings) and secured by landscape staples to prevent livestock injury. The pitfall trap design was modeled after guidelines provided during a study on the habitat associations of carrion beetles (Engasser et al., 2021). Guidelines on pitfall trapping for repeatability with true replication followed Engasser et al. (2021).

Pitfall traps were collected 11 times (every three weeks) between April and December 2018 (24 sample points pooled into 8 transect observation points; replicated 11 times for 88 transect observation points). This time frame was chosen to ensure the detection of both early-season and late-season dung beetles (Bertone, 2005).

Preserved pitfall traps were sifted with a fine-mesh strainer and sorted using dissecting microscopes (AmScope SE306R-PZ Stereo Microscope; 80X magnification). Contents of the pitfall traps were sorted into the following groups: subfamily Scarabaeinae (individuals identified for this study), subfamily Aphodiinae and family Trogidae (scarabaeoids sorted for possible future analysis); and by-catch (non-target insects and invertebrates). We have chosen to omit dwelling (endocoprid) species from this study because they spend their lives eating, breeding, and depositing eggs directly into the dung pat and do not closely interact with soil outside the dung pat. Individuals from the subfamily Scarabaeinae were identified to species level using identification keys (Ratcliffe and Paulsen 2008) and the Wichita State University Invertebrate Collection (WICHI). Species richness, abundance, evenness, and diversity were

recorded for each site and each transect from pooled sample points. Voucher specimens are deposited at Wichita State University Invertebrate Collection, Division of Entomology at the University of Nebraska State in Lincoln (UNSM), the Kansas State University Museum of Entomological and Prairie Arthropod Research (KSU-MEPAR), Z Bar Ranch, and Turner Enterprises, Inc.

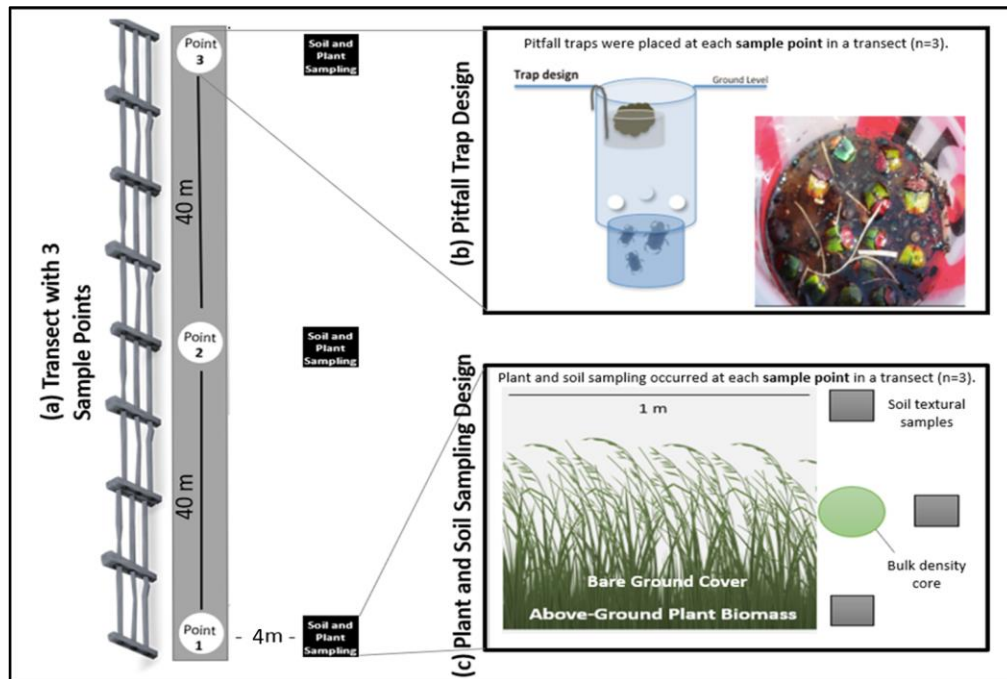


Figure 2. Experimental design showing (a) transect and sample points, (b) pitfall trap method, and (c) plant and soil sampling method.

2.3 Soil and Plant Collection

To investigate the relationship between dung beetle abundance and environmental factors, we conducted soil and plant sampling in October 2019. Soil and plant sampling plots were established four meters east of each sample point (pitfall trap location) to avoid sampling soils compacted by livestock and farm machinery (Figure 2). One m² quadrat was placed 4

meters east of the sample point and fence line for each sample point. Soil cores were taken 5-10 cm east of the m² quadrat, and plant biomass collection and bare ground examination were conducted inside the quadrat. Soil texture was recorded as a possible driver for habitat preference.

Bulk density, or the mass of dry soil per unit volume, including air space, is a measure of soil compaction and was collected as an indicator of soil quality and possible driver for habitat preference. Bulk density values vary by soil texture, and soils characterized by high bulk density can restrict root growth. Separate bulk density cores were taken 4 meters directly east of each sample point using a 5.5 cm diameter ring sampler. Intact soil cores were trimmed to the ring's size and placed in sealed plastic bags to retain moisture until weighing. To explore the effects of bulk density on dung beetle abundance and community structure and explore possible effects of dung beetle abundance on soil productivity, we conducted bulk density analysis using the weight of soil and the volume of the ring sampler on soil cores at each sample point.

2.4 Soil Analysis

To explore the effects of the soil interface on dung beetle assemblages, we conducted soil texture and particle size analysis on soil cores at each sample point using the sieve method (Smith, 2000). Soil cores from each sample point were air-dried and ground with a mortar and pestle. Pulverized soil samples were shaken through a series of Hubbard Scientific Company sieves (#5, #10, #60, #270). The contents of each sieve were weighed and compared to the total weight of the sample to accurately calculate a single point texture class based on percent sand. Percent sand, silt, and clay were estimated using a guide to soil texture by feel (Thien, 1979). Soil texture was analyzed with total beetle abundance and individual species abundance as a

covariate to grazing to explore the effect of the soil interface on dung beetle community structure.

2.5 Plant Sampling and Processing

To explore possible relationships between the habitat surface and dung beetle abundance and community structure, plant biomass (an approximation of plant abundance) data were collected inside m² quadrats placed 4 meters to the east of each sample point. Additionally, bare ground, rock cover, and dung pat cover percentages were collected within this quadrat using a cover card to estimate coverage percentages (Floyd and Anderson, 1987). All above-ground plant biomass rooted inside the quadrat was collected with shears, dried (60° C for 48 hours), and weighed. Litter accumulation and woody growth from previous years were not collected or factored into the data. Plant biomass was also analyzed with total dung beetle abundance to explore the effects of increased dung beetle abundance on soil productivity.

2.6 Statistical Analyses

The relative abundance of Scarabaeinae beetles present at each sample point was obtained by identifying specimens collected in pitfall traps on 11 collection events from April to December 2018. Abundance data were log-transformed to meet normality assumptions. Proportional data (% sand; % bare ground) were arcsine transformed, and non-proportional data (plant biomass; bulk density) were log-transformed to meet normality assumptions. Species of low abundance ($n \leq 25$) were removed before PerMANOVA analysis and NMDS ordination ($n=4$; Table 1), but all species and individuals were used in community abundance, diversity, and evenness comparisons ($n=17$). For this study, we assumed a significance level of $\alpha \leq 0.05$.

R (version 3.3.2) was used to calculate the Shannon-Weiner species diversity index (H' ; quantifies species diversity in a community by weighing values by their frequency) and evenness (J') for each site (bison grazed; cattle grazed) (“vegan” in RStudio [Oksanen et al. 2016]). The effective species number, which conveys the “true diversity” in a community and is suitable for directly comparing sites or sites, was also calculated for each site (Jost, 2006). Temporal trends in abundance were examined in 12 species for which we had adequate sample sizes ($n \geq 25$).

Dung beetle species were classified into functional guilds (Table 1) based on information in Ratcliffe and Paulsen (2008) to explore the relationship between dung beetle guild abundance and environmental factors. Guild and individual species responses to various environmental factors were analyzed using simple linear regression in PAST 4.05. PAST is free software for scientific data analysis, with functions for data manipulation, plotting, univariate and multivariate statistics, ecological analysis, time series and spatial analysis, morphometrics and stratigraphy (Hammer et al. 2001). Guild and individual species responses to environmental factors were examined for 12 species for which we had adequate sample sizes ($n \geq 25$).

Differences in dung beetle community structure between sites were examined with one-way PerMANOVA in PAST (version 4.05) using the Bray-Curtis similarity index with site (bison grazed; cattle grazed) as the explanatory or grouping variable. 9999 replicates were performed. A two-sample t-test (using Monte Carlo Permutation in PAST; 9999 permutations) was performed on each species to compare mean values by site. To explore how species composition is affected by grazing site and select environmental factors (% sand; % bare ground; above-ground plant biomass; bulk density), we performed nonmetric multidimensional scaling (NMDS) in R. We performed Indicator species analysis (IndVal in PAST) to identify dung beetle species indicative of bison grazed and cattle grazed sites.

Dung beetle community structure and soil texture were examined with one-way PerMANOVA in PAST (using the Bray-Curtis similarity index) with soil textural class (sandy loam, silty loam, silty clay, sandy clay loam, loam) as the explanatory variable. 9999 replicates were performed.

CHAPTER 3

RESULTS

3.1 Dung Beetles Associated with Bison and Cattle Grazed Sites

A total of 225,268 dung beetles representing 17 species were captured during this study (Table 1). *Onthophagus pennsylvanicus* (Harold, 1871) was the most abundant dung beetle in this study (n=156,580), followed by *Canthon pilularius* (Linnaeus, 1758) (n=40,222), *Onthophagus oklahomensis* (Brown, 1927) (n=16,736) and *Phanaeus vindex* (Macleay, 1819) (n=4,896). *Canthon viridis* and *Ateuchus histeroides* were found only at the cattle-grazed site (n = 1 and 13, respectively).

Temporal abundance data show seasonal trends for species captured in this study (Appendix Figure 1). Analysis of these trends shows each species' unique temporal distribution: the common tunneling dung beetle species *Phanaeus vindex* and *Copris fricator* display bimodal seasonality. The abundance of the non-native *Digitonthophagus gazella* (Fabricius, 1787) (n=1,303) peaked in September and then quickly declined by late October (Supplemental Document, Figure 1). Abundance peaked in July for *Onthophagus pennsylvanicus* and *Canthon pilularius*, the two most abundant dung beetles in this study.

There was no significant difference in total or mean dung beetle abundance between the cattle-grazed and bison-grazed sites. ($p=0.29$). The cattle-grazed site had higher species richness

(17 species) than the bison-grazed site (15 species), but there was no remarkable difference in diversity indices (H'), evenness (J), or effective species number between the two sites (Table 2). Indicator species analysis found that *C. pilularius* and *D. gazella* were indicative of the bison-grazed site, while *C. vigilans*, *C. fricator*, *O. medorensis*, *M. nigricornis*, *C. ebenus*, and *A. histeroides* were indicative of the cattle-grazed site (Appendix Figure 3).

Total dung beetle abundance was comprised of 81% tunneling species ($n=182,694$) and 19% ($n=42,574$) rolling species. While there was no significant difference in the mean abundance of tunnelers between the two study sites ($p=0.29$), we did find a significant difference in the mean abundance of rollers between the two sites ($p=0.0001$) (Figure 3).

There was no significant difference in the mean values of bulk density between the two sites ($p=0.13$), but there were significant differences in the mean above-ground plant biomass ($p=0.002$), bare ground ($p=0.0001$), and percent sand ($p=0.0001$) between the two sites (Figure 4), indicating that the cattle grazed site is significantly sandier in soil texture, and that the bison grazed site is significantly associated with increased plant biomass.

Dung beetle communities associated with cattle grazing differed from those associated with bison grazing (NMDS Figure 5, stress =0.12; Appendix Figure 4). Dung beetle communities and individual species were strongly correlated with plant biomass and percent sand (NMDS vectors $\text{Pr}(>r) = 0.004$ and 0.002 , respectively) and slightly correlated with bare ground (NMDS vector $\text{Pr}(>r) = 0.08$). Interestingly, dung beetle communities were not significantly associated with bulk density (NMDS vector $\text{Pr}(>r) = 0.41$).

Table 1. Dung beetle species abundance at the cattle-grazed site versus bison-grazed sites.

Species are sorted from most abundant (*O. pennsylvanicus*) to least abundant (*C. viridis*). Guild

classification indicated with **T** (tunneler) and **R** (roller) based on information in Ratcliffe and Paulsen (2008). Common species ($n \geq 25$) encountered in the study were included in multivariate analyses.

Species	Guild	Cattle-Grazed	Bison-Grazed
<i>Onthophagus pennsylvanicus</i>	T	75535	81045
<i>Canthon pilularius</i>	R	14194	26028
<i>Onthophagus oklahomensis</i>	T	8332	8404
<i>Phanaeus vindex</i>	T	2521	2375
<i>Onthophagus hecate</i>	T	1131	1306
<i>Canthon vigilans</i>	R	986	331
<i>Digitonthophagus gazella</i>	T	426	877
<i>Melanocanthon nigricornis</i>	R	589	111
<i>Onthophagus medorensis</i>	T	390	47
<i>Canthon ebenus</i>	R	202	88
<i>O. orpheus pseudorpheus</i>	T	74	90
<i>Copris fricator</i>	T	106	13
<i>Canthon praticola</i>	R	13	11
<i>Canthon probus</i>	R	14	6
<i>Atechus histeroides</i>	T	13	0
<i>Phanaeus difformis</i>	T	6	3
<i>Canthon viridis</i>	R	1	0
Total Abundance		104533	120735

Table 2. Community richness, evenness, and diversity measures for the cattle-grazed and bison-grazed sites. All species were included in community measures (n=17).

	Cattle-Grazed	Bison-Grazed
Abundance	104,533	120,735
Richness	17	15
Evenness (J)	0.16	0.18
S-W Diversity (H')	0.99	0.98
Effective Species #	2.69	2.66

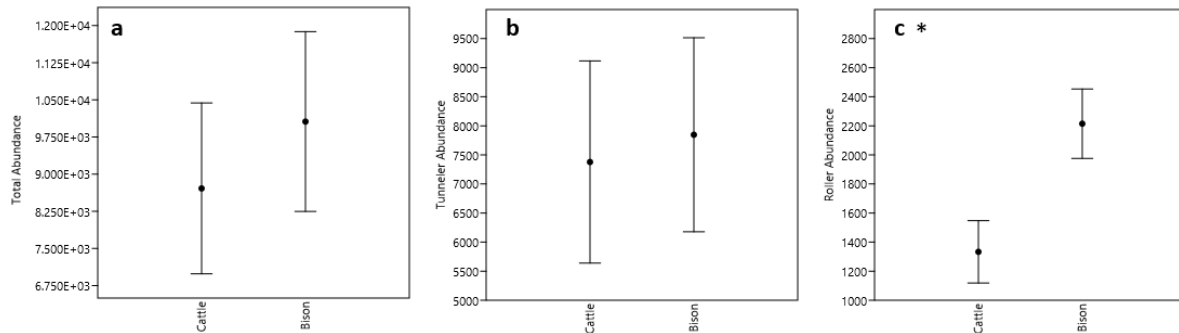


Figure 3. Dung beetle abundance of cattle-grazed and bison-grazed sites. Whiskers indicate 95% interval. **(a)** Total dung beetle abundance (two sample t-test $p=0.29$). **(b)** Total \pm S.E. guild abundance by site: rollers (two sample t-test $p=0.0001$) and tunnelers (two sample t-test $p=0.29$). Significantly different comparisons ($p < 0.05$) are marked with an asterisk (*).

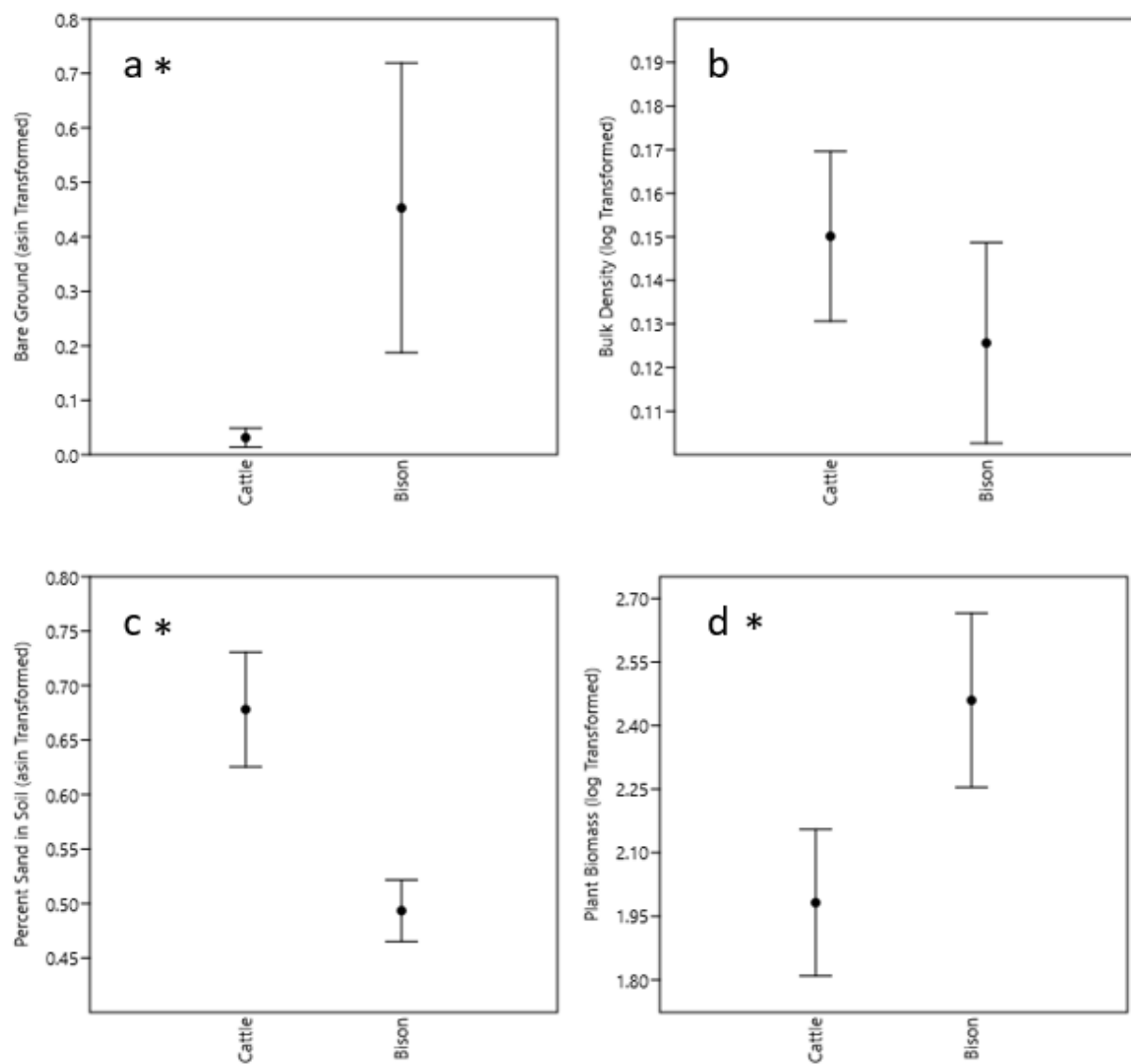


Figure 4: Examination of environmental factors compared between grazing sites; **a** (bare ground), **b** (bulk density), **c** (percent sand in soil), **d** (plant biomass). Whiskers indicate 95% interval. Significantly different comparisons ($p < 0.05$) are identified with an asterisk (*).

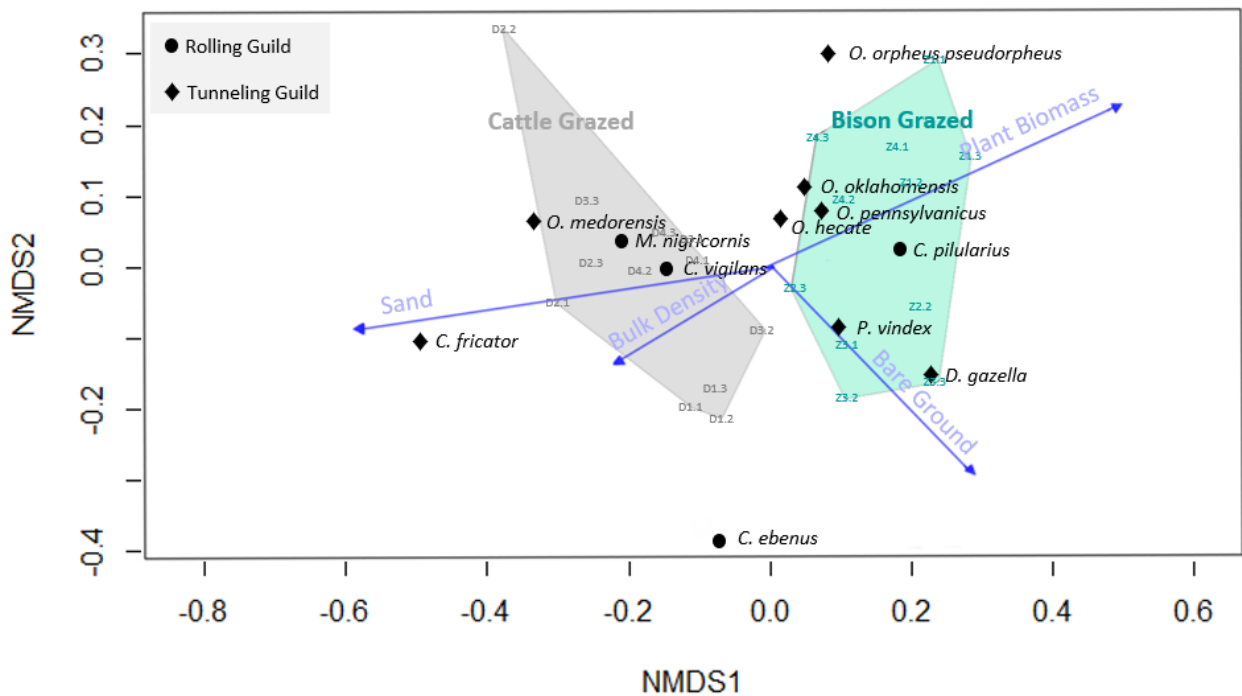


Figure 5: Dung beetle community ordination plot showing the results of NMDS analysis of the cattle-grazed (grey polygon) and bison-grazed sites (turquoise polygon). showing distinct dung beetle communities are associated with bison-grazed and cattle-grazed sites. Biplots of explanatory environmental variables are overlain to observe interactions. The biplots show that plant biomass and sand were significant predictors of the dung beetle communities; bare ground was slightly significant and bulk density was not significant. Sample points within each site are indicated within their respective polygons (e.g., D3.3, Z4.1). The position of each species in ordination space is determined by its abundance and the sample points where it was found. Species are represented by the first three letters of the genus and the first three letters of the species (Table 1). Stress is 0.12.

3.2 Soil Texture and Dung Beetle Guilds

Dung beetle abundance and community structure showed variable responses to soil texture. Total dung beetle abundance was not significantly associated with percent sand in soil ($p=0.67$, Appendix Figure 2). Results suggest different dung beetle communities associated with silty clay loam and sandy loam soils ($p=0.03$), but the NMDS ordination of dung beetle communities associated with soil texture is less clear (Appendix Figure 4). The abundance of dung beetles in the roller guild was significantly, negatively associated with percent sand in the soil ($p=0.001$) but positively associated with percent bare ground ($p=0.001$) (Table 3), and the abundance of five dung beetle species was positively associated with percent sand in the soil (*C. pilularius*, *C. vigilans*, *M. nigricornis*, *O. medorensis*, *C. fricator*) (Table 4).

Table 3: **A**, results from univariate analysis (two-sample t test using the Monte Carlo permutation) comparing the mean abundances of rolling and tunneling guilds between the cattle (C) and bison (B) sites. Significant comparisons are marked in bold text. **B**, results from linear regression analysis of environmental factors (% sand, % bare ground, above-ground plant biomass, bulk density) vs. guild abundance. Guild abundances that are negatively associated with an environmental variable are marked with (-), and guild abundances that are positively associated with an environmental variable are marked with (+). Significant comparisons are marked in bold text.

		A		B		
Guild	<i>n</i>	Cattle v Bison Treatment	% Sand	% Bare ground	Above-Ground Plant Biomass	Bulk Density
Tunneler	182,694	0.65	0.95	0.50	0.76	0.90
Roller	42,574	(B) 0.0001	(-) 0.001	(+) 1.87 E-05	(+) 0.008	0.50

3.3 Plant Biomass, Bare Ground, Bulk Density, and Dung Beetle Abundance

Some significant relationships between plant biomass and dung beetle abundance, and community structure were observed. Total dung beetle abundance was not significantly associated with plant biomass ($p=0.91$) or bare ground ($p=0.84$) (Appendix Figure 2). The abundance of dung beetles in the roller guild was positively associated with above-ground plant biomass ($p=0.008$) and not significantly negatively associated with percent bare ground ($p=0.12$) (Table 3). Two similar species, *Canthon pilularius* and *C. vigilans* exhibited opposite associations with above-ground plant biomass and bare ground (Table 4). The abundant rolling

dung beetle *C. pilularius* was significantly, positively associated with plant biomass and significantly, negatively associated with percent bare ground. Conversely, the abundance of *C. vigilans* was significantly negatively associated with plant biomass and significantly positively associated with bare ground ($p=0.28$) or bulk density ($p=0.10$).

The tunneling species *Onthophagus medorensis* was significantly, negatively associated with above-ground plant biomass ($p=0.0001$), but not associated with bare ground ($p=0.22$) or bulk density ($p=0.60$). Another tunneling species, *Copris fricator*, was significantly negatively associated with above-ground plant biomass ($p=0.003$) but not associated with the bare ground ($p=0.28$) or bulk density ($p=0.10$)(Table 4).

Total dung beetle abundance was not significantly associated with bulk density ($p=0.10$) (Appendix Figure 2) and only one rolling species (*Canthon ebenus*, $p=0.05$) was significantly positively associated with bulk density (Table 4).

Table 4: Species organized from most abundant (*O. pennsylvanicus*) to least abundant (*C. fricator*). **A**, results from univariate analysis (two-sample t test using the Monte Carlo permutation) comparing the mean abundances of individual species between the cattle (C) and bison sites. **B**, results from linear regression analysis of environmental factors (% sand, % bare ground, above-ground plant biomass, bulk density) vs. individual species abundance. Species abundances that are significantly negatively associated with an environmental variable are marked with (-), and species abundances that are significantly positively associated with an environmental variable are marked with (+); Significant comparisons are marked with bold text.

Species	n	A		B		
		Cattle v Bison Treatment	% Sand	% Bare ground	Above-Ground Plant Biomass	Bulk Density
<i>Onthophagus pennsylvanicus</i>	156,580	0.64	0.98	0.54	0.85	0.75
<i>Canthon pilularius</i>	40,222	(B) 0.0001	(-) 0.001	0.10	(+) 0.003	0.20
<i>Onthophagus oklahomensis</i>	16,730	0.56	0.87	0.42	0.92	0.49
<i>Phanaeus vindex</i>	4,896	0.71	0.99	0.22	0.64	0.11
<i>Onthophagus hecate</i>	2,437	0.94	0.86	0.08	(-) 0.05	0.85
<i>Canthon vigilans</i>	1,317	(C) 0.0003	(+) 0.009	0.18	(-) 2.18 E-05	34
<i>Digitonthophagus gazella</i>	1,303	0.14	0.11	0.06	0.75	0.12
<i>Melanocanthon nigricornis</i>	700	(C) 0.0001	(+) 0.003	(-) 5.31 E-05	0.06	0.41
<i>Onthophagus medorensis</i>	437	(C) 0.0001	(+) 0.004	0.22	(-) 0.0001	0.60
<i>Canthon ebenus</i>	290	0.07	0.16	0.29	(-) 0.04	(+) 0.05
<i>Onthophagus orpheus pseudorpheus</i>	164	0.83	0.66	0.72	0.96	0.31
<i>Copris fricator</i>	119	(C) 0.0007	(+) 3.59 E-05	0.28	(-) 0.003	0.10

CHAPTER 4

DISCUSSION

4.1 Does Dung Beetle Abundance and Community Structure Differ on Bison Grazed Versus Cattle Grazed Grasslands?

Because bison were historically abundant in the Great Plains but later replaced by cattle as the prominent grazer species, we aimed to compare the relative dung beetle abundances and dung beetle communities associated with bison and cattle. Tiberg and Floate (2011) did not find significant differences in dung beetle abundance between cattle and bison dung on similar and different diets, and many dung beetle species are generalist foragers, so we did not expect to find differences in the dung beetle communities associated with bison and cattle. Like Tiberg and Floate (2011), we did not find a significant difference in dung beetle abundance or species richness between cattle-grazed and bison-grazed sites. Tiberg and Floate (2011), however, did not examine the dung beetle community structure associated with bison and cattle; our study provides evidence that the dung beetle communities associated with bison and cattle-grazed sites are unique (Figure 5).

Examining individual species' responses to key environmental factors between sites (Appendix Table 5) explained some differences in these communities. The dung beetle community associated with the bison-grazed grasslands was strongly influenced by above-ground plant biomass, while the dung beetle community associated with cattle-grazed grasslands was strongly influenced by the percent of sand in the soil and the percent of bare ground. These

community compositions appear to be shaped by several tunneling and rolling dung beetle species' unique habitat preferences. This finding is fascinating because bison and cattle demonstrate fundamental ecological differences in habitat use (van Vuren 1983; Allred et al. 2011), forage use (Peden et al. 1974; Plumb and Dodd 1993; Towne et al. 2005), and behavior (Plumb and Dodd 1993) (Kohl et al. 2013). While foraging, for example, cattle selectively graze high plant biomass, whereas bison selected for intermediate plant biomass (Kohl et al. 2013). In this study, we found that increased above ground plant biomass was characteristic of the bison-grazed site. Dung beetle communities may be shaped not by the host species' dung, but by the interaction of the grazer species with its local environment. This is an interesting relationship that must be examined with future research, as there are currently no other studies on this topic.

Tiberg and Floate (2011) found that dung beetles were more responsive to diet changes than to changes in host species and that dung beetles historically associated with bison are most likely still extant, utilizing cattle dung. Similarly, an analysis based on fossilized animal tracks, oral tradition, archaeological findings, and dung beetle distribution (Kohlmann et al. 2018) suggested that the Costa Rican dung beetle *Copris subpunctatus* probably fed on bison dung and switched to cow dung after Spanish colonizers introduced cattle. Although fewer bison roam North American grasslands today, the relationship between grazer and dung beetle community structure is of great interest to entomologists and ecologists. Future studies investigating dung beetle communities associated with bison and cattle should use replicated grazed sites for more statistically robust results. Further, it is crucial to standardize the veterinary products being used between sites because commonly-used livestock parasiticides such as Ivermectins and moxidectins are detrimental to dung beetle populations (Lumaret et al. 1993), and toxic residues disrupt dung beetle diversity across multiple generations (Verdú et al. 2018).

4.2 Does the Soil Surface Drive Habitat Selection by Dung Beetle Species?

Because of their close interaction with the soil interface, we predicted that soil texture might significantly influence dung beetle species. We did not find any significant associations between tunneler guild abundance and any factor examined, but roller guild abundance was significantly negatively correlated with percent sand in the soil. There were several tunneler and roller species level associations with percent sand in the soil. For example, the tunneling species *Copris fricator* had an extreme preference for sandy soils (106 individuals associated with the sandier, cattle-grazed site; 13 individuals with the siltier, bison-grazed site). We speculate that this species requires a fast-draining, easily-manipulated, sandy soil texture for breeding and rearing. This hypothesis is supported by the mating and rearing behavior of *C. fricator* (Taruru 1985). Two factors were crucial to the success of this species' laboratory culture: mixing of sand with the soil because excess moisture was detrimental to the beetles, and using moist dung that did not require the addition of water (Taruru, 1985). Future studies investigating this species should include data on soil moisture to corroborate these results.

The common rolling dung beetle *Canthon vigilans* also showed a significant, positive association with the percent sand in the soil. Like *Copris fricator*, *Canthon vigilans* were significantly more abundant at the sandier, cattle-grazed site (n=986) than at the siltier, bison-grazed site (n=331). Interestingly, the total abundance of the morphologically similar species *Canthon pilularius* did not significantly correspond with percent sand in the soil.

We found that the common rolling dung beetle *Melanocanthon nigricornis* was significantly, positively associated with percent sand in the soil and was significantly more abundant at the sandier, cattle-grazed site (n=589) than the siltier, bison-grazed site (n=111).

This species is documented rolling dung across sandy prairies in Wisconsin (Williams and Kriska, 2001) and abundant in sandy areas of the Nebraska Sandhills (Ratcliffe and Paulsen 2008). In a study on dung beetle survival associated with hypoxia in different soil textures, Whipple (2011) found that *Melanocanthon nigricornis* exhibited one of the lowest hypoxia immersion survival times. Oxygen and carbon dioxide diffuse more readily through sand than other soils (Scholtz et al. 2009), and species common to sandy areas may not be exposed to severe hypoxia while in burrows during precipitation events and, therefore, do not require hypoxia tolerance to the degree of other dung beetle species (Whipple, 2013). These differences in critical gas diffusion between soil textures could explain the mechanism behind sandy soil habitat selection in dung beetle species like *Melanocanthon nigricornis*.

The tunneling dung beetle *Onthophagus medorensis* was significantly positively associated with percent sand in the soil and was significantly more abundant at the sandier, cattle-grazed site (n=390) than the siltier, bison-grazed site (n=47). In a review on this species, Branch (2020) determined from data accompanying previous collections (Howden and Cartwright, 1963) that *Onthophagus medorensis* prefers partial to shaded, sandy areas.

This study only examined soil textural class and the percent sand in the soil, but future studies should examine the percent sand, silt, and clay in the soil to reveal additional species-level relationships with soil texture. Further, expanding the study and including sites from different ecoregions would help investigate differences in dung beetle communities by soil type or texture (all transects in this study were located in the Red Hills ecoregion and the soils at each transect were relatively similar).

4.3 Is Dung Beetle Abundance Associated with the Habitat Surface?

Because dung beetles perform key ecological functions that may increase plant biomass, and because beetles in the dung rolling guild must move spheres of excrement amid the above-ground plant stems, we hypothesized that dung beetle abundance and above-ground plant biomass would be positively associated. Our results suggested no correlation between total dung beetle abundance and above-ground plant biomass, indicating that plant biomass is not significantly increased simply by dung beetle activity. However, this is a relationship that must be properly examined in future studies using long-term dung beetle enclosure treatments. Overall, roller guild abundance was strongly associated with increased above-ground plant biomass and decreased bare ground. Species-level interactions with above-ground plant biomass (Table 5) showed that the most abundant rolling dung beetle in this research, *Canthon pilularius*, is associated with increased above-ground plant biomass and decreased bare ground. However, a very similar dung roller, *Canthon vigilans*, is strongly associated with decreased above-ground plant biomass and increased bare ground. The larger species, *C. vigilans* (13.1-20.4 mm long), may navigate above-ground plant biomass differently than the smaller *C. pilularius* (12.1-17.0 mm long) (Ratcliffe and Paulsen 2008). This difference may provide insights into dung beetle niche partitioning, the mechanism by which nearly identical organisms can occupy the same habitat (Finke and Snyder 2008). Many studies have found strong effects of vegetation structure in tropical dung beetle communities (Davis 1994; Hill 1996; Halffter and Arellano 2002), but few have explored the effects of vegetation structure in grassland dung beetle communities. Future studies on this relationship could help determine if niche partitioning of dung rollers is structured based on above-ground plant biomass and increased bare ground in grassland ecosystems.

Is it possible that certain dung beetles are unable to navigate through dense vegetation?

We found a significant, negative association between above-ground plant biomass, the abundance of the dung rolling species *C. vigilans*, and the dung tunneling species *O. medorensis* and *C. fricator*. Further studies on the relationship surrounding dung beetle abundance and above-ground plant biomass should record stem density and examine dung beetle size to determine if decreased mobility through dense vegetation could explain these interactions.

4.4 Is Dung Beetle Abundance Associated With the Soil Interface?

Because dung beetles are closely associated with soil, and tunneling dung beetles must dig through soils that can be compacted, we hypothesized that dung beetle abundance and bulk density (a measure of soil compaction) would be positively associated. Our results showed no association between total dung beetle abundance and bulk density, indicating that bulk density is not significantly increased by beneficial dung beetle activity.

Species-level interactions with bulk density showed that the abundance of three species (*Phanaeus vindex*, *Canthon ebenus*, *Copris fricator*) is significantly associated with increased bulk density. In these species, these results may be indicative of a preference for compacted soils. In a study on the influence of soil bulk density and soil moisture on habitat selection of a tunneling dung beetle in the Netherlands, decreased bulk density resulted in fewer dung brood balls even when sufficient dung was available (Brussard and Slager 1986). This behavioral response supports our observation of abundance and increased bulk density in *Phanaeus vindex*, *Canthon ebenus*, and *Copris fricator*. Interestingly, we did not observe any species that were significantly negatively associated with bulk density.

Future studies aiming to explore the species-level relationships associated with bulk density should choose transects possessing a wide variety of bulk density values and should investigate species-level interactions with bulk density. Further, based on the fact that some dung beetles are significantly affected by bulk density, studies concerning soils in ranchland ecosystems should consider soil compaction caused by vehicles or livestock in the experimental design.

CHAPTER 5

CONCLUSIONS

5.1 Conclusions

Our study is the first to examine dung beetle communities associated with bison-grazed and cattle-grazed sites and only the second to examine the differences in dung beetle abundance between bison-grazed and cattle-grazed sites. Although we found no significant difference in total dung beetle abundance between the two grazing sites, we observed apparent differences in the two dung beetle communities. Our results suggest that dung beetle communities associated with bison and cattle are unique, and these differences are driven by factors at the habitat surface (above-ground plant biomass and bare ground). We speculate that these environmental factors may be influenced by the differing grazing behavior of bison and cattle. Additionally, we found that dung beetle communities are driven by the soil interface (measured as soil) texture – a factor that is not affected by bison and cattle's differing behavior. Interestingly, total dung beetle

abundance was not associated with increased soil health and productivity (bulk density and above-ground plant biomass). Instead, we found that grazer species and environmental factors associated with vegetation structure (above ground plant biomass) and the soil interface (above-bare ground and soil texture) shape dung beetle communities through species-level habitat preferences, interactions, and competitive niche partitioning.

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APPENDIX

APPENDIX

Table 1: PerMANOVA and NMDS results of dung beetle communities associated with bison grazed and cattle grazed sites. **a**, Permutation test using the bray-curtis dissimilarity index, 999 permutations. Results suggest slight differences in the dung beetle communities associated with grazing site. **b**, Vectors associated with the NMDS of bison grazed and cattle grazed sites. Results suggest significant influences of plant biomass and percent sand in the soil, and slight influence of bare ground on dung beetle communities associated with the grazing sites. Number of permutations: 999. **c**, NMDS goodness of fit test indicating significant goodness of fit for the model. Significant comparisons are marked with an asterisk: . $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p \leq 0.001$.

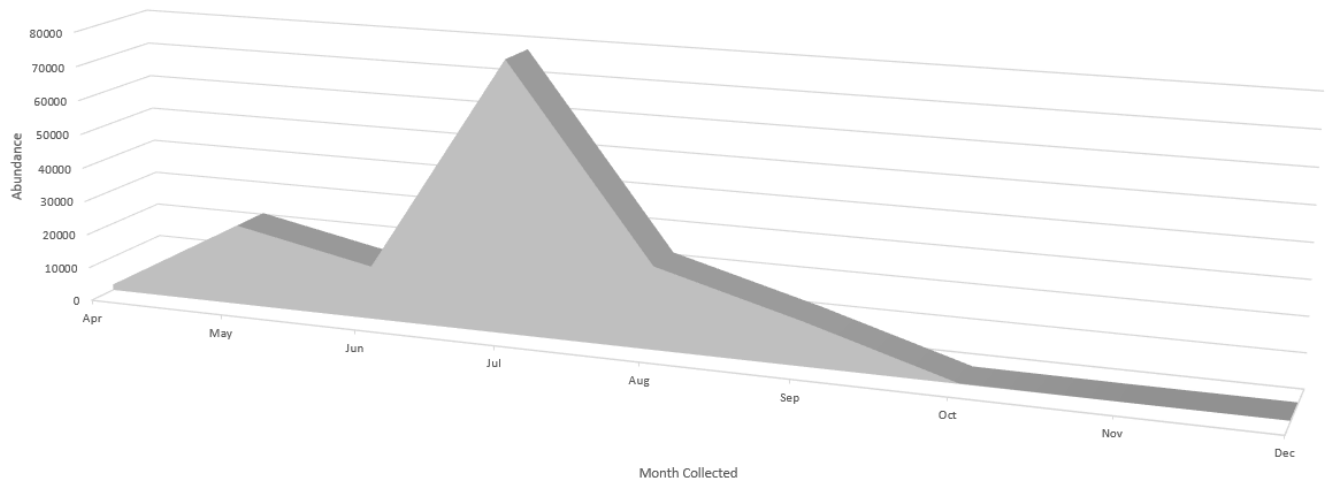
a	Df	SS	R2	F	Pr (>F)
Treatments	1	0.09	0.11	2.83	0.09 .
Residual	22	0.76	0.88		
Total	23	0.85	1.00		

b	NMDS1	NMDS2	R2	Pr(>r)
Bare Cover	0.70	-0.71	0.21	0.08 .
Bulk Density	-0.85	-0.53	0.08	0.41
Plant Biomass	0.91	0.40	0.38	0.004 **
Sand	-0.99	-0.15	0.45	0.002 **

c	R2	Pr(>r)
Treatments	0.47	0.001 ***

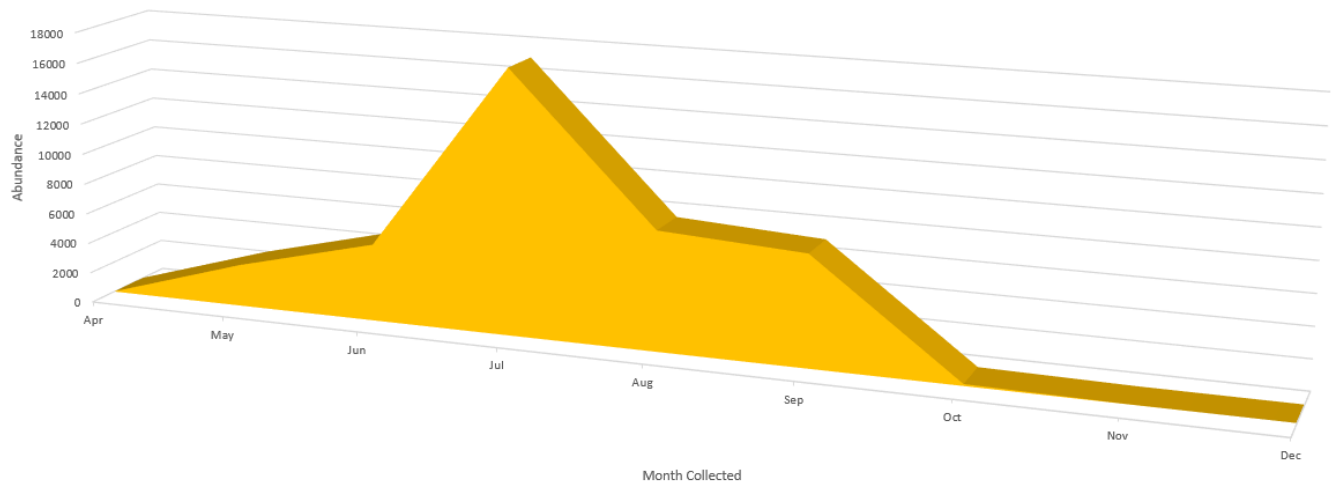
a

Onthophagus pennsylvanicus Seasonal Abundance



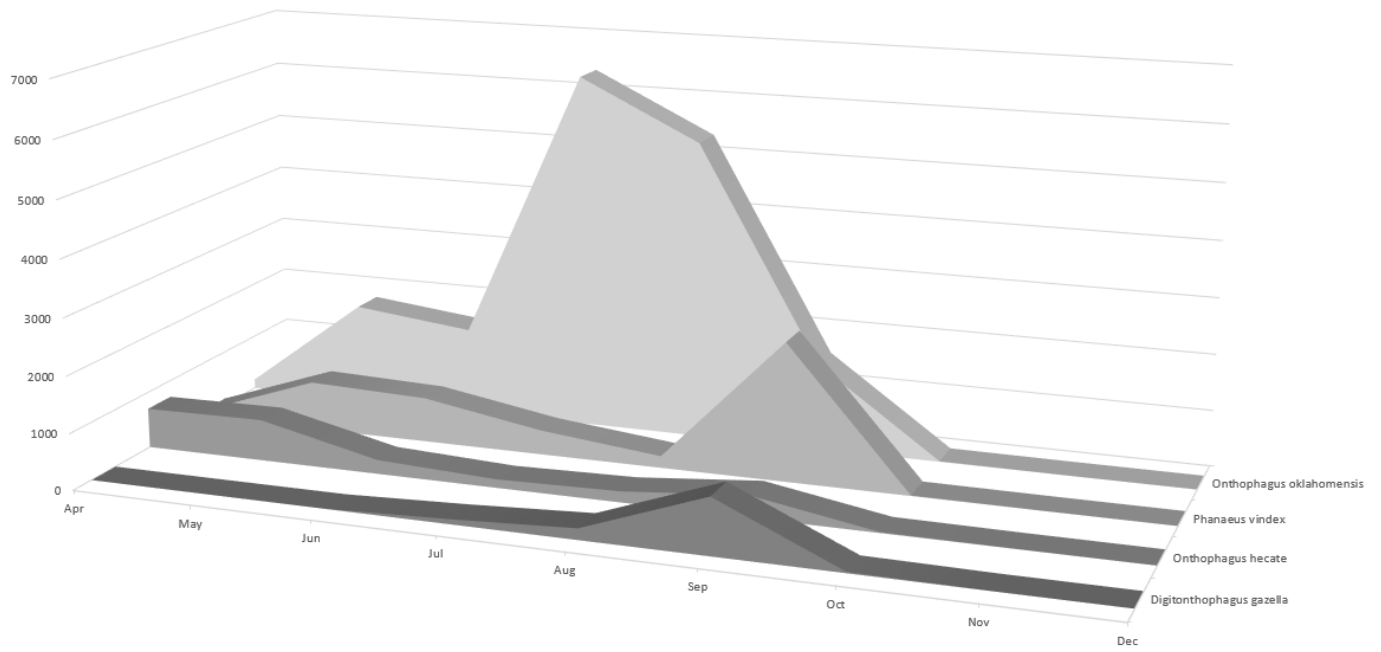
b

Canthon pilularius Seasonal Abundance

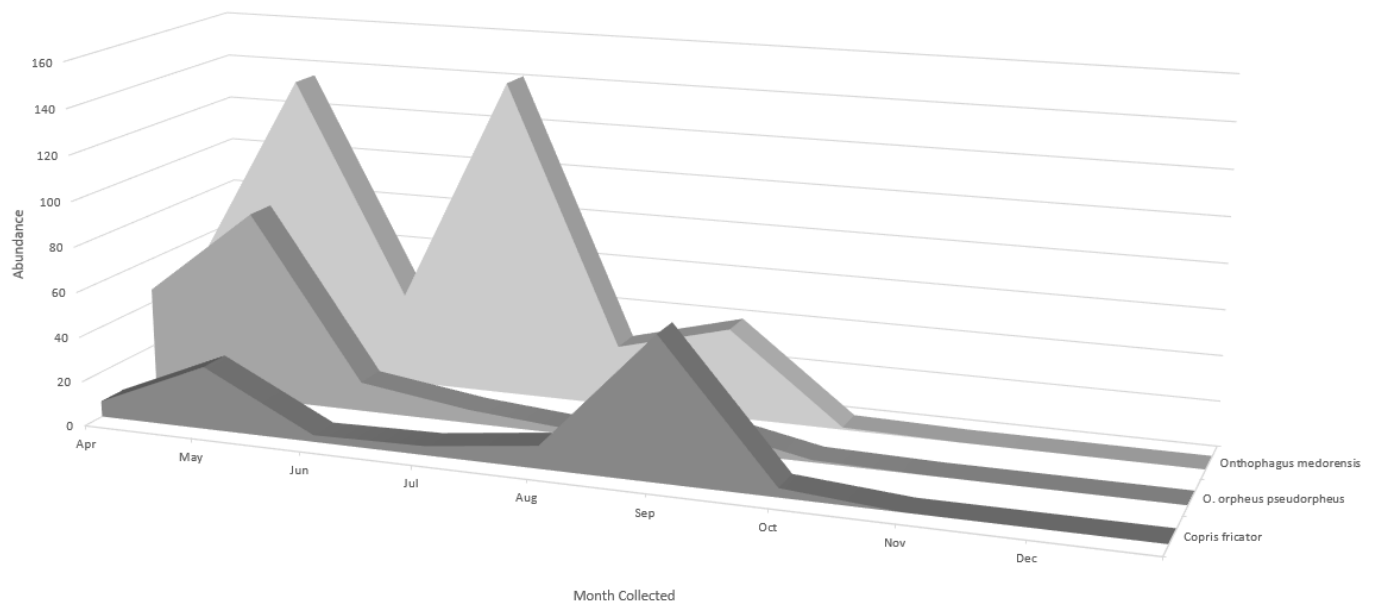


c

Tunneler Guild Seasonal Abundance

**d**

Tunneler Guild Seasonal Abundance



e

Roller Guild Seasonal Abundance

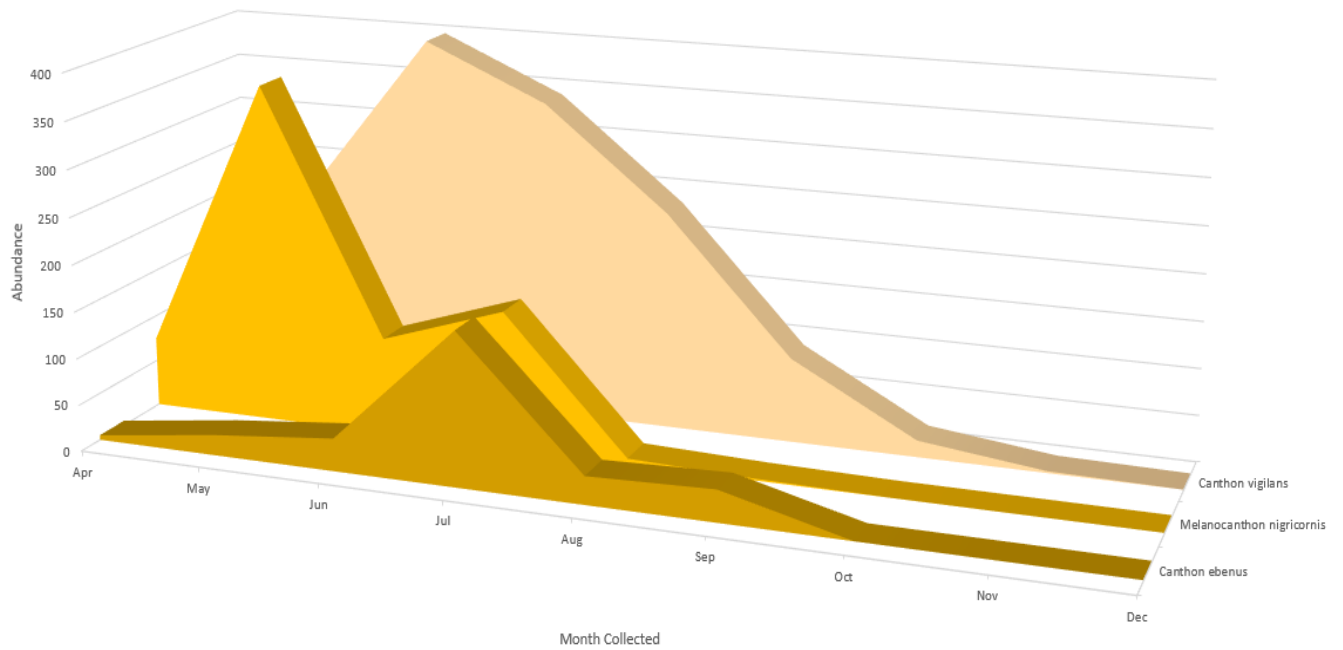


Figure 1: Abundance trends for common dung beetle species ($n > 25$) encountered in this study; **a**, The most abundant tunneler in this study, *O. pennsylvanicus*. **b**, The most abundant roller in this study, *C. pilularius*. **c**, **d**, Tunneling dung beetle species seasonal abundance. **e**, Rolling dung beetle seasonal abundance. Trends are split into multiple graphs due to a drastic spread of abundances (y axis).

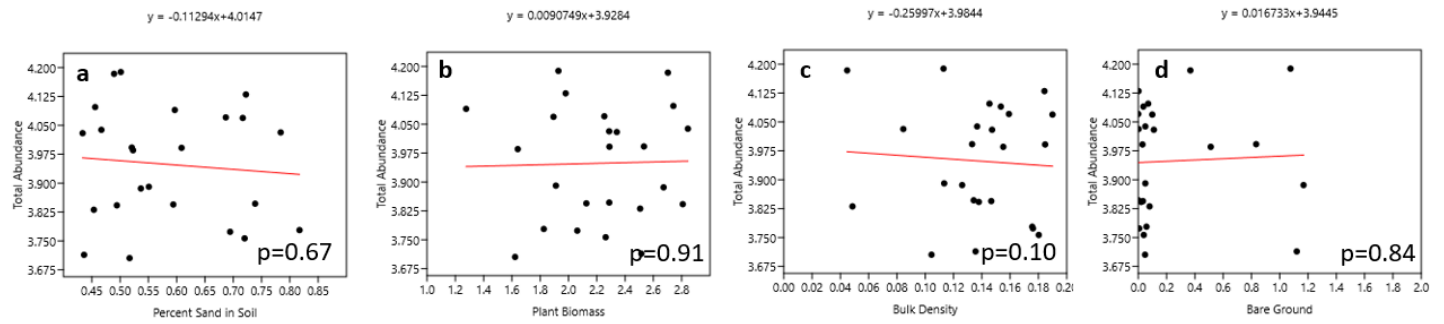


Figure 2: Linear Regression of total dung beetle abundance (y axis) versus environmental factors (x axis) **a**, percent sand in soil; **b**, above-ground plant biomass; **c**, bulk density; **d**, bare ground.

Total abundance, plant biomass, and bulk density were log transformed and percent bare ground and percent sand in the soil were arcsine transformed.

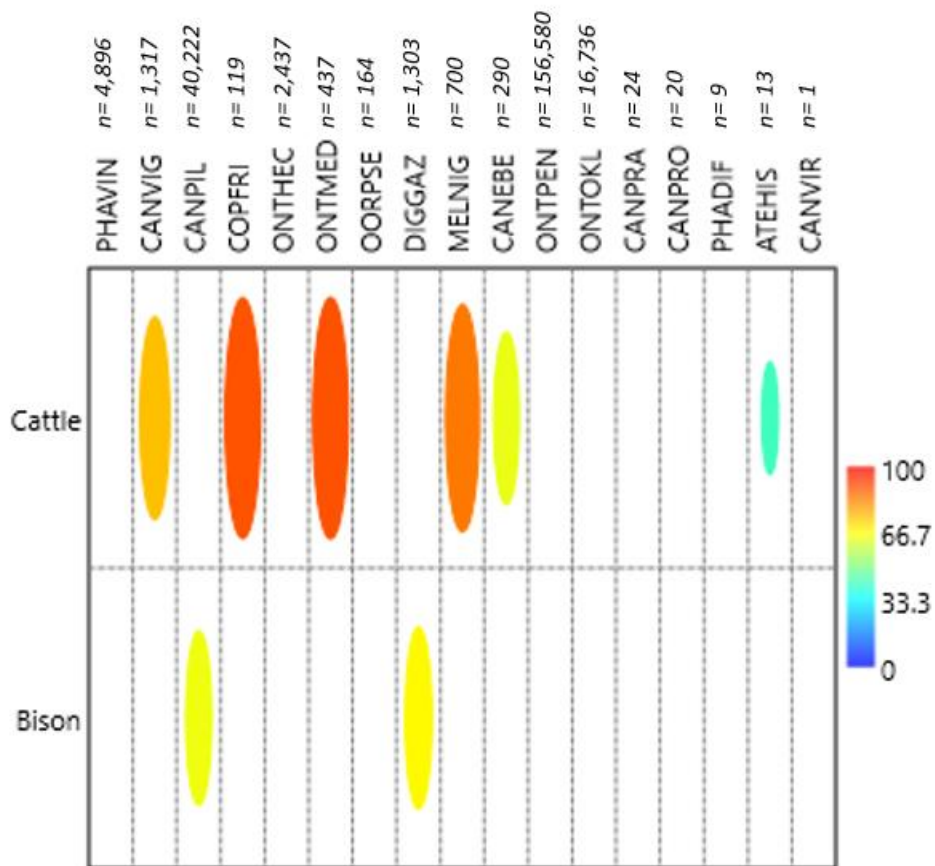


Figure 3: Analysis of the indicator species associated with bison grazed and cattle grazed sites.

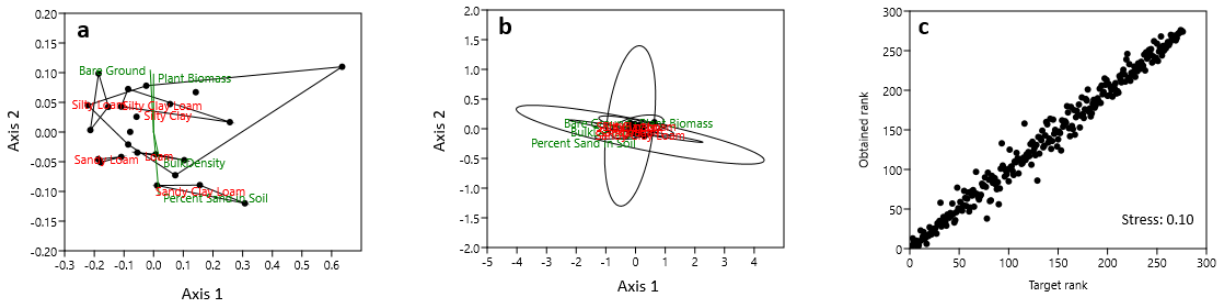


Figure 4: **a**, NMDS analysis showing dung beetle communities associated with different soil textural classes. Biplots of explanatory environmental variables are overlain to observe interactions. We did not find different dung beetle communities associated with soil texture. **b**, NMDS analysis including 95% ellipses indicating that the dung beetle communities associated with soil textural classes are not significantly different. **c**, Shepard plot indicating stress of 0.07. PerMANOVA indicates a significant difference between the dung beetle communities associated with silty clay loam and sandy loam soils ($p=0.03$).

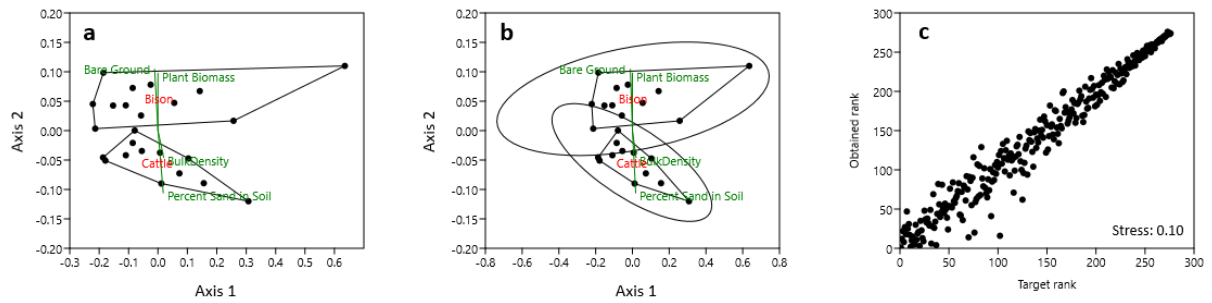


Figure 5: **a**, NMDS analysis showing dung beetle communities associated with cattle and bison grazing sites. Biplots of explanatory environmental variables are overlain to observe interactions. We did find different dung beetle communities associated with bison and cattle grazing sites. **b**, NMDS analysis including 95% ellipses indicating that the dung beetle communities associated with bison and cattle grazing site are significantly different. **c**, Shepard plot indicating stress of 0.10. For an NMDS with species overlay, see Figure 5.