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Effects of herd management and the use of ivermectin on dung arthropod communities in grasslands

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Abstract

Agroecosystems represent a large geographical footprint in most terrestrial landscapes, and management decisions within these systems affect their function in species conservation. We evaluated the effects that rangeland management systems (based on stocking density, rotation frequency, and the number of avermectin applications) have on conserving the dung arthropod community in the Northern Great Plains of North America. Comprehensive bioinventories of arthropods were collected from 16 rangelands using core samples of dung pats. Ivermectin was quantified in pats from each ranch using enzyme-linked immunosorbant assay (ELISA). Arthropods in dung were abundant (116,244 specimens) and diverse in eastern South Dakota (172 morphospecies). Rangelands managed with more regenerative practices (frequent rotation at high stocking densities and lack of ivermectin applications) had greater species richness, diversity, predator species abundance, and dung beetle abundance than more conventionally managed rangelands. Ivermectin quantity in cattle pats was negatively correlated with dung beetle abundance and diversity. This work shows that herd management (specifically high-intensity, frequent rotational grazing and eliminating prophylactic ivermectin use) that aims to mimic intensive grazing of large migrating herds of ruminants can foster dung arthropod community structure, a key trait correlated with nutrient cycling, pest suppression, and productivity of cattle-grazed rangelands.

Keywords: Agroecology; Avermectin; Dung beetles; Grasslands; Regenerative agriculture

Introduction

Agroecosystems currently occupy a large geographic footprint globally, and species conservation and promotion efforts are strongly affected by management decisions within this habitat. For example, rangelands (including unirrigated land, grazed grasslands, and other areas of native vegetation) are estimated to comprise 40–50% of terrestrial surface globally (Yoshitake, Soutome, & Koizumi 2014). In the United States in 2015, beef production on rangelands was valued at nearly $60 billion (NASS 2018), and constitutes a major part of the economy in the Northern Plains of North America (i.e., 29% [$879 million] of agricultural revenue in South Dakota came from beef production in 2015; NASS, 2018). In addition to livestock production, other economic and ecological returns from rangelands include ecosystem services such as soil erosion control, increased water filtration, carbon sequestration, and habitat for a wide variety of plant and animal

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species (Goldstein et al. 2011; Steiner et al. 2014; Stanley et al. 2018). Management decisions, specifically pesticide use, herd size, and rotation frequency, can affect the ability of rangelands to function as habitat for wildlife and provide ecosystem services.

The costs and benefits of different cattle management strategies are regularly debated (Briske et al. 2011; Norton, Barnes, & Teague 2013; Teague, Provenza, Kreuter, Steffens, & Barnes 2013; Roche, Cutts, Derner, Lubell, & Tate 2015). In continuous season-long grazing systems, cattle live on a single pasture for a substantial portion of the year. Continuous grazing systems are commonly implemented due to the ease with which a rancher can manage even large herds of cattle with minimal fencing, water sources and transportation costs (Briske et al. 2011). The benefits of this system must be weighed against the potential loss in long term productivity and sustainability of a pasture (Lodge 1970; Gillen, McCollum, Tate, & Hodges 1998; Briske et al. 2008). In continuously grazed pastures, cattle will often choose to graze some areas more heavily, spending a disproportionate amount of time in localized areas, while leaving others relatively untouched (Senft et al. 1987). A multi-paddock system where animals are grazed at high densities can lead cattle to graze more plant species within a pasture (Barnes, Norton, Maeno, & Malechek 2008). A key aspect of these high-density grazing systems is that herds are frequently moved, and the soil and plant community are allowed a regrowth and recovery period. This practice requires an understanding of the landscape and local optimal plant regrowth rates, but results in higher forage quality in subsequent grazing periods (Teague et al. 2013). It has been argued that by mimicking the intensive grazing patterns of ancestral large ruminant herds, high density, multi-paddock grazing systems can foster greater ecosystem services, higher quality forage, support greater and faster weight gain and healthier animals, and improve the ranch resiliency over continuous grazing systems (Walton, Martinez, & Bailey 1981; Norton et al. 2013).

There are a variety of pesticides and parasiticides that are used to manage internal and external pests of cattle; one of the most widely used chemicals are avermectins. Avermectins came to dominate the livestock pesticide market due to their strong antihelminthic and insecticidal activity (Campbell, Fisher, Stapley, Albers-Schonberg, & Jacob 1983). Five years after the advent of ivermectin (the most widely sold avermectin derivative), it was sold in 46 countries and administered to 320 million cattle (Campbell 1985); more recent estimates are that 56% of all U.S. cattle are administered avermectins (Omura & Crump 2004; Losey & Vaughan 2006). Avermectins are the result of fermentation of an actinomycete bacterium *Streptomyces avermitilis*, which is highly toxic to nematode and insect pests (Burg et al. 1978). Avermectins' broad-spectrum toxicity to pest arthropods and nematodes may also pose hazards to non-target species on rangeland with treated cattle. A substantial portion (80–98%) of administered avermectin is excreted in the dung (Alvinerie, Sutra, & Galtier 1998; Floate, Sherratt, Boxall, & Wardhaugh 2005). Risk assessments have revealed that avermectins frequently reduce the populations of non-target dung arthropods, although risk posed by dung contamination depends on timing of application, method of administration, and concentration of the product administered (Wall & Strong, 1987; Sommer et al., 1992; Floate et al., 2005). Arguably, this pesticide use is more associated with continuous grazing systems, and may be one mechanism whereby different grazing systems affect dung arthropod communities.

This study tests the hypothesis that regenerative rangeland systems affect dung arthropod communities. The systems were defined by the ranchers, and represented a continuum of practices from those that were considered fully conventional to those that approximate the grazing patterns of migrating herds of ruminants. As part of testing this overall hypothesis, we evaluated whether ivermectin use in cattle affects dung arthropod communities, particularly beneficial species. This information can help ranchers make informed decisions regarding how their management decisions affect the financial and ecological contributions of dung arthropod communities to their operations.

Materials and methods

Experimental design

Sampled cattle operations (n = 16; 10 in 2015 and six in 2016) represented a variety of cattle management practices in the Northern Great Plains of North America. The 16 cattle operations span 7935 km^2 across eastern South Dakota. All sites were grazed by cattle for at least 5 y, but among ranches annual grazing intensity and grazing period varied. Herds ranged from 20 to 120 individuals, and the cattle differed in size, breed, and how or whether avermectin products were administered. The systems were ranked from regenerative to conventional based on several practices (Table 1). The three management systems used throughout the study were designated as regenerative (n = 5 operations), intermediate (n = 5 operations), and conventional (n = 6 operations). These management systems were categorized based on three of the practices of importance to rangeland management or potential to impact dung arthropods. These practices were stocking density, rotation frequency, and use of ivermectin products, and the cattle operations were categorized based upon their combination of these practices to define the different systems. Use of ivermectin in the ranches was categorized as high (multiple applications during a year; scored as 0), low (single annual use, not applied during grazing period; scored as 1) and no ivermectin (scored as 2). Operations' stocking densities (animal units [AU] per ha), were categorized as fewer than 5 animal units (AU) per ha (scored as 0), 5–10 AU per ha (scored as 1), and more than 10 AU per ha (scored as 2). Operations were categorized as having a rotation frequency (moving animals between paddocks) of 30 d or more (scored 0), between 10–30 d (scored as 1),

Table 1. Ranch (n = 16) systems were categorized based on their use of ivermectin, stocking density of cattle, and rotation frequency of the herd. Management practices of cattle operations were scored 0–2 based, with higher numbers reflecting practices that promote biodiversity and soil quality. Ivermectin application frequency was divided into multiple applications (0), single application not during grazing season (1), and no avermectin use (2). Stocking density (animal units; AU) was divided into <5 AU/ha (0), 5–10 AU/ha (1), and >10 AU/ha (2). Rotation frequency was divided into >30 d rotation (0), 10–30 d rotation (1), and <10 d rotation (2). The highest scoring 30% of ranches were identified as regenerative, and the lowest 30% as conventional ranches.

Location (closest town)	Year surveyed	Ivermectin	Stocking density	Rotation frequency	System designation
Bruce, SD	2016	1	0	0	Conventional
Castlewood, SD	2016	1	2	1	Intermediate
Clear Lake, SD	2015	2	2	2	Regenerative
Estelline, SD	2015	1	1	1	Intermediate
Estelline, SD	2016	0	1	0	Conventional
Flandreau, SD	2015	0	0	0	Conventional
Gary, SD	2016	2	2	2	Regenerative
Goodwin, SD	2016	2	2	2	Regenerative
Madison, SD	2015	0	1	1	Conventional
Milbank, SD	2015	1	1	1	Intermediate
Milbank, SD	2015	0	0	0	Conventional
Sioux Falls, SD	2015	2	2	2	Regenerative
Summit, SD	2016	1	1	1	Intermediate
Thomas, SD	2015	1	1	2	Intermediate
Twin Brooks, SD	2015	2	2	1	Regenerative
Volga, SD	2015	0	0	0	Conventional

and less than 10 d (scored as 2). Ranches with the top 33% of scores were considered regenerative, the middle 33% of scores were intermediate, and the lowest third of scores was considered conventional. This same approach was used to distinguish regenerative and conventional corn fields in a recent published study (LaCanne & Lundgren, 2018). In our study, the designation of management systems was based upon the grouping of several management practices that were sometimes all present on the same cattle operation. This grouping approach was based on findings that these practices' impact the rangeland ecosystem and specifically the dung arthropod community (Senft, Rittenhouse, & Woodmansee, 1985; Lumaret et al. 2007; Errouissi & Lumaret 2010; Norton et al. 2013; Teague et al. 2013; Verdu et al. 2015).

Sampling procedure

Each of the ranches was sampled monthly from May to September. Two- to 5-day-old dung pats (n = 10 per ranch) were randomly selected from each ranch; this age of pat has peak arthropod abundance and diversity (Kessler & Balsbaugh 1972; Lee & Wall 2006), and sampling intensity is based on previous experience in the region. Arthropod communities remain at their peak abundance and diversity when pats are aged 2–7 days old (Pecenka & Lundgren 2018), and this is also when ivermectins are at their highest concentrations in the pats. Ranchers kept records of when the cattle were moved from a sampled pasture to help us target pats within this age range. A core sample (10 cm diameter, 10 cm deep) was collected from each selected pat and the underlying soil, and the arthropods within each pat were extracted using a Berlese system over 7 d; at that point the core had completely dried and all arthropods had left the dung pat. Arthropods from each core were stored in 70% ethanol. All extracted arthropods were identified microscopically and cataloged; each unique specimen was identified to the lowest taxonomic level possible representing a functional morphospecies. Each morphospecies was placed into a trophic guild (coprophage, predator, parasitoid, or herbivore) based upon previous descriptions of the biology of the arthropod community in dung pats (Mohr 1943; McDaniel, Boddicker, & Balsbaugh 1971; Cervenka & Moon 1991).

Ivermectin quantification

The amount of ivermectin in dung pats was quantified using a direct, competitive enzyme-linked immunosorbent assay (ELISA) following kit instructions (Product #5142B, Abraxis, Warminster, PA). ELISA is relatively inexpensive and requires less sample volume to detect low quantities of a pesticide relative to chromatographic approaches. A 500 μL (approximately 0.65 ± 0.02 g; mean ± SEM) sample was collected from five of the dung pats per field. This sample was vortexed with 100 μL of water and 100 μL of ethanol for 1 min. The mixture was centrifuged at 14,000*g* for 2 min and 50 μL of the resulting supernatant was analyzed. Absorbance values at 450 nm were recorded for each well on 96-well plates (μQuant, Biotek Instruments, Winooski, VT). To quantify ivermectin in the dung samples, a standard curve series with concentrations of 1, 0.5, 0.25, 0.1, 0.05, 0.025, and 0.01 ng ivermectin/μL dung was included on each plate. Additionally, a negative control series of 0 ppm ivermectin was included in three wells on each plate. To distinguish positive samples from background absorbance of the matrix, the mean and standard deviation of the negative control series were calculated for each plate; any samples with a lower optical density (direct competitive ELISAs have an absorbance negatively associated with ivermectin concentration) than the mean minus three times the standard deviation of this series were considered positive for ivermectin.

Data analysis

All statistics were conducted using Systat 13 and SigmaPlot 13 software (SYSTAT Software, Inc; Point Richmond, CA). Two-way ANOVAs were used to investigate how month and management system impacted arthropod community characteristics of abundance, species richness, and species diversity as well as their effect on arthropod functional groups of coprophages, predators, herbivores, and parasitoids. The effects of month and management system on ivermectin content in dung was also observed. Linear regressions were generated to compare the quantity of ivermectin found in dung to arthropod abundance, species richness, and diversity as well as the abundance of beetle larvae and members of Scarabaeidae.

Results

Description of dung arthropod community

In sum, 116,244 arthropod specimens were identified representing 172 morphospecies. These species were represented by six classes of arthropods across 14 orders (Acarina, Araneae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Isopoda, Julida, Lepidoptera, Lithobiomorpha, Protura, Pseudoscorpiones, and Thysanoptera). Due to the difference in ecological function of larvae and adults, larvae were considered distinct morphospecies. The highest number of morphospecies were Coleoptera adults, Hymenoptera, Coleoptera larvae, Diptera adults, and Araneae containing 79, 24, 16, 14, and 11 morphospecies, respectively. The most abundant groups collected were Acarina (43,757), Coleoptera adults (24,945), Diptera larvae (17,988), Collembola (13,324), and Hymenoptera (6610). All species collected were divided trophically into coprophages (74,703 individuals representing 53 morphospecies), pests (20,282 individuals representing 21 morphospecies; all Diptera), predators (18,861 individuals representing 54 morphospecies), herbivores (2159 individuals representing 27 morphospecies), and parasitoids (239 individuals representing 17 morphospecies). Across all 16 ranches there was an average species richness of 34.76 ± 0.85 (mean ± SEM) species found per site per month with an overall average diversity (Shannon H') of 2.07 ± 0.04. In total 18,501 ± 1385 arthropods were found per m^2 of cattle dung throughout the study. A complete inventory of arthropod specimens can be seen in Supplementary Appendix A (summarized in Table 2).

Dung community over time and as affected by management system

Arthropod communities in dung changed over the summer and were different among the management systems (Table 2). The number of arthropods differed among months of the season, but abundance was not affected by the management systems (month: $F_{4, 65} = 4.38$, $p = 0.003$; management: $F_{2, 65} = 0.34$, $p = 0.72$; interaction: $F_{8, 65} = 0.24$, $p = 0.98$). Species richness was significantly affected by both time of season and management system (month: $F_{4, 65} = 6.94$, $p < 0.001$; management: $F_{2, 65} = 10.69$, $p < 0.001$; interaction: $F_{8, 65} = 1.89$, $p = 0.08$). Arthropod abundance started low in May (8815.69 ± 1034.38 arthropods per m^2); the remaining months were indistinguishable from each other, but there were significantly more arthropods than in May. Species richness was similarly lowest in May; the remaining months had significantly more arthropods than in May, but the remaining season did not vary statistically. Management system had a significant effect on the diversity of arthropods, but month did not (month: $F_{4, 65} = 1.38$, $p = 0.25$; management: $F_{2, 65} = 7.77$, $p = 0.001$; interaction: $F_{8, 65} = 0.54$, $p = 0.82$) (Fig. 1B). Species richness and diversity were found to be significantly lower in pastures with continuous grazing, lower stocking densities and high ivermectin use compared to the more regenerative systems.

Systems with the most regenerative practices had a species richness of 38.24 ± 1.19 species per site per month sampled versus 31.03 ± 1.35 in the conventional system; diversity in regenerative systems was 2.24 ± 0.06, and 1.90 ± 0.05 in conventional systems (statistics presented above). Predator abundance was significantly affected by month and management system (month: $F_{4, 65} = 3.58$, $p = 0.01$; management: $F_{2, 65} = 3.71$, $p = 0.03$; interaction: $F_{8, 65} = 0.28$, $p = 0.97$). Pastures managed conventionally had significantly fewer predators than the more regenerative ranches. Month sampled had a significant effect on parasitoid abundance, while management system did not (month: $F_{4, 65} = 3.65$, $p = 0.009$; management: $F_{2, 65} = 1.10$, $p = 0.30$; interaction: $F_{8, 65} = 0.48$, $p = 0.87$). The months of May, August, and September had significantly fewer parasitoids than June or July. Herbivore abundance was not significantly affected by sampling month or management system (month: $F_{4, 65} = 1.39$, $p = 0.25$; management: $F_{2, 65} = 1.21$, $p = 0.23$; interaction: $F_{8, 65} = 0.41$, $p = 0.83$). Abundance of the entire coprophage assemblage was found to be significantly affected by month sampled but not by management system (month: $F_{4, 65} = 3.88$, $p = 0.007$; management: $F_{2, 65} = 0.218$, $p = 0.81$; interaction: $F_{8, 65} = 0.30$, $p = 0.96$). Management systems had a significant effect on maggot populations, and there was a marginally significant seasonal effect on maggot abundance (month:

Table 2. Arthropod community characteristics of dung pats from the Northern Great Plains of North America.

Community characteristics	Regenerative systems	Intermediate systems	Conventional systems	Statistics
	Abundance (ind./m^2)			
All arthropods	18,686 ± 2,865	19,796 ± 2,165	17,292 ± 1,912	$F_{2,65} = 0.34$, $P = 0.72$
Coprophages	14,712 ± 2,422	16,214 ± 1912	14,562 ± 1,708	$F_{2,65} = 0.218$, $P = 0.81$
Predators	**3,561 ± 494 A**	**3,375 ± 281 A**	**2,228 ± 387 B**	**$F_{2,65} = 3.71$, $P = 0.03$**
Parasitoids	41 ± 9	35 ± 7	39 ± 11	$F_{2,65} = 1.10$, $P = 0.30$
Herbivores	372 ± 246	172 ± 62	463 ± 401	$F_{2,65} = 1.21$, $P = 0.23$
Dung beetles	**828 ± 141 A**	**406 ± 79 B**	**267 ± 65 C**	**$F_{2,65} = 9.06$, $P < 0.001$**
Species richness	**38.24 ± 1.19 A**	**35.76 ± 1.52 A**	**31.03 ± 1.35 B**	**$F_{2,65} = 10.69$, $P < 0.001$**
Diversity (H’)	**2.24 ± 0.06 A**	**2.09 ± 0.06 A**	**1.90 ± 0.05 B**	**$F_{2,65} = 7.77$, $P = 0.001$**
Evenness (J’)	**0.62 ± 0.02 A**	**0.59 ± 0.01 AB**	**0.56 ± 0.01 B**	**$F_{2,65} = 3.14$, $P = 0.05$**

The mean ± SEM of each community characteristic was taken across the three management systems per month. Abundance values for community characteristics are extrapolated from samples from a 10 cm diameter core to 1 m^2. Different letters indicate differences between management systems ($\alpha = 0.05$).

$F_{4,65} = 2.31$, $p = 0.06$; management: $F_{2,65} = 2.87$, $p = 0.047$; interaction: $F_{8,65} = 0.59$, $p = 0.79$).

Dung beetle abundance was significantly affected by the pasture’s management system, but no differences were seen among months (month: $F_{4,65} = 1.86$, $p = 0.13$; management: $F_{2,65} = 9.06$, $p < 0.001$; interaction: $F_{8,65} = 0.69$, $p = 0.70$). Regenerative pastures, with frequent rotations, high stocking densities and no ivermectin use, had significantly more dung beetles (827.52 ± 140.63 beetles per m^2 of dung) than conventionally managed pastures (267.09 ± 65.30 dung beetles per m^2). The diversity of dung beetles was significantly affected by both month and management system (month: $F_{4,65} = 5.52$, $p = 0.001$; management: $F_{2,65} = 6.83$, $p = 0.002$; interaction: $F_{8,65} = 1.37$, $p = 0.23$). The most numerous dung beetle species were *Aphodius haemorrhoidalis* (n = 1396), *A. rubeolus* (n = 476), *A. erraticus* (n = 363), *A. fossor* (n = 299), *Onthophagus hecate* (n = 223), and *A. fimetarius* (n = 130). While the overall abundance of dung beetles was not significantly different over the season, the individual species had significant changes over time. *A. fossor* and *A. erraticus* were found at 12–13 of the 16 ranches on the May and June sampling dates and by August fewer than three ranches contained either of the two species. Inversely, *A. fimetarius* was found on only one ranch in May and nine ranches in September. *A. rubeolus* was found in 14–15 ranches in June, July, and August while in May and September only six ranches had any *A. rubeolus*. *A. haemorrhoidalis* and *O. hecate* were found consistently across the entire sampling period.

Ivermectin ELISA quantification

The average ivermectin in cattle dung pats across all 16 ranches was found to be 187.56 ± 19.25 ng of ivermectin per mL of dung. The amount of ivermectin (ng/mL of dung) was found to be significantly affected by the month sampled and the management system (month: $F_{4,65} = 3.08$, $p = 0.02$; management: $F_{2,65} = 55.36$, $p < 0.001$; interaction: $F_{8,65} = 1.69$, $p = 0.12$) (Fig. 2). Ivermectin in May was significantly higher than all other months except September, and ivermectin quantity in September similar to that found in every month but May. Management systems had significantly different quantities of ivermectin found in dung pats. The most conventionally managed systems had the highest ivermectin contamination, with 329.79 ± 29.59 ng/mL. Intermediately managed systems had half the 180.66 ± 21.16 ng/mL and the regeneratively managed pastures had only 23.78 ± 7.31 ng/mL of dung.

Ivermectin correlations to arthropod metrics

Ivermectin in dung pats influenced many aspects of the arthropod community. While the entire community abundance was not correlated to ivermectin ($F_{1,78} = 3.21$, $p = 0.08$), there was a negative correlation of species richness ($F_{1,78} = 21.90$, $p < 0.001$), and species diversity ($F_{1,78} = 7.06$, $p = 0.01$). There were no correlations to ivermectin and coprophagous arthropods, ($F_{1,78} = 2.36$, $p = 0.13$); however, predatory species were negatively correlated to higher ivermectin quantities ($F_{1,78} = 6.93$, $p = 0.01$) (Fig. 3B). Dung beetle numbers were negatively correlated with higher ivermectin levels in dung ($F_{1,78} = 18.13$, $p < 0.001$) as were all coleopteran larvae ($F_{1,78} = 5.46$, $p = 0.02$). Maggot abundance was positively correlated to a higher ivermectin content in dung pats ($F_{1,78} = 4.21$, $p = 0.047$).

Discussion

Ranchers that abandoned ivermectins often used a high-density and frequently-rotated grazing system that more closely resemble the natural grazing patterns of large migrating herds of ruminants. Categorizing the management system according to a range of practices was necessary to fully understand the effects of management on the arthropod community. Management system significantly influenced the dung arthropod communities found in these rangelands. Regenerative systems had 19% more species and greater Shannon diversity than the conventionally managed pastures. The losses in

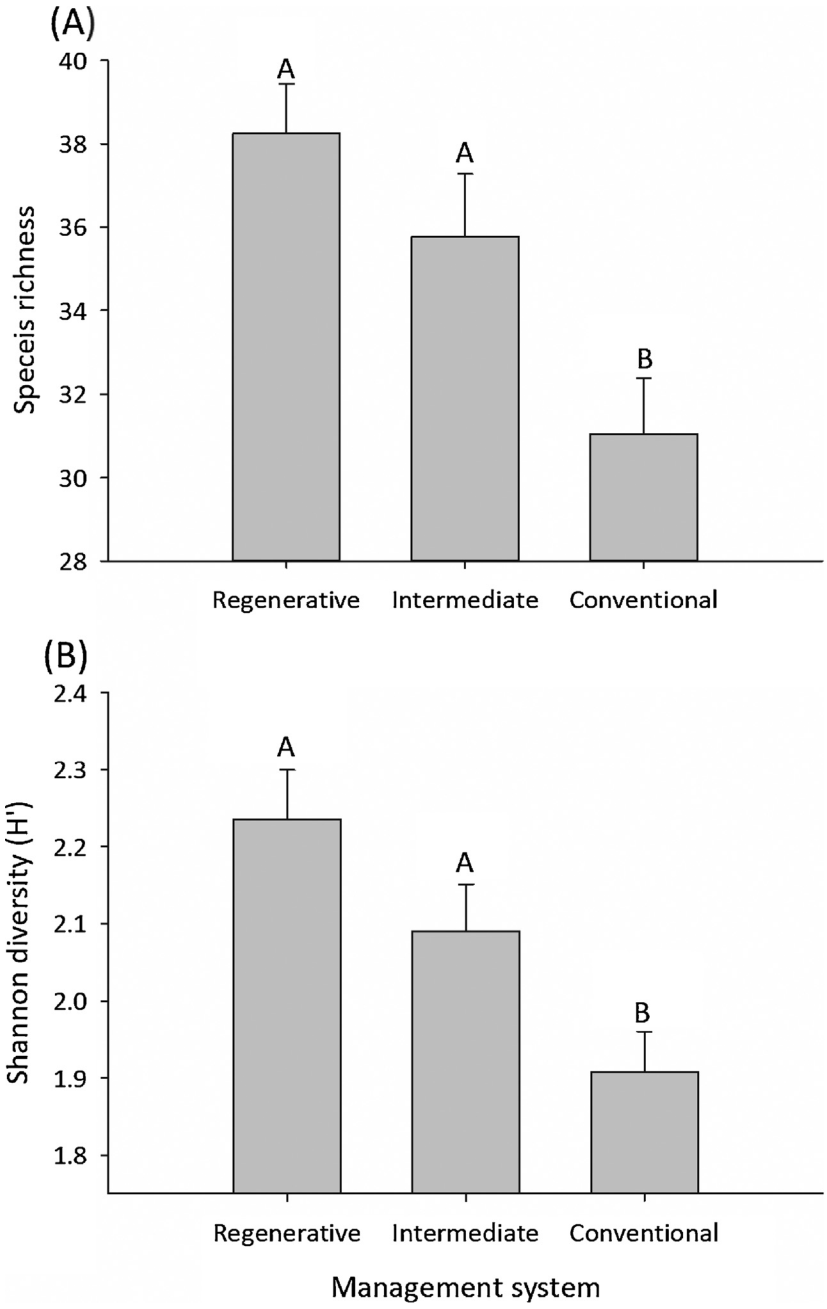

Fig. 1. Species richness and diversity of dung arthropod communities in eastern South Dakota ranches (n = 16) under different management practices. Species richness (A) and diversity (B) were averaged (mean ± SEM) across dung pats sampled from May to September for three management systems: regenerative (frequent rotation, high stocking density, low/no ivermectin use), intermediate (moderate rotation, medium stocking density, low ivermectin use), and conventional (continuous grazing, low stocking density, multiple ivermectin applications). A different letter over the bar indicates significantly different community characteristic between pasture qualities ($\alpha = 0.05$).

arthropod community structure in conventionally managed ranches may limit the ability of the community to provide ecosystem services (Hooper et al. 2005; Wagg, Bender, Widmer, & van der Heijden 2014; Manning, Slade, Beynon, & Lewis 2016; Verdu et al. 2015). Dung beetles are a major driver of community diversity and function, and their abundance was significantly reduced in conventionally managed systems. Two inter-related differences in these management systems may have driven community patterns: grazing intensity and ivermectin use.

Our study revealed a diverse community of arthropods in cattle dung that changes seasonally. In total, 172 unique morphospecies were found in dung from this area of the Northern Great Plains (Supplementary Appendix A). This species richness was comparable to other studies of dung communities, where 108–275 species have been recovered (Cervenka &

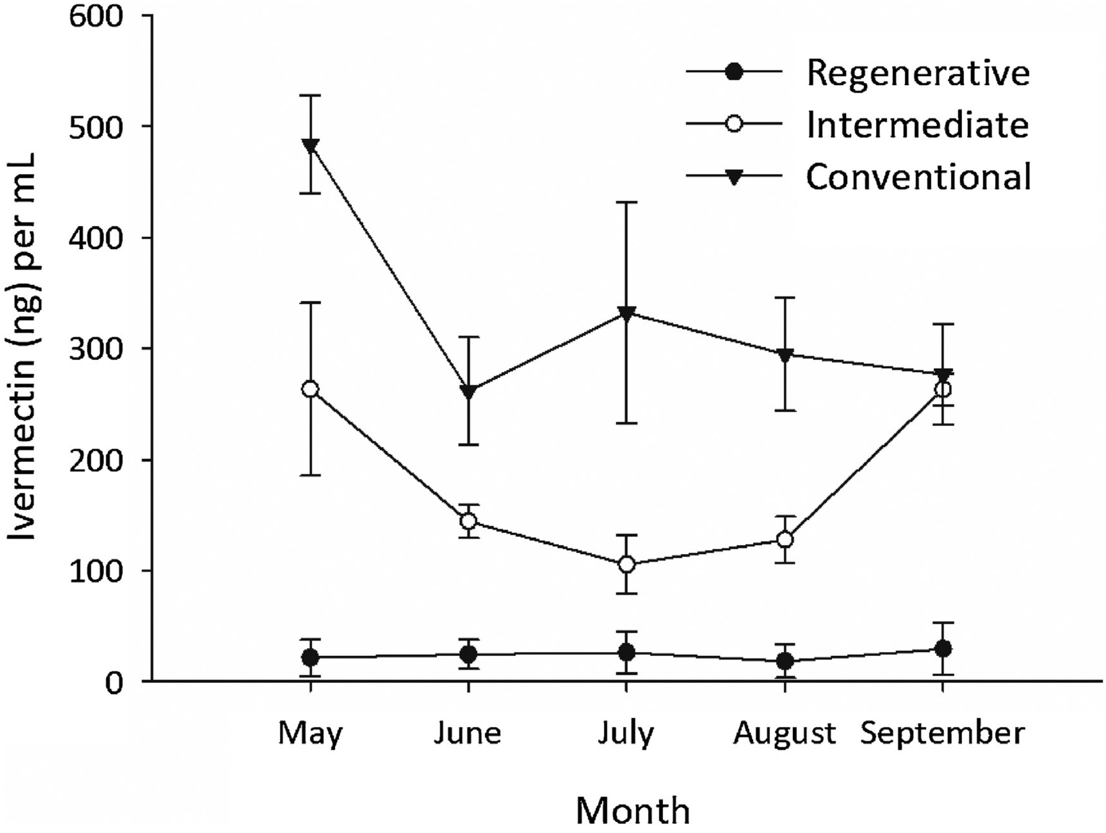

Fig. 2. Ivermectin found in 2- to 5-day-old dung pats (mean ± SEM) sampled over the season (2015–2016) from differently managed pastures: regenerative (frequent rotation, high stocking density, low/no ivermectin use), intermediate (moderate rotation, medium stocking density, low ivermectin use), and conventional (continuous grazing, low stocking density, multiple ivermectin applications). Ivermectin concentrations were measured using ELISA.

Moon 1991; Skidmore 1991). Arthropod abundance and species richness were lowest in May with all following months containing significantly higher values but not distinguishable from one another. This lag time in community growth may be because, with conventional management, dung pats, in May have the highest ivermectin residues. There was little observed change in abundance metrics across the months sampled but the composition of communities changed throughout the season. For example, overall dung beetle abundance was not significantly different over the summer but diversity varied substantially over the season. Even within the genus *Aphodius*, we found distinct seasonal shifts in which species dominated the community of dung pats which allow this complex community to persist on a single, discrete resource (Hanski & Koskela 1977; Hanski 1980). Dung may support such a diverse community because of the rapid renewal of the primary resource. Even though dung represents an attractive resource, not all the 172 morphospecies found in the dung pat system are coprophagous. There were many predator, herbivore, and parasitoid species found that all respond to the dung resource for reasons other than simply feeding on the pat itself. Even within coprophagous arthropods, species partition the dung resource based on moisture content, fiber content, and particle size of the dung (Holter & Scholtz 2007; Tixier, Lumaret, & Sullivan 2015; Holter 2016). The different reproductive and overwintering strategies among species further contribute to when dung taxa dominate the community (Gittings & Giller 1997). All of this is to say that multiple factors influence the species observed in a single snapshot of the dung community, and ultimately may contribute to the function of this important group of insects.

The cattle grazing practices of stocking density and rotation frequency may affect dung arthropods in several ways. First, changes in forage diversity, quantity, and quality affect the relative nutrition/composition of dung pats (Van Vuuren & Meijs 1987). Grazing patterns alter resources available to cattle within a pasture, and rotational grazing leads to more homogenous grazing and less bare ground within the pasture over a 4 y period (Jacobo, Rodriguez, Bartoloni, & Deregibus 2006). In addition to changing the diversity and biomass of forage, plants from pastures that are grazed intensively and then allowed to rest are higher in calcium, magnesium and crude protein (Walton et al. 1981; Earl & Jones 1996; Barnes et al. 2008; Teague et al. 2013). These changes in nutrition of the forage affect dung pat composition, and can lead to a more attractive resource for dung beetles and other dung arthropods (Holter & Scholtz 2007). Another explanation that may have driven the greater arthropod abundance and diversity in regenerative systems is the relative concentration of dung within

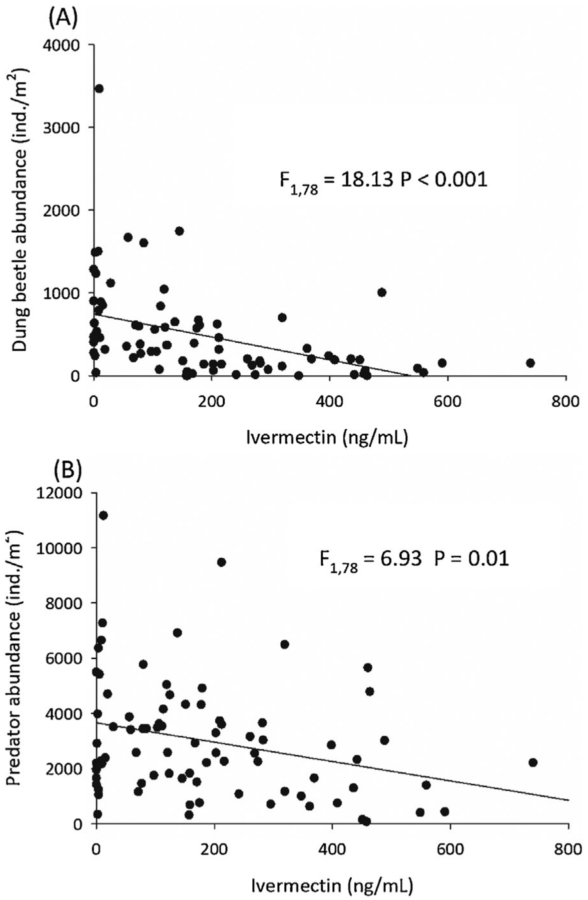

Fig. 3. Correlation between the abundance of different dung arthropod functional groups and the amount of ivermectin found in dung. Abundance of dung beetles (A) and predators (B) found in dung pats across ranches (n = 16) in 2015–2016 was run in a linear regression to observe the correlation to the amount of ivermectin (ng per mL of dung). There was a significant and negative correlation between both functional groups and ivermectin ($\alpha = 0.05$).

a pasture. High stocking density produces a concentration of dung resources that may have been relatively more attractive to dung arthropods (Finn & Gittings 2003; Dormont, Epinat, & Lumaret 2004). High stocking density also likely increases trampling that might alter the physical characteristics of the dung, perhaps affecting its accessibility to a greater number of dung arthropod species (Merritt & Anderson 1977; Strong, 1992). Some or all of these factors likely influenced the dung as a resource in the regenerative and conventional systems.

One of the factors associated with the regenerative pasture management is reduced reliance on ivermectin in the system. Ivermectins are designed to control arthropod pests, however, this efficacy comes with risks to non-target species (Wall & Strong 1987; Strong 1992; Verdu et al. 2015). Each site had dung ivermectin residues quantified throughout the season and higher quantities were found in systems that administered ivermectins more frequently (Fig. 2). Risk assessments on ivermectin's toxicity to dung beetles have shown that ivermectin levels present in dung are toxic to larvae of the dung beetles *Aphodius constans* (LC_{50}: 470–780 ng per g of dung), *A. fimetarius* (LC_{50}: 540 ng per g) and *Volinus distinctus* (LC_{50}: 500–620 ng per g) (Errouissi, Alvinerie, Galtier, Kerboeuf, & Lumaret 2001; Hempel et al. 2006; Lumaret et al. 2007; Römbke et al. 2010). Sub-lethal effects, such as extended larval development or decreased larval size, occur at even lower levels (O'hea, Kirwan, Gillard, & Finn 2010). Values for the lowest observed effect concentration (NOEC) to dung beetle larvae range from 38 to 310 ng per g of dung (Errouissi et al. 2001; Hempel et al. 2006). These affected communities have reduced ecological function within treated pastures; dung pats often degrade more slowly, sometimes taking years when ivermectins are heavily applied to livestock (Wall & Strong 1987; Madsen et al. 1990; Strong 1992; Herd 1995; Dadour, Cook, & Neesam 1999; Floate, Colwell, & Fox, 2002 Römbke et al. 2010). Ivermectin levels of 780 ng per g (dry weight dung) and higher were found to significantly slow the decomposition rate of dung pats. Ivermectin levels collected from conventionally managed ranches were often within the range where lethal or sub-lethal effects could be experienced by dung beetle larvae (Hempel et al. 2006; Römbke et al. 2010). The toxicity of avermectin, coupled with its insect-repellent properties, can disrupt community structure (Floate 2007; Webb, Beaumont, NAger, & McCracken 2010). The loss of structure and complexity within an arthropod community can lead to a failure to provide ecosystem services of dung degradation and pest suppression (Pecenka & Lundgren 2018).

We hypothesize that dung beetle community characteristics partially drove the relative abundances of other dung taxa in these different management systems. In systems with the most conventionally managed pastures and highest ivermectin use, there were 66% fewer dung beetles than in regenerative pastures. This lower abundance not only represents a decrease of an important coprophagous group, but dung beetles' multifunctionality and role as keystone species means that fewer numbers may have knock-on effects on the remaining arthropod community (Verdu et al. 2018). Dung beetles facilitate dung pat degradation and pest suppression (Fincher, 1981; Lee & Wall 2006; Losey & Vaughan 2006). Dung beetles are early colonizers to dung pats, and their large body allows them to make tunnels and aerate pats; these tunnels then facilitate colonization by other species (Sanders & Dobson 1966). Dung beetles, along with other coprophagous arthropods, directly compete with cattle parasites and pests for the dung resource (Doube 1990; Ridsdill-Smith & Edwards 2011). Dung pats with a network of beetle-formed tunnels open pathways whereby predators can infiltrate the pats; these perforated pats produce fewer pest maggots (Valiela 1969a,b). In conventional systems both predators and dung beetles were significantly fewer compared to the regenerative systems (Fig. 3). If a management system reduces dung beetles, then the ecosystem services that they provide could be reduced as well, furthering a reliance on chemical products that come at an ecological and economic cost to the rancher.

By implementing regenerative practices that approximate the conditions under which plant, insect, and ruminant communities evolved, a rancher can provide a food source and habitat for thousands of arthropods that increase the profitability and natural resource base of a ranching operation. Improved management has been shown to reverse the causal mechanisms of degradation by decreasing bare ground, increasing water infiltration rates, enhancing soil carbon, enhancing soil fertility, increasing soil and ecosystem community biodiversity, and restoring the dominance of the most productive plant species. These functions are all strongly linked to shifts in soil microbial and biological community composition, carbon and nitrogen cycling. In addition to soil microbes, key organisms such as dung beetles and earthworms have a strong influence on ecological function and farm management can be adjusted to optimize the benefits they provide (Herrick & Lal 1995; Richardson & Richardson 2000; Wardle & Bardgett 2004; Blouin et al. 2013).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.baae.2019.07.006.

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