

DUNG BEETLES, IVERMECTIN, AND SOIL FERTILITY: A RANGELAND STUDY

by

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ABSTRACT

Dung beetles provide essential ecosystem services in rangelands by recycling Nitrogen, Phosphorus, Potassium, Sulfur, and Organic Matter from cattle dung pats back into the soil. However, the use of macrocyclic lactones, like ivermectin, may hinder dung beetles from performing this ecosystem service. This study evaluated the specific impact of ivermectin-treated dung on local populations of dung beetles and resulting soil fertility. To test this, three dung treatments were established from cattle dung that was either left untreated and contained no ivermectin residues or from dung that was manually treated with ivermectin to achieve one of two residue levels, 0.4 (low) and 4.0 (high) ppm. A randomized complete block design with four treatments was established at two sites in northcentral Montana in June 2024 or 2025, where eight-inch dung pats were manually formed from untreated, low-residue, and high-residue dung and placed in the corresponding research cells. A fourth ‘empty’ treatment was established by leaving certain cells without a dung pat to measure the soil changes in the absence of dung. I found that dung beetles transferred more ($p<0.05$) nutrients from untreated and low-residue pats than from high-residue pats, which did not differ ($p>0.05$) from empty cells. With the onset of a drought in the second year of the study, I hypothesized that the lack of dung beetle effects in 2025 are due to drought conditions. This oxidation relationship resulted in no statistical differences ($p>0.05$) among treatments in the second year of the study for phosphorus and sulfur. Yet, for nitrogen and potassium, analyses indicated that greater ($p<0.05$) transfer occurred in the control and low compared to the high and empty treatments. Levels of organic matter did not differ ($p>0.05$) among treatments in either year of the study. These results show that while dung beetle ecosystem services remain a primary driver of rangeland ecosystems, the presence of ivermectin needs to be monitored within a proposed management plan to help benefit cattle ranchers and the environment.

CHAPTER ONE

LITERATURE REVIEW

Introduction

In the US, there are approximately 86.7 million head of cattle (NASS, 2003) with each cow excreting approximately 10 dung pats (hereafter ‘pats’) a day (Heinrichs, 2023), much of which is incorporated by dung beetles into the soil profile (Nadir Ali Shah, 2022). Dung beetles greatly benefit agriculture by burying and recycling dung underground (Byk & Piętka, 2018; Owen, 2006) and by consuming dung, up to 175–530% of their body weight each day (Floate, 2011), which leads timely pat degradation and improved soil fertility and water holding capacity (Nadir Ali Shah, 2022).

Dung beetles provide ecosystem services by accelerating the decomposition of cattle pats, which can reduce pests. There are over 300 other species of invertebrates that use pat resources to varying degrees (Floate, 2023), including dung beetles and several livestock pests such as horn fly (Funasaki, 1988) and face fly (Moon, Loomis, & Anderson, 1980). Dung beetles use pats as reproductive resources which disrupts pat ecology by reducing moisture content through tunneling (Stebnicka, 2001), thereby reducing pest fly survivorship (Holter, 2007), which also places dung beetles as biological control agents. Dung beetle activity also improves the rate of pat degradation, which minimizes pat smother, the amount of time land under pats lies idle, and without vegetative growth. Without timely pat degradation, grasses and plants are smothered and killed while livestock avoid grazing around pats to minimize exposure to diseases and parasites,

all of which decrease forage availability (Weeda, 1967) by up to 0.2 m² per animal per day (Floate, 2011). It is widely recognized that dung beetles promote plant growth and increase the available biomass for grazing in areas that otherwise would have been avoided by degrading these pats (Nichols et al., 2008).

The introduction of parasiticides, such as ivermectin (IVM), a popular macrocyclic lactone commonly used in livestock production, has affected dung beetle ecology (Verdú et al., 2018). Once IVM is administered to an animal, it is only partially metabolized, with a portion excreted in varying concentrations in dung; depending on the delivery method, dosage, and diet of the animal (Céline M. Laffont, 2003). Evidence suggests that IVM residue in pats disrupts dung beetle assemblages, pat degradation rates, and soil nutrient cycling, along with functional beetle activity that is necessary to process dung ecologically (Verdú et al., 2018). For example, when a pat with an IVM concentration of at least 0.3 mg/kg of dung (fresh weight) is ingested by dung beetles, it causes a decrease in adult beetle olfactory and locomotor functions, limiting their ability to find, ingest, and reproduce in additional pats (Verdú et al., 2015) and in turn decreasing rates of pat degradation. It is estimated that timely pat degradation yields \$2 billion in added value through improved forage production, increased soil nitrogen, and biological control of livestock pests (John E. Losey 2006). Marked up for inflation, this would represent \$3.24 billion in 2026.

Dung Beetle Ecology

Dung beetles are among the most important insects in biological pest control and soil fertilization (Nichols et al., 2008). They are comprised of functional guilds, including rollers, dwellers, and

tunnelers (Bornemissza, 1976) where each guild has its own mechanism for pat degradation and incorporation into the soil (Bornemissza, 1976; Doube, 1990).

Dung beetles also provide ecosystem services by removing and recycling animal dung beneath the soil surface (Anderson, Merritt, & Loomis, 1984), which can be defined as the ground surface area once covered by pats. In agricultural systems, dung beetles are highly efficient at breaking down and removing cow pats from the surface by feeding on the liquid pat contents and use the remaining pat for brood housing and provisions for their young (Halffter & Edmonds, 1982). This then helps improve soil aeration and water-holding capacity (Macquen & Beirne, 1975)

Three functional guilds of dung beetles are prevalent in Montana: rollers, tunnelers, and dwellers. Dwellers live in the cow pat (Floate, 2011) and create burrows to build nests and hatch young (Bornemissza, 1976; Christensen, 1976). Tunnelers burrow into the soil, approximately 5–5 cm directly beneath the pat, where they place dung balls that serve as egg deposition sites and larval provisions after egg hatch (Simmonds, 1929). Rollers are similar to tunnelers in that they excavate dirt burrows to place provisionary dung, but, instead of digging burrows below the pat, rollers dig burrows some distance away from the source dung pat and then ‘roll’ dung balls to the burrow for burial (Simmons, 2011). Rollers are larger than both dwellers and tunnelers as they need to roll dung significantly larger than themselves to place it into their predetermined hole (Hanski, 1991a). Rollers and dwellers mostly scatter the pat, while tunnelers cause less pat destruction (Doube, 2014).

A primary ecological role of dung beetles is to recycle nutrients such as nitrogen (N), phosphorus (P), and potassium (K), and sulfur (S) back into the soil, thereby activating microorganisms involved in nutrient cycling and stimulating plant growth (Yamada et al., 2007). Phosphorus and K can be lost to runoff when left on the soil surface; however, dung beetle activity incorporates these dung nutrients back into the soil and helps safeguard against field-level loss (Gillard, 1967; Nichols et al., 2008). Further research investigating dung beetles' ecological role in rangeland ecosystems will continue to emphasize their importance and provide information on the economic and ecological benefits they provide to working landscapes.

Pat Degradation

As cattle consume forage and uptake its nutrients, they leave behind dung, in the form of pats, and urine (Haynes & Williams, 1993; Wu & Sun, 2010). The degradation of these pats is highly relevant to nutrient cycling and aids in plant growth. When pats remain undegraded and on the soil surface, it leads to pasture fouling and smothering (Floate, 2011) of the plant growth within the area (Holter, 2007; MacLusky, 1960; Pecenka & Lundgren, 2018). When cattle excrete dung onto the soil surface, the failure of the pat to break down can pose challenges for the underlying grass to grow and produce on grazing rangelands (Fincher, 1981). When dung beetles have adequate feed material, it is buried and shows an increase in both dry matter yields and nitrogen content of the herbage as well, thus leading to improved rangeland productivity quantified by above-ground biomass and nutrient uptake of plants (Bang et al., 2005). These findings suggest that a healthy beetle population can improve rangelands while removing pats from the soil surface. However, when cattle are administered Ivermectin, a portion of the dose is lost into the feces, where it is shown to have an insecticidal effect on the dung beetle populations (Barth et

al., 1993). Because of this veterinary drug's nontarget effects on dung beetles, the rate of pat degradation is dramatically affected (Adler et al., 2016).

Pat degradation occurs primarily by dung beetles and microbial populations. Initially, dung beetles dig within the pat, making holes that allow colonization by beneficial microbes, which in turn accelerates bacterial growth and degradation (Breymeyer, Jakubczyk, & Olechowicz, 1975) and ultimately improves soil aeration and water-holding capacity through incorporation of the pat into the soil (Macquen & Beirne, 1975).

Incorporating dung into rangeland soils increases AUM's (Animal Unit Months) by bioturbation, which is the displacement and movement of sediment particles, and in this case, is moving soil from underground to the surface during beetle excavation (Mittal, 1993). This results in capturing essential nutrients for the surrounding forage plants. Bioturbation improves soil aeration, which also increases water infiltration, improving plant growth and helping protect against mudslides and floods (Nichols et al., 2008).

Overview of Macrocylic Lactones

Macrocylic lactones are a class of antiparasitic drugs that are used to control endo- (internal) and ecto- (external) parasites in livestock (Lifschitz et al., 2024). Macrocylic lactones are divided into two families: avermectins and milbemycins. Avermectins include the drugs ivermectin, doramectin, eprinomectin, and abamectin (Vardanyan & Hruby, 2016). Milbemycins include moxidectin and milbemycin oxime. All macrocylic lactones bind to the nerve and muscle cells of invertebrates, hindering neurotransmission and reproduction (Lifschitz et al., 2024), resulting in parasite death. Avermectins have a slightly different structural basis than

milbemycins, which can influence their efficacy against specific parasites (Shoop, Mrozik, & Fisher, 1995). Milbemycins are often considered to have a better safety profile, particularly for non-target species and sensitive animals. The administration methods for both families are the same: topical pour-on, injectable, or oral drench (Darrington & Grussing, 2021).

Effects of Ivermectin

IVM residue in cattle dung is associated with slower pat degradation rates due to how it affects the presence of insects and their sensitivity to the environment (Wall & Strong, 1987). Research suggests that IVM in dung can cause paralysis and death to dung beetles, as is evidenced by research conducted on *Scarabaeus cicatricosus*, (Verdú et al., 2015). When *S. cicatricosus* consumed dung with IVM residue, a dose-dependent response was documented, indicating that concentrations of 0.3 mg/kg will cause sensory and locomotor disorders, while higher concentrations ranging from 0.001mg/kg to 0.2 mg/kg dung (fresh weight) result in ataxia and death more quickly over time as concentration increases. Therefore, it is hypothesized that IVM can disrupt the dung degradation process by dung beetles and prevent them from performing their key ecological functions by altering their physiological and behavioral effects (Verdú et al., 2018).

Along with the mortality rates of dung beetles, research indicates that IVM also decreases the muscle force of certain dung beetle species (*Scarabaeus cicatricosus*). Spontaneous isometric muscle contraction recordings of an IVM-free control and dung beetles treated with an application of IVM in dung showed a significant decrease in the control vs. treatment groups based on spontaneous muscle control force tests (Verdú et al., 2015). Because of this, the average

muscle force and the peak muscle force are affected, suggesting that IVM can alter the locomotory function of dung beetles in the field. This research provides insight into the toxicity of IVM to dung beetle species and into the potential consequences of its administration. Highlighting the importance of considering the broader ecological implications of pesticide use is a starting point for finding new management practices.

Routine treatment with macrocyclic lactones, like IVM, can negatively affect plant pasture heterogeneity, diversity, and ecosystem function (Wall & Beynon, 2012). This is due, in part, to how macrocyclic lactones affect adult dung beetle reproduction, foraging, olfactory, and locomotor capacities, resulting in negative downstream effects on beetle populations and ecosystem services (Ambrožová et al., 2021). Other studies have also suggested that IVM causes relocation of dung beetle communities and decreased total beetle abundance on ivermectin-treated sites (Sands & Wall, 2018). Newly emerged *Copris hispanus* beetles had a 90% mortality rate in dung dropped by calves administered a 200 µg/kg dose of IVM just two to three days prior to beetle exposure (Wardhaugh & Rodriguez-Menendez, 1988). These studies reinforce the concept that IVM negatively affects dung beetle populations and the ecosystem functions they provide.

Larvae

The development and survival of dung beetle larvae is a critical step to performing their numerous ecosystem services when hatched as an adult, and exposure to IVM and other macrocyclic lactones can have hindering effects on this process. A study completed by (Mackenzie et al., 2022) investigated if larvae of three dung beetle species (*Onthophagus*

binodis, *Onitis viridulus*, *Sisyphus rubrus*) would pupate after exposure to a macrocyclic lactone. The study proceeded with equal numbered groups of larvae being introduced to either pats treated with the macrocyclic lactone Abamectin or to untreated pats. The larvae of each of the species were assessed for growth over time, and age in days was recorded. Throughout the experiment, all larvae, regardless of the species, reported higher mortality from treated pats at 1, 7, and 14 d post-exposure (Mackenzie et al., 2022). These results indicate that larvae that feed on treated pats express higher mortality in the early stages of development.

Another study investigated larval response on brood balls that were made with treated IVM pats at 0.01, 1.0, and 100mg/kg of wet dung. Researchers recorded that as larvae fed on the IVM-contaminated provisions, their feeding rate slowed which led to either death or protracted juvenile development (Cruz Rosales et al., 2012). Without the necessary development through instars, dung beetle larvae express a decreased probability of development to adulthood and overall survival. Supporting research (O’Hea et al., 2010) also indicates that larvae reared on untreated dung balls had an 80% greater chance of developing beyond instar III. On the contrary, the probability of larvae reared on dung balls treated with IVM (0.2 mg of IVM/kg) dropped to 15%. As IVM concentrations increase, so do the negative effects on the development and survival of the larvae.

Fecundity

Dung beetle populations grow slowly compared to other insects as they exhibit naturally low fecundity in the field (South Dakota State University Extension, 2025). This, in turn, can have a

downstream effects by reducing the ability of dung beetles to colonize pats, which leads to reduced ecological services within cattle-grazed rangelands (Nichols et al., 2008). Different concentrations of parasiticides in dung can have varying effects on reproduction and larval development (Rodríguez-Vivas et al., 2020). For example, Martinez et al. found that at 10 µg IVM, the beetles were unaffected, yet when increased to 31.6 µg IVM/kg fresh dung weight, both female fecundity and larval emergence were negatively impacted, along with a 30% decrease in brood ball production (Martínez et al., 2017). Because of a decline in breeding females and total species egg production, larvae numbers would be reduced, potentially leading to a reduction in overall fecundity, thus suggesting a time-specific cascading effect could take place, leading to continual population decline.

IVM effects on soil nutrients and health

Soil nutrients are a key factor that affects rangeland and farmland health. The availability of nutrients, such as N, P, K, and S is imperative to soil fertility. Dung beetle activity helps improve earthworm populations, soil water retention, and , and carbon sequestration (Doubé, 2008) with one of the biggest ecological roles being recycling plant nutrients (i.e., N, P, K, S) from dung back into the soil. Dung beetles also influence the soil's hydrological properties by increasing soil porosity and water infiltration, while also reducing water runoff from the soil surface (Brown et al., 2010).

With the widespread use of ivermectin, it may have unintended consequences on beneficial dung beetles. Research by (Verdú et al., 2018) suggests that there are significant changes in soil

functionality when IVM is introduced to the soil. Regarding the environmental fate of IVM in soil, (Halley, Jacob, & Lu, 1989) report that IVM has strong sorption with clay loam and silty loam soils. Meaning it is immobile and unlikely to leach deeper into the soil profile. Thus, with the intensification of IVM use on range and pasturelands, the functional diversity of dung beetles, ecosystem resilience, and vegetation diversity may be seriously affected (Verdú et al., 2018). This highlights the need for further research into the persistence of IMV in soils, particularly in the state of Montana, where it is understudied.

Conclusion

This literature displays the profound and direct impact that IVM can have on dung beetle populations and the indirect ecosystem services that they provide. These studies indicate that larvae feeding on macrocyclic-contaminated dung face significant developmental challenges, which ultimately impact their survival rates. Higher concentrations exacerbate these effects, resulting in death in most cases. These disruptions to the dung beetle's natural developmental processes have direct effects on their fecundity as fewer larvae develop into adults, thereby threatening populations.

The non-target effects of IVM go beyond dung beetle populations and their functions, as they affect ecosystems across a broader ecological spectrum. Without the incorporation of pats into the soil, nutrient availability for plant growth is limited and breeding sites for livestock pests (i.e., face fly, horn fly) are left undisturbed. The disruption of ecosystem services, when chemical stressors are introduced, can result in a decline in soil fertility, increased pest pressure, and a

measurable decline in agricultural field productivity. When IVM is introduced, ecosystem services can be altered by reducing beetle activity; thus, pat degradation slows, leading to undecomposed pats and smothering of native rangeland plants that provide forage and cover for livestock and wildlife populations.

Therefore, I present the following hypothesis: I hypothesize that increasing concentrations of Ivermectin in cattle dung will reduce dung beetle activity and subsequently decrease the incorporation of dung-derived nutrients into the underlying soil.

Predictions

1. Soil beneath pats that allow normal dung beetle activity will contain greater concentrations of dung-derived nutrients than soil beneath pats where beetle activity is reduced.
2. Control and low-ivermectin treatments are expected to exhibit similar nutrient concentrations due to continued dung beetle activity, whereas high-ivermectin and empty treatments are expected to show reduced nutrient incorporation due to minimized beetle activity.

CHAPTER TWO

DUNG BEETLE NUTRIENT TRANSFER

Abstract

Dung beetles provide essential ecosystem services in rangelands by recycling nitrogen, phosphorus, potassium, sulfur, and organic matter from cattle dung pats back into the soil. However, the use of macrocyclic lactones, popular veterinarian deworming drugs, may hinder dung beetles from performing this ecosystem service. This study evaluated the specific impact of ivermectin-treated dung on local populations of dung beetles and resulting soil fertility. To test this, three dung treatments were established from cattle dung that was either left untreated and contained no ivermectin residues or from dung that was manually treated with ivermectin to achieve one of two residue levels, 0.4 (low) and 4.0 (high) ppm. A randomized complete block design with four treatments was established at two sites in northcentral Montana in June 2024 or 2025, where eight-inch dung pats were manually formed from untreated, low-residue, and high-residue dung and placed in the corresponding research cells. A fourth ‘empty’ treatment was established by leaving certain cells without a dung pat to measure the soil changes in the absence of dung. I found that dung beetles transferred more ($p < 0.05$) nutrients from untreated and low-residue pats than from high-residue pats, which did not differ ($p > 0.05$) from empty cells. With the onset of a drought in the second year of the study, I hypothesized that dry soils would mask the effects of dung beetles because certain nutrients would not undergo oxidation and would therefore accumulate in the soil in non-plant available forms that standard soil tests do not detect. This oxidation relationship resulted in no statistical differences ($p > 0.05$) among treatments in the second year of the study for phosphorus and sulfur. Yet, for nitrogen and potassium, analyses indicated that greater ($p < 0.05$) transfer occurred in the control and low compared to the high and empty treatments. Levels of organic matter did not differ ($p > 0.05$) among treatments in either year of the study. These results show that while dung beetle ecosystem services remain a primary driver of rangeland ecosystems, the presence of Ivermectin needs to be monitored within a proposed management plan to help benefit cattle ranchers and the environment.

Introduction

In the US, there are approximately 86.7 million head of cattle (NASS, 2003), which drop on average 10 dung pats (hereafter ‘pats’) per day per cow (Heinrichs, 2023), resulting in approximately 867 million pats daily. (NASS, 2003). The efficient incorporation of this animal byproduct into the soil profile is driven primarily by dung beetles, a bioindicator species that aids in soil fertility and water retention (Brown et al., 2010). Dung beetles provide ecosystem services by burying the dung underneath the soil surface and by consuming dung at rates 175% – 530% greater than their body weight (Floate, 2011). Categorized into functional guilds, rollers, dwellers, and tunnellers, each group employs a different technique to break down these pats and incorporate them into the soil profile (Doubé, 1990).

Dung beetle activity can also result in pest fly population management by manipulating pats and destroying fly habitat, thus improving both ecological and economic gains to cattle operations (Mendes & Linhares, 2002) while helping clear land surface areas, thus promoting plant growth, which in turn benefits livestock operations (Nichols et al., 2008) and wildlife populations (Kie & Thomas, 1988)

However, with the widespread use of parasiticides in Montana, such as ivermectin (hereafter ‘IVM’), can disrupt the ecosystem services that dung beetles provide. Post administration to cattle, IVM is partially metabolized, with a remainder excreted in dung in varying concentrations, which is primarily based on administration method (i.e., injection and pour on) and volume of dose (Verdú et al., 2015). Research suggests that pats with IVM concentrations

can disrupt dung beetle assemblages and impair their ability to transfer nutrients into the soil (Verdú et al., 2018).

While the general impacts of IVM on dung beetles have been documented, the result of subsequent nutrient transfer from the dung pat into the soil is under-researched. If IVM can disrupt dung beetle behavior and survival, then their ability to transfer nutrients into the soil should be disrupted as well. I hypothesize that increasing concentrations of IVM in cattle dung will reduce dung beetle activity and subsequently decrease the incorporation of dung-derived nutrients into the underlying soil.

Materials and Methods

Study Site

This research area was located in the Brown Glaciated Plains south of Malta, MT (48.09619, -107.81876), in rolling terrain at ~700m. The dominant vegetation is comprised of western wheatgrass (*Pascopyrum smithii*), needle and thread grass (*Hesperostipa comata*), threadleaf sedge (*Carex filifolia*), little bluestem (*Schizachyrium scoparium*), and blue grama (*Bouteloua gracilis*) (NRCS, 2025). Daily temperatures in the summer months range between 9 °C and 28.7 °C, with an annual precipitation average of 304 mm (Washington State University, 2025).

Commercial agriculture is the dominant land use in dryland farming or livestock grazing, with all pastures being ungrazed during this study.

Experiments were placed on two private ranches. Ranch “F” is located 20 miles south of Malta, MT (48.09619, -107.81876; altitude 2,291 ft), and ranch “B” is 27 miles SE of Malta, MT

(48.02013, -107.55011; altitude 2,392) (Figure 1).

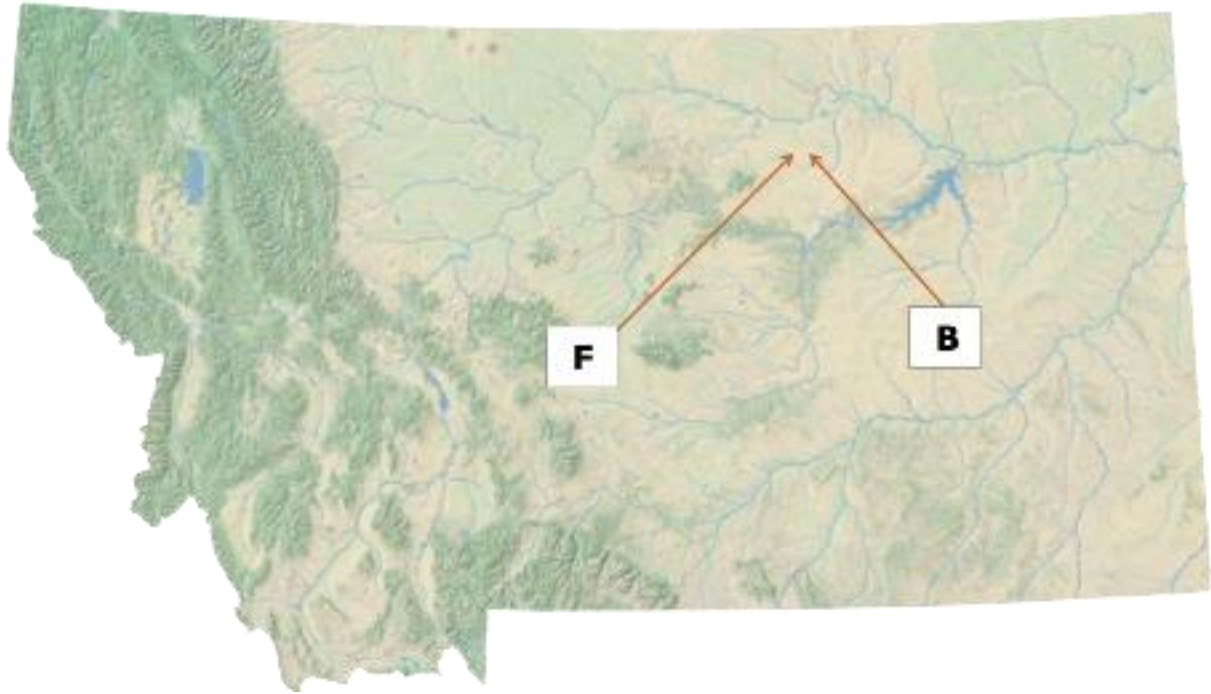


Figure 1. Location of F and B study sites in Phillips County, Montana.

Experimental Design

Cattle dung used in this study was collected from the Montana State University herd, which was maintained anthelmintic and insecticide-free for 9 months before initiation of this study (Kellan Marlow, personal comm.). Fresh dung was collected in pastures and placed into 5-gallon buckets with sealable lids and frozen at -20 C. When a sufficient quantity was collected, all dung was thawed and uniformly homogenized using a paint mixer (Husky Tools, Bristol, TN) and a cordless drill (Dewalt INC, Towson, MD) to create consistent dung to use in experimental treatments. Following homogenization, dung was weighed, placed into a treatment-specific shallow plastic wading pools (Summer Escape, Hong Kong, China), and dosed with either a low rate (0.04 mg/kg IVM per fresh weight dung) or a high rate (4.0 mg/kg IVM per fresh weight

dung). The high-rate treatment was derived from the expected residual IVM levels found in the dung of a 1,200 lb. cow dosed at the label rate. The low-rate treatment was subsequently established as a 100-fold dilution of the high-rate treatment. Treated dung was again manually homogenized using treatment-specific paint mixers to ensure even IVM distribution. Dung was then placed back into treatment-specific buckets and re-frozen to ensure chemical stability and olfactory attractiveness to dung beetles (Bezanson, Dovell, & Floate, 2021). Dung was then transported to the research sites where artificial pats were arranged in a randomized complete block with pat as the experimental unit. Randomization was achieved by assigning each treatment a number (1 = untreated control, 2 = low rate, 3 = high rate, 4 = empty), which was entered into a random number generator (Table 1). Empty cells were defined as having no pat placed on the site. Artificial pat was formed using treatment-specific eight-inch cake pans (Nordick Ware, Minneapolis, MN). Hand-constructed cages, made from inverted tomato cages wrapped in metal-stranded poultry netting (Mazel and Co., Chicago, IL), were placed over the top of each pat to prevent other wildlife (i.e., birds) from interfering with the beetles and pats during the study time period.

2	1	4	3	1
3	4	1	2	2
1	2	3	4	3
4	3	2	1	4
Block 1	Block 2	Block 3	Block 4	Block 5

Table 1. Randomized complete block design of the treatments at ranch F.

4	1	3	2	1
3	2	1	4	2
1	4	2	3	3
2	3	4	1	4
Block 1	Block 2	Block 3	Block 4	Block 5

Table 2. Randomized complete block design of the treatments at ranch B.

Soil Sampling.

All pats at both sites were left exposed for 30 days, after which each pat was turned over to expose the soil so that dung beetle tunnel holes could be counted as documentation of adult

survivorship and tunneling activity. The soil surface, below each pat and in empty cells, was cleared of all debris (fecal and vegetative) to remove any materials that would artificially bias soil nutrient samples. Soil cores ($n = 2$) were taken using a 1-1/8 in. diameter soil probe, where each core was painstakingly separated into one-inch incremental categories by depth down to six inches (i.e., 0–1, 1–2, 2–3, 3–4, 4–5, 5–6 inches).

Once collected, soils were immediately cooled with ice packs to stop microbial respiration and preserve sample integrity, transported to Montana State University campus in Bozeman, and placed into a forced air-drying oven at (87.7 °F, 4.6% humidity) for 48 hours. After drying, samples were placed into plastic-lined soil sample bags (Agvise Laboratory, Northwood, ND) and shipped for testing (Agvise Laboratories, Northwood, ND). Testing comprised of Nitrate-N (Gelderman & Beegle, 2015), sulfate-S (Franzen, 2015), P (Frank et al., 2015), SOM (Combs & Nathan, 1998), and K (Warncke & Brown, 1998). It should also be noted that due to the low amounts of soil per bag (~30g), some samples could not be tested, resulting in missing values.

Statistical Analyses

Data were assessed for both Site X Treatment and Site X Year interactions using the PROC GLM procedures of SAS v. 9.4 (SAS Institute 2023) to assess if soil nutrient data could be combined across both sites and years of study. Data were then subjected to an unbalanced analysis using the PROC GLIMMIX procedures of SAS v. 9.4 (SAS Institute, 2023) with pat as the random effect with 12 observations per pat to account for assessing nutrient treatment differences.

Response variables were defined as soil parameters nitrogen (N), phosphorus (P), potassium (K),

sulfur (S), and soil organic matter (SOM), Treatment, Year, and Treatment means were separated using Fisher's Least Significant Difference (LSD).

Results

Statistical Results and Justification

Soil nutrients did not differ ($p > 0.05$) among treatments below the two-inch soil sampling depth, only data from zero to two-inch sampling depths are presented. To increase statistical power, data from zero to one and from one to two-inch depths were combined for analyses.

Site X Treatment interactions did not differ for N ($F = 2.35$; $df = 3, 77$; $p = 0.08$), P ($F = 1.37$; $df = 3, 74$; $p = 0.26$), K ($F = 0.74$; $df = 3, 72$; $p = 0.53$), S ($F = 1.27$; $df = 3, 77$; $p = 0.29$), or SOM ($F = 0.68$; $df = 3, 70$; $p = 0.57$), therefore data were pooled across sites for analyses. Year X Site interactions did not differ for N ($F = .08$; $df = 1, 157$; $p = 0.30$), K ($F = 0.39$; $df = 1, 149$; $p = 0.53$), and SOM ($F = 0.11$; $df = 1, 142$; $p = 0.74$); therefore, the data were also pooled across study year. However, Year X Site nutrient interactions were significant for P ($F = 3.89$, $df = 1, 154$, $p = 0.05$) and S ($F = 12.01$, $df = 1, 157$; $p < 0.01$), so these data are analyzed and presented by study year.

Regarding nitrogen, when combined across year and site, the control and low treatments did not differ, nor did the high and empty treatments; however, control and low differed from high and empty (Figure 2) ($F = 12.91$, $df = 3, 150$, $p < 0.01$). Full model parameters and Least Squares Means for Nitrogen are displayed in Table A1. Potassium analyses mirrored nitrogen in that the control and low treatments did not differ, high and empty did not differ; yet control and low

differed from high and empty (Figure 3) ($F = 14.73$, $df = 3,142$, $p < 0.01$). Full model parameters and Least Squares Means for Potassium are displayed in Table A2. With SOM, treatments did not differ (Figure 4) ($F = 0.41$, $df = 3,135$, $p = 0.75$). Full model parameters and Least Squares Means for SOM are displayed in Table A3. Phosphorus analyses, combined across sites but separated by year, during 2024, indicate that control and low treatments did not differ, nor did the high and empty treatments; however, control and low differed from high and empty treatments (Figure 5) ($F = 8.81$, $df = 3,67$, $p < 0.01$). In 2025, P treatments did not differ ($F = 1.19$, $df = 3,72$, $p = 0.32$). Full model parameters and Least Squares Means for Phosphorus are displayed in Table A4 and Table A5. In 2024, S control and low did not differ, and high and empty did not differ, yet control and low differed from high and empty (Figure 6). ($F = 3.19$, $df = 3,70$, $p = 0.02$). In 2025, S treatments did not differ ($F = 1.34$, $df = 3,72$, $p = 0.27$). Full model parameters and Least Squares Means for S are displayed in Table A6 (2024) and Table A7 (2025).

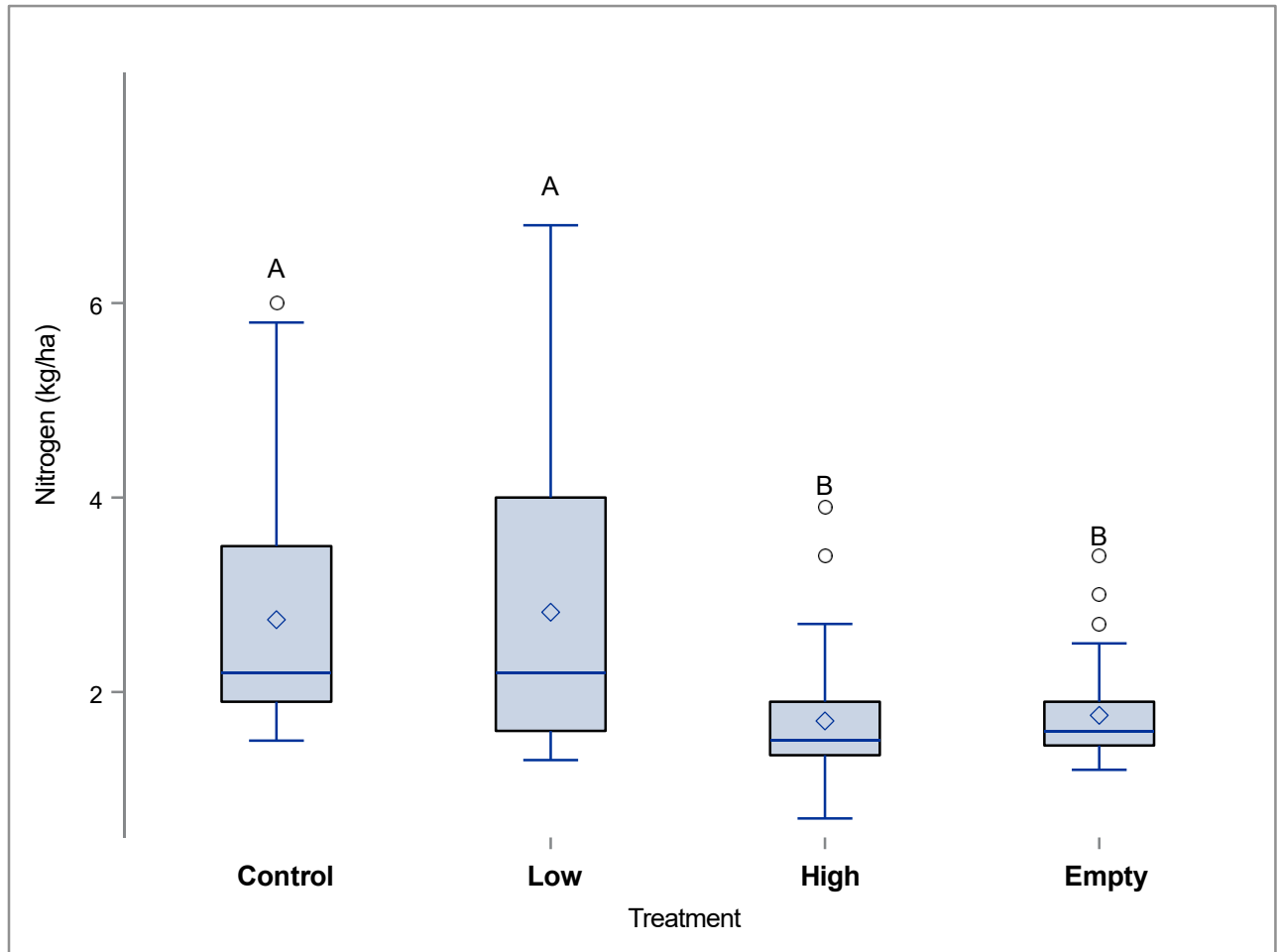


Figure 2: Box plots of nitrogen (kg/ha) combined across sites and years.

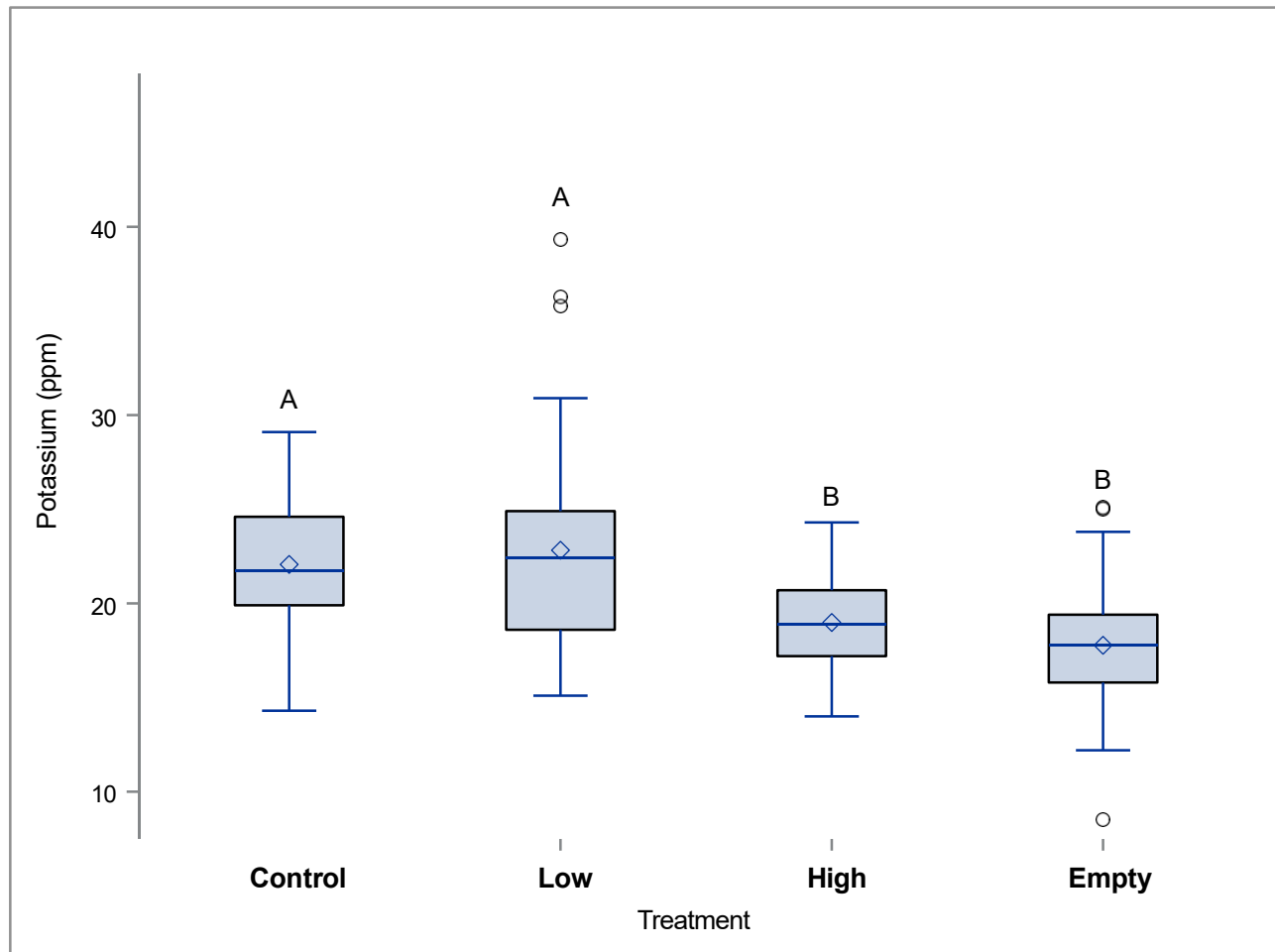


Figure 3: Box plots of potassium (ppm) combined across sites and years.

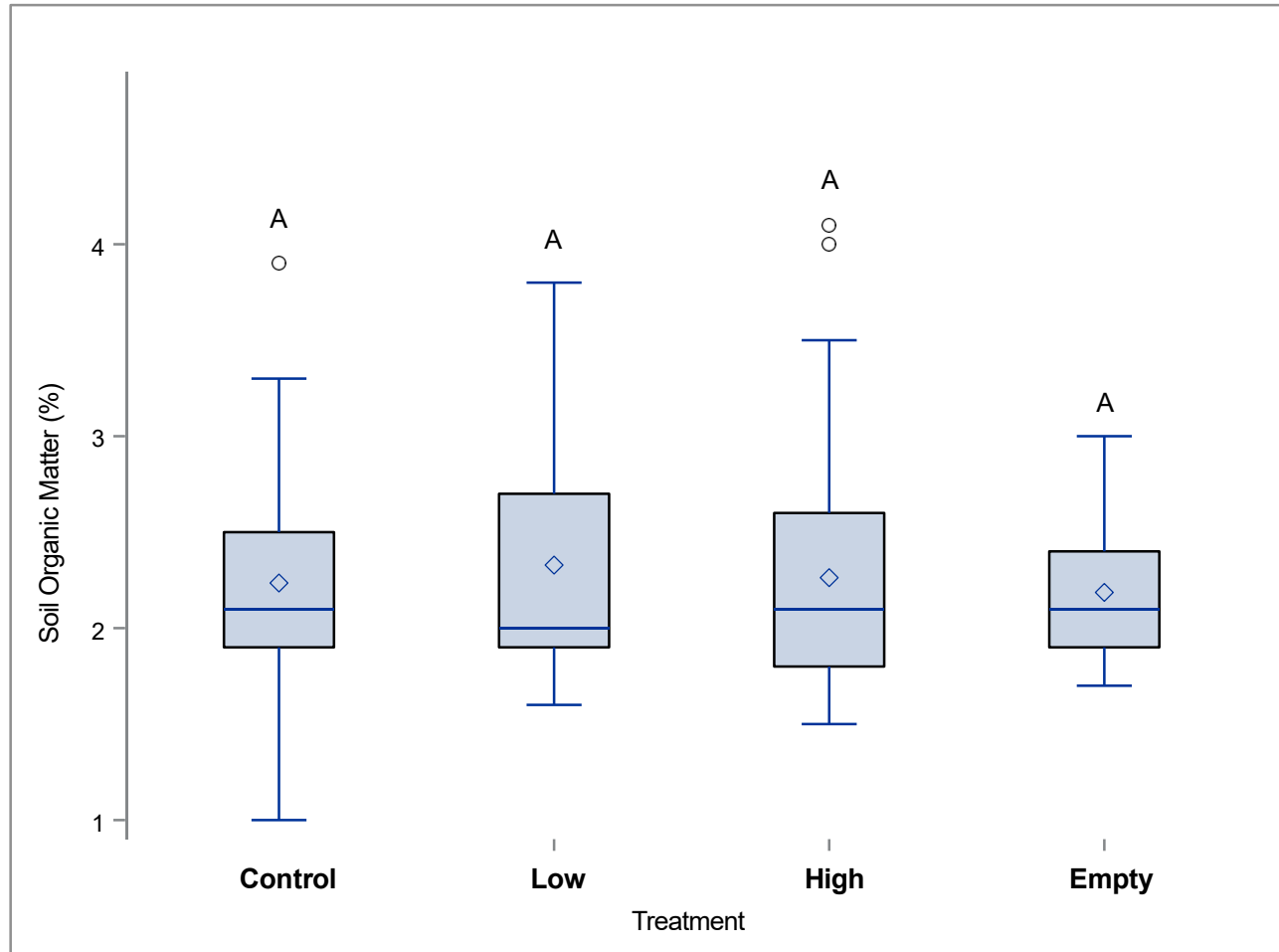


Figure 4: Box plots of SOM (%) across sites and years.

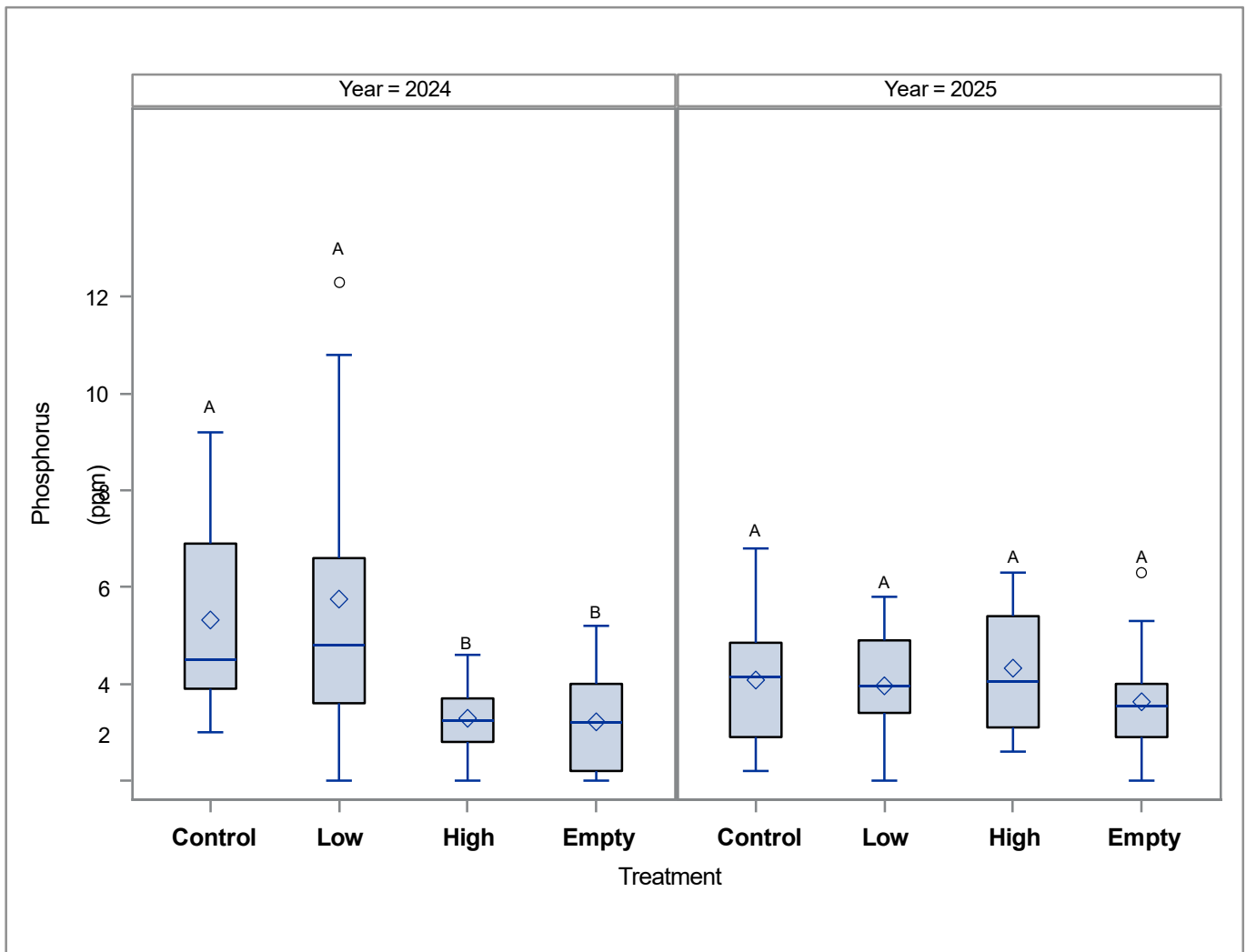


Figure 5: Box plots of phosphorus (ppm) combined across sites and separated by year.

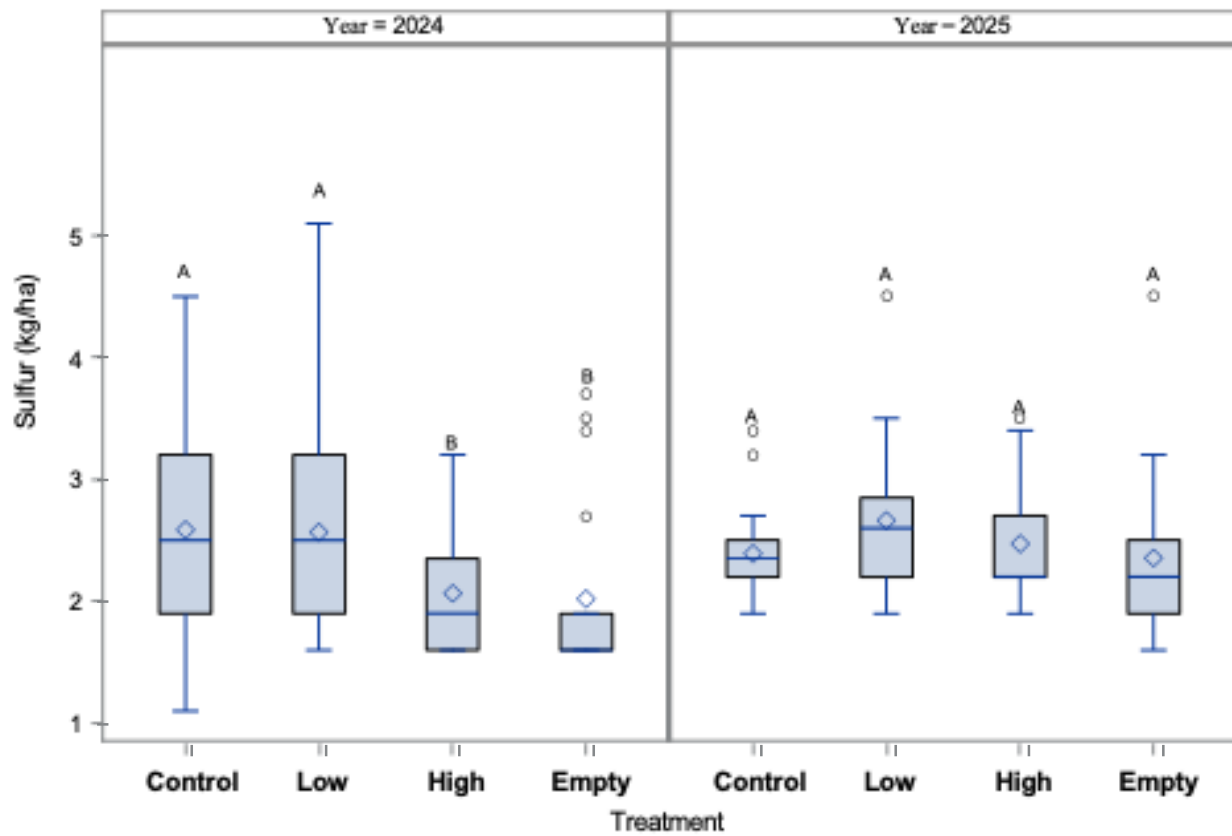


Figure 6: Box plots of sulfur (kg/ha) combined across sites and separated by year.

Discussion

The impact of IVM residue on soil nutrient dynamics was altered by treatment differences in 2024, but not in 2025. In 2024, and across sites and years, all soil nutrients were separated by IVM residue level, where control and low treatments were similar, and high and empty treatments were also similar and comparatively lower; however, in 2025, no treatment effects were recorded for P, and S. SOM did not change over the one-month sampling period in either year. These results indicate that dung beetles do, in fact, transfer significant amounts of nutrients from pats to the soil, certain nutrients are more influenced by drought, and that organic matter is a difficult metric to change in the short term. As I will explain in greater detail below, I suggest dung beetles did, in fact, move significant amounts of P and S during 2025; however, these were not reflected in my soil analyses because tests only measure plant availability of nutrients, which is highly influenced by soil moisture, which led to the lack of detectable beetle effects as a result of 2025 drought.

Nitrogen

Results of site and year combined data indicate there was no difference in soil N between low and control and between high and empty, but that lower N levels were detected in the soil under high residue pats and in empty cells. Thus, suggesting that at my sites, dung beetles exposed to 0.04 ppm IVM can still move the same amount of dung when compared to beetles that colonized

the untreated, no IVM, pats. My results also suggest that the high rate of 4.0 ppm disrupts their ability to move nutrients into the soil, negating any ecosystem service benefits.

The process of ammonification, where organic N is converted to plant-available ammonium (NH_4) in the pat, is a microbial process that starts in the intestines of cattle and continues inside the pat after it is dropped from the animal (Petersen, 1992). Additionally, the process of nitrification, where ammonium is converted to plant-available nitrate (NO_3), is also a microbe-driven process that is happening both at the pat-soil interface and in the tunnels beneath the pat where wet dung is being brought down (Kazuhira et al., 1991). This is further enhanced by the beetle's ability to increase aeration in the soil underneath the pats, creating a micro-environment for nitrification. These processes result in up to 25% of N in dung being classified as immediately plant available within the first few hours after deposition (Gary M. Pierzynski, J. Thomas Sims, & Vance, 2005), suggesting that my soil sampling captured differences in plant available NO_3 below control and low pats compared to high pats and empty cells, as a function of dung beetle activity, or lack of activity, where dung beetles become modifiers of microenvironment conditions enabling dung transport and nitrification.

Interestingly, when soil N is separated by year, I see that during 2024, when soil moisture was near normal, N levels were 60% lower, possibly due to plant uptake combined with downward leaching. Compared to 2025, the cumulative soil N was 2.5X greater. Increasing relative amounts of soil nutrients is common during a drought (Homyak, 2017) because low soil moisture can lead to a buildup of available N in the soil due to decreased plant use (Sujani De Silva, 2025). This primarily suggests that dung beetles are actively performing their ecosystem services during

drought. With the drought preventing plant uptake of N, and the beetles putting N in the soil, this results in elevated concentrations in soil tests.

Potassium

Results for K mirrored N in that there was no difference between control and low and between high and empty; however, levels of K were in high and empty treatments compared to low and control. This indicates that there was less K underneath pats that were treated with a high-rate dose, which was similar to empty cells with no pat on the soil surface. This suggests that, similar to N, K movement from dung beetle tunneling is inhibited when beetles are exposed to high-dose IVM. As dung beetles recycle nutrients, potassium exists as the K^+ ion, which is already plant available without the need for microbial oxidation in the soil (Eckhardt et al., 2018). Because K levels remained detectable regardless of soil moisture, this supports the premise that dung beetles are actively ecosystems services during drought conditions. Interestingly, and as I recorded with N, soil K ppm was 13% higher in 2024 than 2025. This again is likely due to limited plant uptake during 2025 due to drought and subsequent dry soils resulting in a ‘banking’ of soil K. This is supported by the fact that there was a ~15% increase in K level in 2025, compared to 2024.

Phosphorus

During 2024, I observed no difference between control and low, and between high and empty treatment, yet control and low did differ from high and empty. In 2025, I recorded no difference between any treatments. Phosphorus is typically immobile in the soil and only moves from a site via runoff or soil surface erosion. Even though P ppm levels did not differ in 2025, I hypothesize

that the dung beetles still successfully transferred dung; however, this dung still contained P in its organic form, which was not detected in my soil samples. The soil test method used in this study was the Olsen P Test, which tests P in its plant-available inorganic state known as orthophosphate. Without adequate soil moisture, microbes do not mineralize (i.e., convert) organic P into its oxidized plant-available orthophosphate state, which would bypass detection in my soil tests.

Sulfur

Sulfur analyses indicated that during 2024, control and low treatments did not differ nor did high and empty treatments; yet, control and low differed from high and empty. In contrast, during 2025, there was no detectable difference among any treatments. Similar to P, I hypothesize that, due to low soil moisture, there was little if any soil microbial activity and so S remained attached to dung and in its organic state. Unlike N, the majority of S contained in dung is plant-unavailable (Cardelli et al., 2008), and without the moisture-driven process of bacterial oxidation, which converts organic S into plant-available sulfate-S, it remained undetectable in my soil analyses (Turner & Haygarth, 2001).

Soil Organic Matter

Building higher levels of SOM in the soil is inherently difficult due to the slow process of long-term organic inputs. While dung beetles redistribute organic material into the soil, measurable changes in SOM typically require sustained inputs over longer time periods than in my study. With this study being conducted over 2 years, we were not able to detect fluctuations in SOM as measurable changes over our 1-month sampling period, which takes 6–10 years to shift (Smith,

2004). Dung inputs may also affect microbial activity first and before SOM, suggesting that the readily available nutrients in dung favor microbes, which may have limited SOM buildup.

Decoupling of Nutrient Cycling

When dung is dropped from a cattle it is about 80% water, 2.5 to 4% N, 0.7% P, 2.0% K, and 0.1% S by dry weight (R. Marsh, 1970). However, the integration of these nutrients is dependent on dung beetle activity. Along with the need for soil moisture to initiate microbial activity to convert nutrients like P and S into their inorganic plant-available forms (Oldham, 2021; Rishi Prasad, 2019).

Under drought conditions, microbial processing and plant uptake can become disconnected from nutrient inputs, leading to a temporary accumulation of nutrients in the soil (Clain Jones, 2017).

This decoupling may reduce the detectable influence of dung beetle-mediated nutrient redistribution. I hypothesize that the transition from a wet year (2024) to a dry/drought year (2025) has led to a decoupling of nutrient mineralization. This ultimately led to an overshadowing of dung beetle activity in the second year of the study, where the nutrients observed were already present in the soil, not those transferred by dung beetles.

Climate Context

Due to year-to-year weather variability, the climate may have altered P and S dynamics, leading to a measurable decrease in inorganic forms of plant nutrients (i.e., orthophosphates and sulfate) (Zhang, 2020). Drought also decreased soil P microbial biomass, and can inhibit microbial growth, and kill microbial cells. This resulted in large amounts of P being released from the microbial biomass, leading to a reduction of P (Turner & Haygarth, 2001). Dry conditions have

been shown to reduce microbial activity, in turn reducing plant-available sulfate, which is released into oil from SOM (Narayan et al., 2023). Tables 5 and 6 show the monthly rainfall data from the AGRIMET MATM station (48.3733 -107.7764) accessed through the US Pest pest risk modeling platform (Washington State University, 2025), showing that 2024 was drier than 2025. In 2024, soil moisture was above historical averages (Figure 7). Yet, in 2025, soil moisture was below the historical average, resulting in abnormally dry conditions at the time I took soil samples (Figure 8).

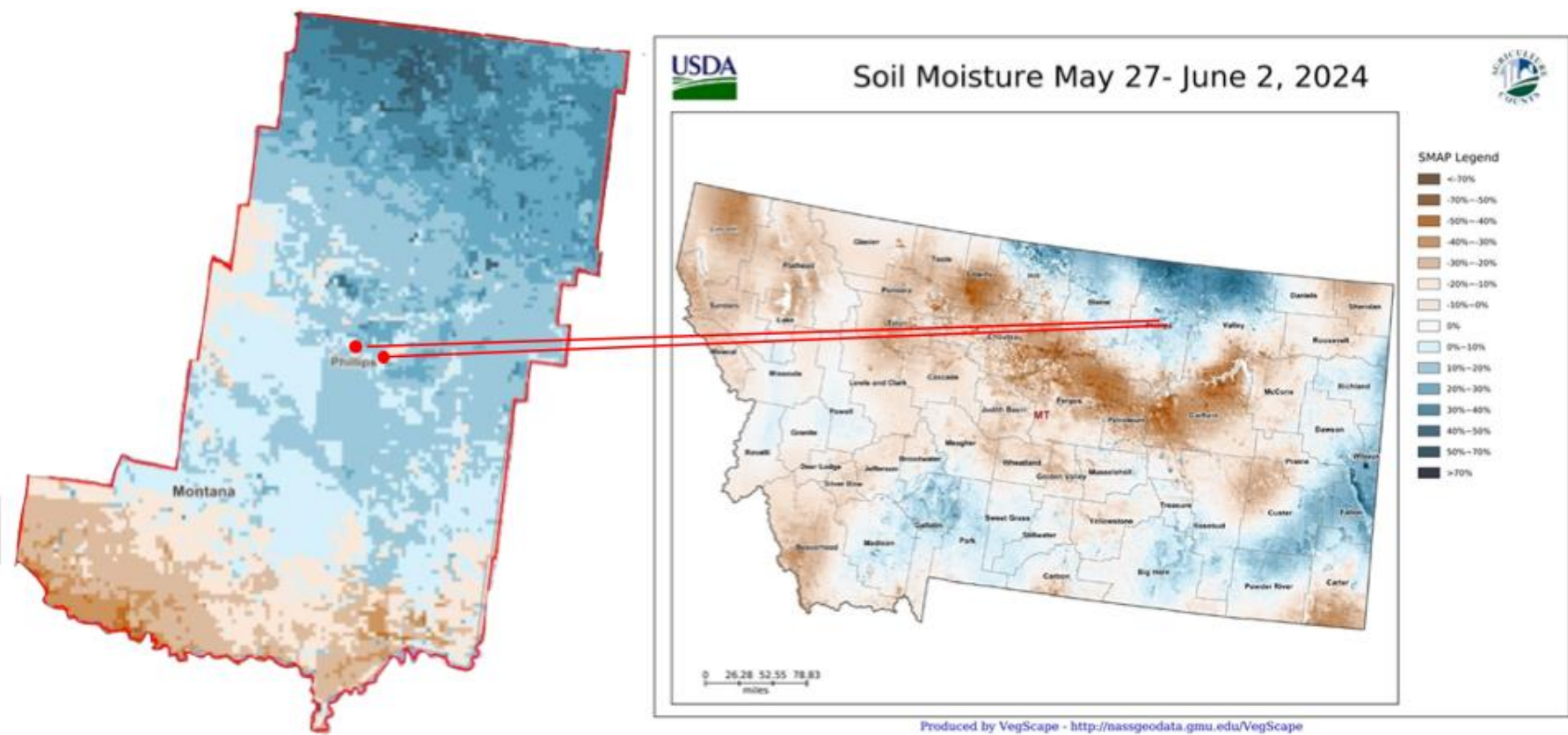


Figure 7: Soil Moisture Anomalies at research sites in Phillips County, Montana, from CropCASMA between May 27 and June 2, 2024.

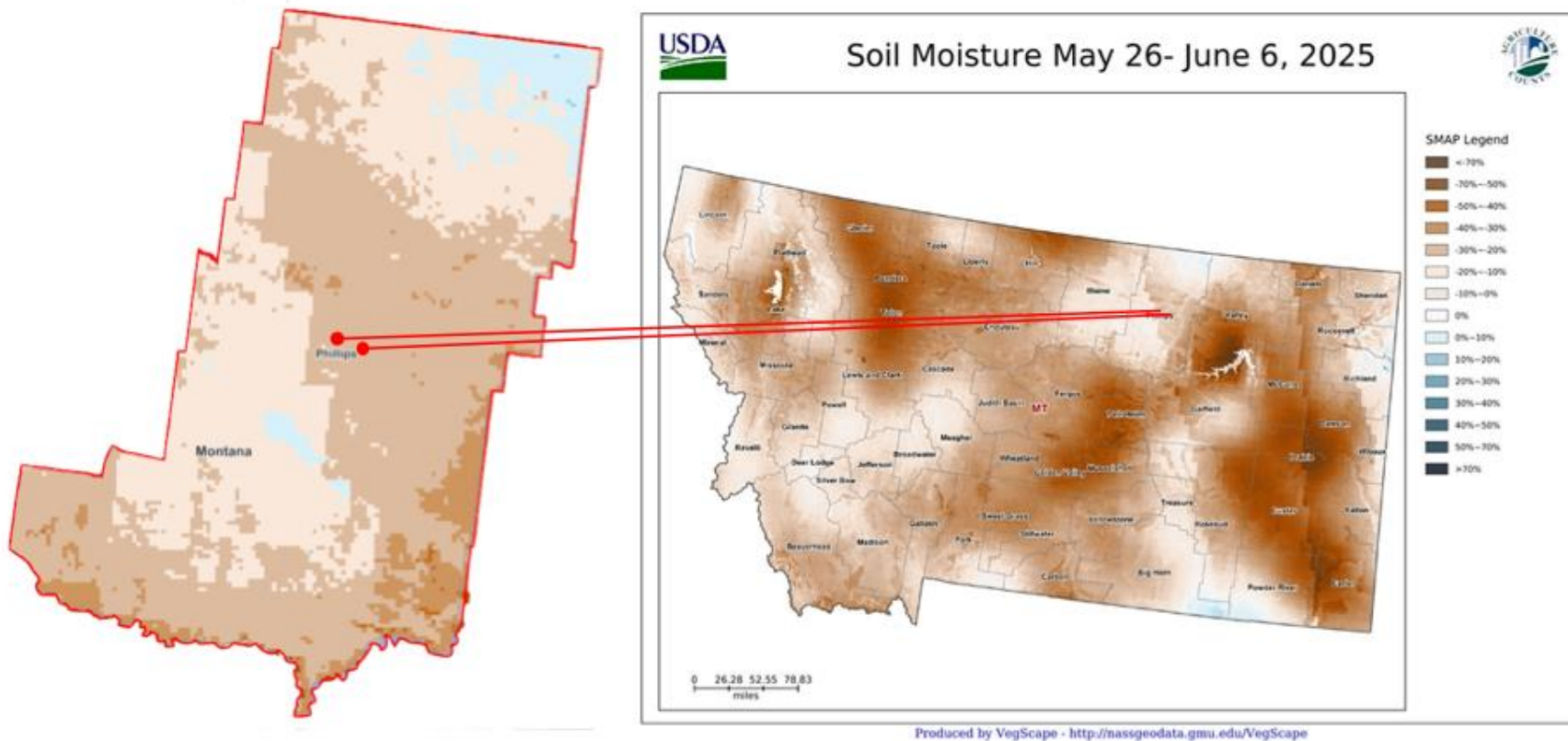


Figure 7: Soil Moisture Anomalies at research sites in Phillips County, Montana, from CropCasma between May 26 and June 6, 2025.

Month	Rainfall (inches) (2024)	Rainfall (inches) (2025)
March	0.49	0.06
April	1.14	0.77
May	2.31	1.43
June	2.51	1.56
July (1–17)	1.36	0.59
TOTAL	7.81	4.41

Table 3: Annual Rainfall from AGRIMET MATM Station in Malta, MT across months in 2024 and 2025.

Ecological Implications

Based on results from the N and K transfer, this suggests that climatic conditions during my study did not strongly influence dung beetles and their nutrient cycling ecosystem service. Dry soils, however, do reduce microbial activity, which may in turn limit the immediate redistribution of nutrients, like P and S, from dung into plant-available pools, resulting in a temporary accumulation in plant-unavailable forms that, in the short term, masks dung beetle nutrient cycling. The nutrients, however, are not lost from the systems, and after a moisture event, soil microbial activity could resume breaking down organic matter, converting macronutrients into plant-available forms (Szejgis et al., 2024). Dung beetle activity creates localized microsites where moisture and aeration conditions differ from bulk soil, allowing nitrification to proceed even under drought conditions, whereas P and S cycling remain constrained by broader soil moisture limitations.

With adult beetles using this dung for reproduction, with residual IVM concentrations, the larvae that are developing in these pats are also exposed to IVM and may be subjected to lethal concentrations. Locomotor and olfactory senses can be impacted in IVM-exposed adults, which can inhibit their overall fitness, but it does not immediately impact adult survival (Verdú et al., 2015). Although we did not directly measure this, dung beetle larvae, being smaller, experience higher rates of mortality with varying levels of macrocyclic lactone exposure (Kadiri, Pérez, & Lumaret, 2018). The resulting larvae being killed by IVM pats can initiate a long-term population decline of dung beetle populations and nutrient cycling (Wall & Strong, 1987).

The presence of IVM residue in pats poses a problem for pasture and rangeland productivity because, without proper decomposition, pats can smother underlying vegetation. Dung dropped by animals like sheep and deer can decompose in 3 to 8 weeks, while dung from cattle can take 12 months to decompose fully from the soil surface. (P. H. Williams, 1995). Dung left on the soil surface for at least 15 days resulted in 75% mortality of grass tillers and rooted nodes, which then causes a reduction in pasture growth and regrowth (B. N. Macdiarmid, 1971). These effects on pasture and rangelands can be reduced with the presence of dung beetles, which break down pats and return nutrients to the soil. With the acceleration of fecal matter breakdown, it can help mitigate the smothering effect that cattle pats have on rangelands. As a result, Animal Unit Months (AUMs), which are a measurement of available forage, can increase as the grazing area expands (Stam, 2018). As a result of faster pat and degradation occurring, the dung buried shows an increase in both dry matter yields and nitrogen content of the herbage. Therefore, there is improved nutrient uptake and an increase in above-ground biomass, which ultimately leads to a more improved rangeland (Bang et al., 2005). This not only has a beneficial impact on grazing livestock, but also on wildlife.

Finally, livestock operations are businesses, and the adoption of new practices is often economically driven. Therefore, it is appropriate to estimate the economic value of nutrient transfer in my study. I used March 2026 fertilizer prices to calculate individual nutrient prices per kg (N = \$0.68, K = \$0.53, P = \$0.97, S = \$0.74). These values were combined with inputs that one cow drops 10 pats per 24 h period, and that each pat is 1 ft² in surface area. Based on the mean (control + low IVM) nutrient (N, P, K, S) increases from my soil's tests, and the inputs

I described above, the monetary value of total plant nutrient cycling is \$17.20 per cow every 30 days.

When calculating the total nutrient cycling value, we used the fertilizer equivalent for all of the nutrients assessed. For N, Urea was used, which is priced at \$688/ton, and at an application rate of 4.22lbs/acre, it equates to \$3.16/acre. For K, we saw a 168ppm increase, which is 336 lbs./acre and was valued using Potash (0–0–60) priced at \$487/ton, totaling \$164.72/acre.

Phosphorus showed a 20.3 ppm increase, and when converted to lbs./acre of MAP P_2O_5 (11–52–0) at \$880/ton, the value was \$78.70/acre. Finally, Sulfur resulted in a 2.4lb/acre increase, with Ammonium Sulfate priced at \$678.08, which is about 28% sulfur; it equates out to \$3.38/acre.

Combined prices per acre are \$249.51 worth of plant available nutrients. Based on an average of 10 pats a day, with each one covering 1ft², one cow will provide 300ft² worth of dung coverage in 30 days. The 300ft² was then divided by the square footage of an acre, 43,560ft², and then multiplied by the dollar amount of all combined nutrients, \$249.51 comes out to \$1.72 for all plant available nutrients. Given that approximately 10% of dung-derived nutrients are immediately available to plants, we divided the \$1.72 by 0.1 to finally get the \$17.20 per cow every 30 days.

This results in sufficient soil fertility to produce a 1.5–2.0 ton per acre rangeland forage crop. To fully maximize rangeland productivity, management strategies should be used that balance parasite control with the preservation of ecosystem services provided by dung beetles. While anthelmintic drugs such as Ivermectin are a vital tool in many ranching systems, their residues can impair the functionality of dung beetles (Verdú et al., 2018). Accordingly, I recommend that

IVM be administered to cattle to coincide with dung beetle dormancy. Ivermectin residues in cattle drop to ‘low’ levels 30 days post administration (Heinrich, 2024). Dosing cattle 30 days before March 1, which is approximately the end of winter dormancy and the start of spring emergence, or after November 30, approximately the start of beetle winter dormancy, ensures that adult dung beetle exposure to IVM is minimized, their ecosystem services are maximized, and IVM remains a useful tool for livestock producers to manage herd parasites.

Future work should focus on measuring the quantity of nutrients over a growing season based on soil type and moisture content, while measuring the impact on plant growth. By monitoring nutrient levels and plant growth over the course of a growing season, researchers can better understand how soil texture and moisture play a role in soil fertility and rangeland health.

Conclusion

The results of this study highlight the ecosystem services provided by dung beetles and the decoupling effects of soil nutrients in low soil moisture environments. Within these soils, nutrients were banked with the onset of dry/drought conditions, and pools of N, P, K, and S accumulated in the soil due to minimal nutrient uptake and leaching. In my study, dung beetle ecosystem services were not shown in 2025, likely due to drought; however, dung beetles’ role in the ecosystem remains imperative. By breaking down pats on rangelands, dung beetles increase the amount of available forage while also increasing the grazable land that cattle would have avoided (B. N. Macdiarmid, 1971). To help preserve dung beetles’ ecosystem services, a management plan with anthelmintic drugs is recommended. By timing IVM treatment to

coincide with beetle dormancy, with a 30+ day window before beetle emergence (Heinrich, 2024), producers can manage herd health while also promoting dung beetle activity to improve soil health and grazing areas within fields. Prioritizing the seasonal health of dung beetles ensures that when moisture is present or returns to rangelands, nutrients can then be transferred into the soil, ensuring productivity and preservation of rangeland ecosystems.

CHAPTER THREE

DISTRIBUTION OF DUNG BEETLE SPECIES AND FUNCTIONAL GROUPS

Pitfall Traps

Pitfall traps are an effective and commonly used method for collecting arthropods in the field (Hohbein & Conway, 2018). Pitfall traps consist of two Solo® brand cups, 10 cm in diameter, placed one inside the other and placed flush with the soil surface. The traps were baited with 100 g of fresh cow dung collected from the Montana State University cow herd that was not treated with any deworming drug. Each trap was partially filled with propylene glycol to kill and preserve any collected samples. Squares were cut from a gridded wire fence to go over the top of the cups, and the 100g of dung was placed on top to suspend it while still allowing samples to fall into the trap. All three sampling locations (Ranch F, O, and B) (Figure 8) contained 12 pitfall traps per location and were checked weekly and occasionally biweekly due to distance and unpredictable weather. Beetles were collected and returned to Montana State University – Bozeman MARSH laboratory, and were identified to the species level.

Trapping started on April 15, 2024, and continued until July 17, 2024. The sample collections were then put into Whirl-Pak bags and returned to the MSU laboratory for processing.



Figure 8: Location of sampling locations F, O, and B, in Phillips County, Montana.

Beetle ID

The tunneller species captured were (b.) (*Onthophagus nuchicornis*), (c.) (*Onthophagus hecate*), and captured rollers were (a.) (*Canthon pilularius*), (d.) (*Canthon praticola*) (Figure 9).

The tunneller community, predominated by (*Onthophagus nuchicornis*), was far more common than other beetle functional groups ($n = 6,140$). Because of this group's ability to transfer nutrients into the early soil horizon, we hypothesize that they are directly responsible for the banked nutrients found in the soil in 2025. While species like (*Canthon pilularius*) made up ~28% of the catch ($n = 2,547$), they disperse the pat horizontally, indicating that nutrient transfer was occurring among the tunneller species.

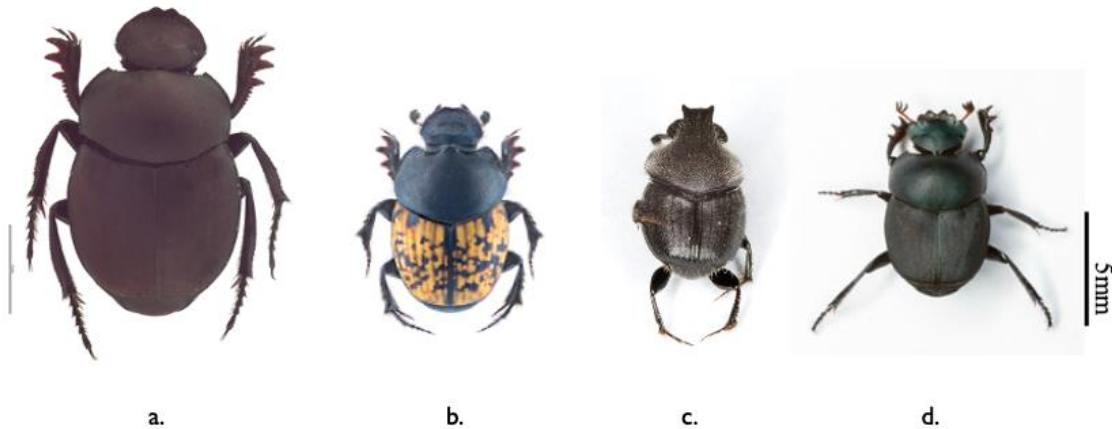


Figure 9: Images of trapped species (a.) *Canthon pilularius*, (b.) *Onthophagus nuchicornis*, (c.) *Onthophagus hecate*, and (d.) *Canthon praticola*.

Onthophagus nuchicornis

Onthophagus nuchicornis is a native of the Palearctic, yet its populations have flourished in North America (Floate & Kadiri, 2013). The tunneller (Paracoprid) guild is very prevalent in the U.S., representing more than 80% of the dung beetle community at latitudes above 44°N (Jones et al., 2019). They create brood balls that are then placed underground to which a single egg will hatch and feed on for the duration of its development (Skidmore, 1991). They are characterized by their 6.5–10mm body size with black and brown elytra (Cornell University, 2024b).

Onthophagus hecate

Unlike *Onthophagus nuchicornis*, *Onthophagus Hecate* is a native North American species whose populations stretch from Florida to southern Canada (Hoebeke & Beucke, 1997).

Onthophagus Hecate is also part of the tunneller (Paracoprid) guild that excavates beneath the pat to bury brood masses in which eggs are laid for provisioning (Arnaudin et al., 2014). It is 5.2–9.5 mm in length with an overhanging horn from the pronotum, and can go through multiple generations in a season based on location (Cornell University, 2024a).

Canthon pilularius

Canthon pilularius, another species that is native to North America, whose populations can be found in the eastern and Northwestern parts of the U.S (Edmonds, 2025). They are part of the roller guild (telecoprid) in which they roll brood balls from the pat to a tunnel or chamber away from the pat, ranging from centimeters to meters away (Halffter & Edmonds, 1982). Similar to the Paracoprid species, these brood balls are where the egg lies and is used as feed as its development continues (Thomas, 2001). These beetles are typically larger, being 10–19mm in length, with an oval shape (Matthews, 1963).

Canthon praticola

Canthon praticola are very similar in appearance to *C. pilularius* but much smaller in size, ranging from 5–8 mm (Edmonds, 2022). They also create and translocate brood balls for nesting purposes for their eggs and can be found from Mexico through to Canada (Robinson, 1948). They have been associated with preferring prairie dogs alongside that of cattle (Gordon RD & OL, 1974)

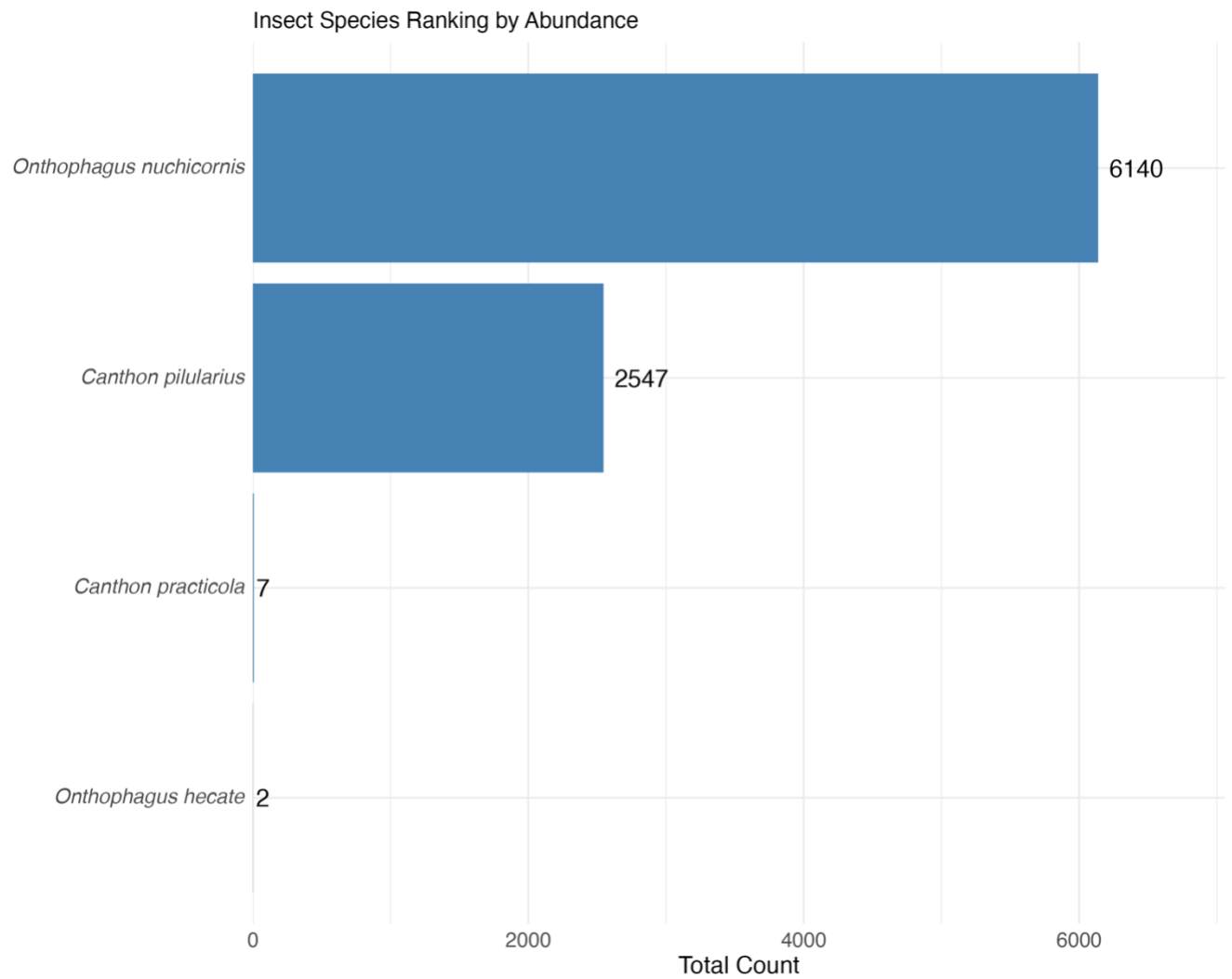


Figure 9: Total count of dung beetles collected from pitfall traps from April 15 to July 17, 2024.

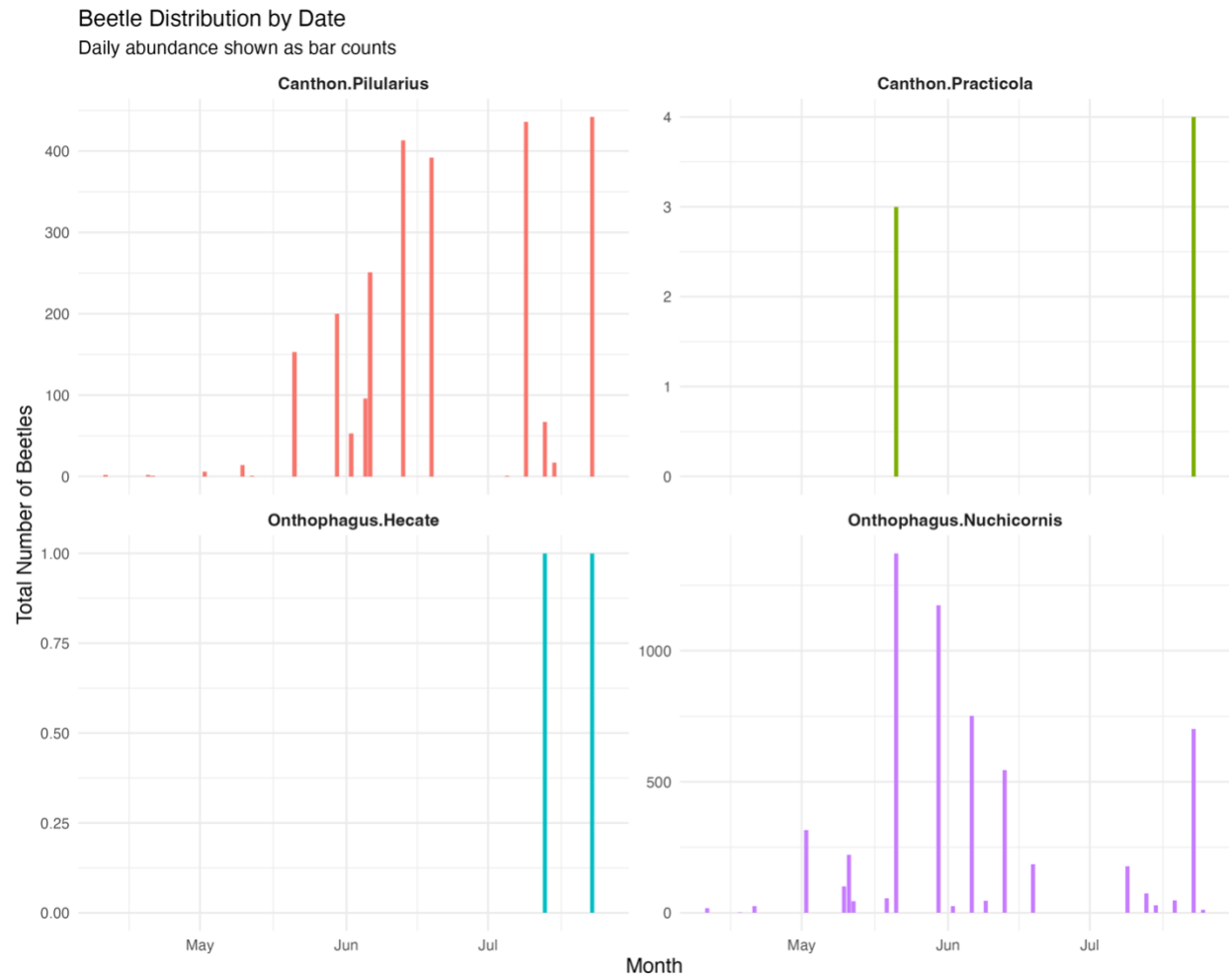


Figure 10: Dung beetle capture rates by sampling date and faceted by species.

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REFERENCES CITED

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APPENDIX

Least Squares Means Tables

Table A1: Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for Nitrogen data combined across two study years (2024, 2025) and two sites (F and B).

Comparison	Estimate	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
		Error							
Control vs. Empty	0.9836	0.2393		150	4.11	<.0001	0.05	0.5108	1.4564
Control vs. High	1.0411	0.2393		150	4.35	<.0001	0.05	0.5683	1.5139
Control vs. Low	-0.07692	0.2408		150	-0.32	0.7498	0.05	-0.5527	0.3989
Empty vs. High	0.05750	0.2378		150	0.24	0.8092	0.05	-0.4123	0.5273
Empty vs. Low	-1.0605	0.2393		150	-4.43	<.0001	0.05	-1.5333	-0.5877
High vs. Low	-1.1180	0.2393		150	-4.67	<.0001	0.05	-1.5908	-0.6452

Table A2: Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for Potassium data combined across two study years (2024, 2025) and two sites (F and B).

Comparison	Estimate	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
		Error							
Control vs. Empty	4.2927	0.8932		142	4.81	<.0001	0.05	2.5271	6.0584
Control vs. High	3.0823	0.8994		142	3.43	0.0008	0.05	1.3043	4.8603
Control vs. Low	-0.7547	0.8815		142	-0.86	0.3934	0.05	-2.4972	0.9879
Empty vs. High	-1.2104	0.9053		142	-1.34	0.1834	0.05	-3.0001	0.5792
Empty vs. Low	-5.0474	0.8875		142	-5.69	<.0001	0.05	-6.8018	-3.2930
High vs. Low	-3.8370	0.8938		142	-4.29	<.0001	0.05	-5.6039	-2.0701

Table A3: Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for SOM data combined across two study years (2024, 2025) and two sites (F and B).

Comparison	Estimate	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
		Error							
Control vs. Empty	0.04902	0.1301		135	0.38	0.7069	0.05	-0.2082	0.3063
Control vs. High	-0.02772	0.1310		135	-0.21	0.8328	0.05	-0.2869	0.2314
Control vs. Low	-0.09344	0.1310		135	-0.71	0.4770	0.05	-0.3526	0.1657
Empty vs. High	-0.07675	0.1319		135	-0.58	0.5617	0.05	-0.3376	0.1841
Empty vs. Low	-0.1425	0.1319		135	-1.08	0.2821	0.05	-0.4033	0.1184
High vs. Low	-0.06571	0.1328		135	-0.49	0.6216	0.05	-0.3284	0.1970

Table A4: : Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for Phosphorus data combined across two study sites (F and B) in 2024.

Comparison	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
	Estimate	Error						
Control vs. Empty	2.1053	0.6304	67	3.34	0.0014	0.05	0.8469	3.3636
Control vs. High	2.0322	0.6391	67	3.18	0.0022	0.05	0.7565	3.3078
Control vs. Low	-0.4316	0.6304	67	-0.68	0.4960	0.05	-1.6899	0.8267
Empty vs. High	-0.07310	0.6391	67	-0.11	0.9093	0.05	-1.3488	1.2026
Empty vs. Low	-2.5368	0.6304	67	-4.02	0.0001	0.05	-3.7952	-1.2785
High vs. Low	-2.4637	0.6391	67	-3.85	0.0003	0.05	-3.7394	-1.1881

Table A5: Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for Phosphorus data combined across two study sites (F and B) in 2025.

Comparison	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
	Estimate	Error						
Control vs. Empty	0.4500	0.3748	72	1.20	0.2339	0.05	-0.2972	1.1972
Control vs. High	-0.2450	0.3748	72	-0.65	0.5154	0.05	-0.9922	0.5022
Control vs. Low	0.1200	0.3748	72	0.32	0.7498	0.05	-0.6272	0.8672
Empty vs. High	-0.6950	0.3748	72	-1.85	0.0678	0.05	-1.4422	0.05221
Empty vs. Low	-0.3300	0.3748	72	-0.88	0.3816	0.05	-1.0772	0.4172
High vs. Low	0.3650	0.3748	72	0.97	0.3334	0.05	-0.3822	1.1122

Table A6: Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for Sulfur data combined across two study sites (F and B) in 2024.

Comparison	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
	Estimate	Error						
Control vs. Empty	0.5642	0.2446	70	2.31	0.0240	0.05	0.07634	1.0521
Control vs. High	0.5192	0.2446	70	2.12	0.0373	0.05	0.03134	1.0071
Control vs. Low	0.01579	0.2477	70	0.06	0.9494	0.05	-0.4783	0.5099
Empty vs. High	-0.04500	0.2415	70	-0.19	0.8527	0.05	-0.5266	0.4366
Empty vs. Low	-0.5484	0.2446	70	-2.24	0.0281	0.05	-1.0363	-0.06055
High vs. Low	-0.5034	0.2446	70	-2.06	0.0433	0.05	-0.9913	-0.01555

Table A7: Treatment comparison estimates, standard errors, t-values, alpha, and lower and upper confidence levels for Sulfur data combined across two study sites (F and B) in 2024.

Comparison	Standard		DF	t Value	Pr > t	Alpha	Lower	Upper
	Estimate	Error						
Control vs. Empty	0.03500	0.1663	72	0.21	0.8339	0.05	-0.2965	0.3665
Control vs. High	-0.08000	0.1663	72	-0.48	0.6319	0.05	-0.4115	0.2515
Control vs. Low	-0.2700	0.1663	72	-1.62	0.1088	0.05	-0.6015	0.06151
Empty vs. High	-0.1150	0.1663	72	-0.69	0.4915	0.05	-0.4465	0.2165
Empty vs. Low	-0.3050	0.1663	72	-1.83	0.0708	0.05	-0.6365	0.02651
High vs. Low	-0.1900	0.1663	72	-1.14	0.2570	0.05	-0.5215	0.1415