

**An Investigation of the Effects of Native and Introduced Grazing on Soil Nitrogen Levels
and Exotic Species Prevalence in the Palouse Prairie of Western Montana**

BIOS 35503: Practicum in Field Biology

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2016

Abstract

The Palouse Prairie grassland is one of the most endangered ecosystems in the United States. Like many other grasslands of North America, primary threats to this particular ecosystem include agricultural conversion of land, invasive species, and the loss of biodiversity, all of which are closely tied to an abiotic soil community. I investigated the similarities and differences between native (*Bison bison*) and introduced (commercial cattle) grazing effects on exotic species prevalence and how this relates to soil nitrogen levels. Three different land types were assessed for this study, at five replicates a land type: bison-grazed land, cattle-grazed land, and ungrazed land. I surveyed forbs and graminoids at each site in addition to taking soil samples. Grazing type was found to have no significant effect on either the amount of total nitrogen present in the soil or on the proportion of introduced to native species present in an area. However, nitrogen content was found to be an important factor in determining exotic species for both bison and cattle-grazed land, with the two land types displaying opposite effects along the same nitrogen gradient: cattle-grazed land increased exotic prevalence with an increasing soil nitrogen gradient, while bison-land decreased exotic prevalence along this same gradient. This study supports the role of the American bison as a keystone herbivore of the Palouse Prairie, and suggests that some sort of competition between native and exotic species is being mediated by herbivory. Further research is needed to dissect this herbivore's key role within this ecosystem and better inform effective land management strategies.

Introduction

In the past century, the western livestock industry has come into prominence in extensive numbers. Due to the minimal capitalization costs following the Civil War, western ranching turned from a small-scale lifestyle into a large-scale business empire. From 1870 to 1900, the

number of beef cattle in the 17 western states skyrocketed 478% to 19.6 million, the number of sheep grew 523% to 25.1 million sheep (U.S. Department of Interior, 2015) and overgrazing became a primary issue for farmers and naturalists alike. Soil erosion emerged as a major problem for the inhabitants of overgrazed areas, causing a profusion of subsequent environmental changes, including but not limited to flooding, drought and the loss of biodiversity (Smith, 1940; Young, 1943). Federal policy, such as the Taylor Grazing Act of 1934 and the Federal Land Policy and Management Act of 1976, have attempted to control the effects of this overgrazing by placing fees on grazing areas and requiring permits for public grazing (U.S., 2015). Though these restrictions did curb the effects of overgrazing noticeably, the topic of grazing in the West remains a hotly contended topic even today (Collins et al., 1998).

The native prairie ecosystem is the largest vegetative province of North America, originally comprising 162 million hectares (Samson and Knopf, 1994); however, surveys have suggested that anywhere up to 99.9% of this native prairie has been either lost or drastically altered since European settlement (Risser, 1988). Invasive plant species have collectively been shown to be one of the greatest threats to biodiversity in the West (USDA Forest Service, 2004) and, furthermore, disturbance of an area has been shown to serve as a conduit for invasive species into an otherwise stable environment (Wein et al, 1992). However, studies have shown mixed results as to whether overgrazing serves as such a form of disturbance, providing an easy route for invasive species into the prairies. While some studies have shown commercial overgrazing to result in a loss of biodiversity of the ecosystem (Lin & Tan, 2007), other studies have shown the grazing of American bison (*Bison bison*)--a keystone herbivore of the plains--to actually increase the stability of biodiversity of an ecosystem (Collins et al., 1998). This

poses the question of whether bison grazing differs fundamentally from agricultural cattle grazing in its effects on the environment.

As for the mechanisms through which exotic species become invasive in an environment, a study by Bennett et al. (2011) enumerated four potential means through which their study organism—the invasive velvetgrass, *Holcus lanatus*—might be dominating coastal prairies: through direct competition, indirect competition mediated by mammalian herbivores, interference competition via allelopathy, and/or indirect competition mediated by changes in the soil community. In particular, certain invasive grasses have been shown to alter the nutrient levels of the soils they invade, to make growing conditions more favorable for themselves over their native counterparts (Perkins et al, 2011). This alteration can come in many different forms, from an alteration of carbon, nitrogen, phosphorous, or other key nutrient levels (Ehrenfeld, 2003) to the actual release of biochemical toxins which can poison the soil, making it impossible for other competing plants to grow in the area (Mangla & Callaway, 2008). However, the potential role of bottoms-up effects--that is, the composition of the soil determining the aboveground community, rather than the reverse--within this community does exist. Therefore, conclusions regarding the top-down mechanisms described above will be evaluated contextually in this study.

Nitrogen serves as one of the primary limitations to plant growth in the Palouse Prairies of the West, alongside moisture (Hunt et al., 1988). For this reason, the alteration of this nutrient could have devastating effects on plants which are naturally found in this ecosystem and are adjusted to low levels of nitrogen. Studies have shown the grazing of large herbivores to affect the cycling of nitrogen in an area (Frank and Groffman, 1998), while other studies have shown various invasive species to both increase (Parker and Schimel, 2010) and decrease (Corbin, J. D.,

& D'Antonio, 2004) nitrogen levels in the soils of areas that they invade. Due to nitrogen's role as a limiting factor in the prairie ecosystem, it serves as a primary target for invasive plants to alter, allowing for their dominance of an invaded area. For this investigation, we analyzed the potential correlation of total soil nitrogen and invasive plants prevalence within the context of grazing. This design allowed us to ultimately assess the potential for top-down effects of herbivory on soil nutrients.

Methods

Study Area

This study was conducted on areas of native Palouse Prairie in Charlo and Ronan, Montana. Palouse Prairie is a grassland ecosystem unique to a small area of the northwest United States, composed primarily of mid-length perennial grasses such as Idaho fescue (*Festuca idahoensis*) and Bluebunch wheatgrass (*Agropyron spicatum*) (Stoddard, 1941). Native Palouse Prairie is one of the most endangered ecosystems in the United States (Noss et al., 1995), making it an important geographic area for studying the mechanisms of habitat and biodiversity loss.

All five bison-grazed sites for this study were located in commonly grazed areas of Montana's National Bison Range, while ungrazed and cattle-grazed sites were located around the area of the National Bison Range, both on the Ninepipe National Wildlife Refuge and on private lands (Table 1). These sites were selected specifically to ensure minimal variability in altitude, proximity to water, anthropogenic disturbance, and spraying.

Data Collection

Five Palouse Prairie sites were selected for each of three different "grazing" categories: bison-grazed, cattle-grazed, and ungrazed within the past five years. Surveys and collections at

these sites were performed from June 22-July 8, 2016. Four scat surveys, each taken within a circle of 5 meter radius, were performed at each site to characterize the relative degree of grazing present at that site. Three subplots were randomly placed at each sites.

Each of the three subplots was 1 meter x 1 meter in size, with a circular subsection of radius 0.2 meter in the top right corner of the plot. The 1 meter x 1 meter area was assessed in its entirety for invasive species of the forb variety, while the 0.2 meter radius section was assessed for graminoid invasive species. All forbs in the 1 meter x 1 meter area and all graminoid species in the 0.2 meter radius plot were collected and identified to species. Each of these identified species was noted as either “native” or “introduced.”

Additionally, a soil sample was collected from each of the three 1 meter x 1 meter subplots at a site using a 40 cm hand probe soil corer, according to the methodology put forth by Dinkins et al. (2010). The samples for the three subplots were pooled by site, and the composite sample for each land type replicate was frozen and stored in a vacuum-sealed plastic freezer bag. A total of 15 total analyses at five per land type were thus collected, and tested at the University of Montana through the Environmental Biogeochemistry Laboratory (Missoula, MT) for total nitrogen content using the combustion method (Rhee, 2001).

Statistical Analysis

The R program was used to run statistical analysis for this study (R Core Team, 2016). We used a one-way ANOVA to first compare land type (ungrazed/cattle-grazed/bison-grazed) to the average number of invasive species found in the three subplots on that land. Invasive species were run as an arcsine transformed proportion of the total species present within the plot, in order to standardize plots. A second one-way ANOVA compared land type to the nitrogen

content of the composite soil sample for that site. Finally, an ANCOVA was run on soil nitrogen content vs. invasive species prevalence for each land type to determine whether there exists any relationship between these two factors.

Results

No significant difference was found to exist among the number of invasive species as a proportion of total species found at any of the three site types ($p = 0.187$). The mean number of invasive species as a proportion of total species was found to be greatest on cattle-grazed and ungrazed sites, with the smallest proportions of invasive species found on bison-grazed sites (Figure 1). No significant difference was found to exist among the total soil nitrogen values for any of the three site types ($p = 0.592$). The average nitrogen content was found to be greatest for cattle-grazed sites, while the least mean nitrogen was found on ungrazed land (Figure 2).

However, significant differences were shown for both cattle-grazed ($p=0.050$) and bison-grazed ($p = 0.032$) sites with regard to the proportion of invasive species detected at a site plotted against the percent nitrogen for that site. No such difference was detected for the ungrazed sites ($p=0.685$). Notably, regression analysis revealed a negative correlation between these two factors for bison-grazed sites, while it revealed a positive correlation for cattle-grazed sites (Figure 3). Scat count was found to be not significant in determining invasive species prevalence for both cattle-grazed ($p=0.343$) and bison-grazed sites ($p=0.316$). No scat was found on ungrazed sites, so these were not included in this analysis. Scat was additionally found to be not significant in determining soil nitrogen content for any site type ($p=0.240$).

Discussion:

While no significant difference in invasive species prevalence was found among the three different land types, interpretation of the graphed data (Figure 1) does suggest that the mean number of invasive species found in bison-grazed areas is lower than the mean number of invasive species found in either of the other two site types. It should additionally be noted that nearly all local ranchers and farmers of the Charlo, Montana area spray for the noxious weed, sulfur cinquefoil (*Potentilla recta*). The data for cattle-grazed plots chosen for this study should thus be interpreted as a low estimate of the true number of invasive species present. While previous studies have suggested that overgrazing can provide a form of disturbance, serving as a conduit for invasive species into an ecosystem (Loeser, 2005), this particular study does not support these findings for the Palouse Prairie ecosystem. The average number of invasive species found in both the ungrazed and cattle-grazed sites were essentially identical, and the average number of invasive species found in the bison-grazed sites was in fact *less* than that at the control sites. This would seem to suggest that the mechanism of invasion suggested by Loeser (2005) is not at work in this particular ecosystem, as we originally predicted.

An alternative study by Parker et al. (2006) showed the relative abundance of exotic plants to in fact be *reduced* by native herbivores, while a similar group of exotic herbivores increased the species richness of exotic plants. There are several potential explanations for why grazing pressure from native herbivores may favor native species over their exotic competitors. One argument states that it was many of the large native herbivores, most of which are now extinct, that served as a keystone pressure for the post-Pleistocene rise of the grassland biome (Axelrod, 1985, Hartnett et al., 1997). According to this theory, the grazing by megafauna, ancestors of the bison, in fact served a disproportionate role in *creating* the Palouse

Prairie ecosystem we see today, along with the other prairie regions of North America. If one accepts this theory, it does not become difficult to imagine American bison playing a keystone role in maintaining the native nature of a prairie which their same species evolved alongside and helped to create. Additionally, the role of bison in shaping ecosystems goes well-beyond their grazing, Knapp et al. (1999) argues; wallowing and horning (i.e., rubbing on trees) are associated exclusively with bison, differentiating them behaviorally from cattle (Coppedge and Shaw, 1997; Hartnett et al., 1997). These behaviors, taken alongside grazing effects, have the potential to increase habitat heterogeneity, alter plant community and even change ecosystem processes (Knapp et al, 1999), substantial evidence in favor of the role of bison as a keystone herbivore to maintaining biodiversity of the plains region (Power et al., 1996). However, another study by Towne et al. (2005) contradicted these findings, showing plant communities in bison and cattle pastures to be 85% similar after 10 years of grazing, and therefore suggesting that the type of grazing of a habitat (native vs. exotic) does not, at least to a significant degree, fundamentally differ.

While our study found no significant difference in soil nitrogen content among site types, it did show a difference in invasive species prevalence with regard to soil nitrogen for different grazing types. Scat count, however, was not found to be significant in determining invasive species prevalence or soil nitrogen content at any site type. Taken together, this might suggest that although grazing type alone is not strong enough of a factor in this study to cause significant differences in either soil nitrogen levels or invasive species prevalence, when grazing *and* nitrogen are taken into account, significant differences in invasive species prevalence do arise. In addition to this, the insignificance of scat count in determining invasive species prevalence at any site type might imply that concurrent bottom-up and top-down effects are at

work in determining the prevalence of invasive species in the ecosystem. Herbivory (top-down) seems to be modulating the competition between native and exotic species along a nitrogen gradient (bottom-up).

Studies have shown a net effect of bison grazing to be an increase in nitrogen cycling (Steinauer and Collins, 1995) in a tallgrass prairie ecosystem, resulting in an alteration in both species composition and patterns of productivity. Given this and other studies (Frank and Groffman, 1998; Pastor et al, 1993) that describe the potential for large herbivores to alter the nitrogen cycle dynamics of an area through grazing, several mechanisms may be at play in this particular study. That either large herbivore of this study, bison or cattle, are directly altering the soil composition through their grazing habits seems to be unlikely, given that there is no significant difference in soil composition among any of the three different grazing-type sites. Additionally, scat density's lack of significance on soil nitrogen would seem to indicate that the presence and density of grazing does not have as strong of impact on nitrogen as it might, given that scat itself has been shown to play a role in contributing nitrogen to a soil system (Knapp et al, 1999) in addition to giving insight into the relative amounts of grazers contributing to and potentially altering an area through grazing (Qi et al., 2011).

The relationship between the levels of nitrogen and degree of exotic species in this study suggests interesting forces at play beyond the idea of a "grazer" in general always producing the same, predictable effects. While cattle-grazed areas of this study showed a positive relationship between total nitrogen and exotic prevalence, bison-grazed areas actually showed the opposite effect: exotic species appeared to decrease along a gradient of increased nitrogen. Interestingly enough, both of these relationships show significant p-values, while the ungrazed control does not show a significant trend. So what potential factors could be at play, altering exotic species in

opposite directions along a nitrogen gradient in two different grazing communities? First, it should be noted that the grazing habits of these two types of animals, alone, do vary. Bison have been shown to consume a higher proportion of graminoids than do cattle, making forb species more common in cattle diets than those of bison (Van Vuren and Bray, 1983; Hartnett et al., 1997). Bison also spend less time grazing than cattle do (Plumb and Dodd, 1993). As both of these species do graze selectively rather than indiscriminately (Senft et al., 1987, Wallace et al. 1995), differences in the forage composition could react differently to similar nitrogen gradients. Knapp et al (1999) have suggested that bison alter plant community composition at the patch scale by selectively grazing species-poor, grass-dominated sites and converting them to sites of locally higher diversity. Field observations taken during this study did note the high variety of forb species present at the bison-grazed sites, a variety of which was clearly lacking at the cattle-grazed sites. These observations, though not quantitative, would support this theory and would be a good route of investigation for future study. Alternatively, studies have shown short-term effects of bison grazing to result in an increase in photosynthetic rates in many graminoid species, for which the grazed plants reallocate their nitrogen stores from roots to leaves (Wallace, 1990). Because the National Bison Range has recently instated an “open gate” policy, that is a policy of letting the bison freely wander the range, the managed grazing of the past has likely been replaced by much more short-term grazing of areas. This might potentially result in this short-term response of reallocating nitrogen away from the soil and into leaves, potentially partially explaining why the bison-grazed areas with more exotic species might also have less soil nitrogen. Vinton and Hartnett (1992) found that these effects do not extend into the long-term, during which plants stop reallocating nitrogen away from their roots to the same extent that they do during short-term grazing. This could potentially explain the opposite effect shown in

cattle-grazed pastures of this study, which have belonged to area farmers and been cattle-grazed for many years.

Much investigation has gone into the potential mechanisms for and effects of the role of American bison as a “keystone species” (Power et al., 1996). This study in particular strongly implies the reality of this role, suggesting that the grazing of American bison fundamentally differs on at least some level from that of introduced cattle in the Palouse Prairies. While an increase in exotic species along a nitrogen gradient for cattle-grazed areas may be due to either the selective grazing of the cattle or the long-term nature of their grazing, among many other potential explanations, a decrease in exotics along the same gradient for bison emerges. This would seem to indicate that bison behavior *may* indeed play a sort of keystone role, as proposed by Knapp et al (1999), increasing the native species of an area through their behavior. Further research into this topic, especially in the form of more trials, are highly suggested in order to better understand the difference that these two types of ungulates may have on the ecosystem. Such understanding could prove essential to informed land management strategy in the future.

Acknowledgements-

The completion of this project would not have been possible without the generous contribution of the Bernard J. Hank Family Endowment Fund. I would also like to thank the University of Notre Dame, and the University of Notre Dame Environmental Research Center (UNDERC) for allowing me this opportunity. A big thanks to my mentor Sarah Russ for her guidance with every aspect of this project, and to Gary Belovsky and David Flagel. Thank you to area ranchers Jerry Hamel and Brent and Patty Powell for allowing the use of their land, in addition to all those

at the National Bison Range, especially Amy Lisk for her insight into the grazing habits of the range's bison. This project would not have been possible without them. Finally, I am greatly indebted to the UNDERC West Class of 2016 for their help and companionship both in the field and with the writing process for this project.

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Tables:

Table 1:

	GPS N ⁰	GPS W ⁰	Altitude (ft)
Bison Site 1	47.22212	114.13236	2701
Bison Site 2	47.1847	114.1123	3957
Bison Site 3	47.211	114.1638	2602
Bison Site 4	47.2042	114.105	2846
Bison Site 5	47.29378	114.24532	2785
Cattle Site 1	47.1641	114.1711	2999
Cattle Site 2	47.291	114.111	3018
Cattle Site 3	47.216	114.1035	2715
Cattle Site 4	47.2814	114.129	2974
Cattle Site 5	47.2835	114.5051	3038
Ungrazed Site 1	47.217	114.1035	2715
Ungrazed Site 2	47.291	114.8023	3014
Ungrazed Site 3	47.2618	114.1211	2926
Ungrazed Site 4	47.2357	114.1036	2921
Ungrazed Site 5	47.2357	114.8059	2845

Table 1. The above table provides the locations of the fifteen study sites used in this paper.

Figures:

Figure 1:

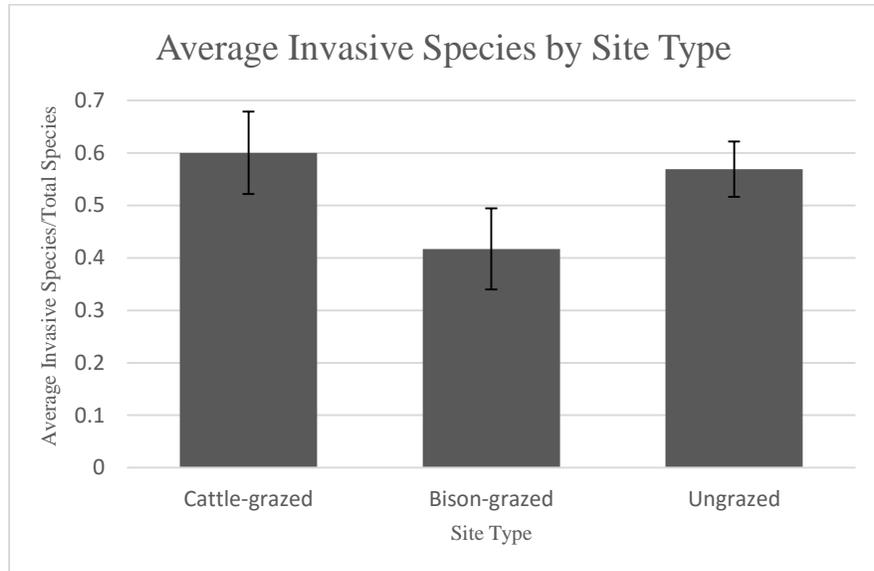


Figure 1. The above figure presents the average proportions of invasive species to total species for three different grazing categories. Error bars are represented by Standard Error.

Figure 2:

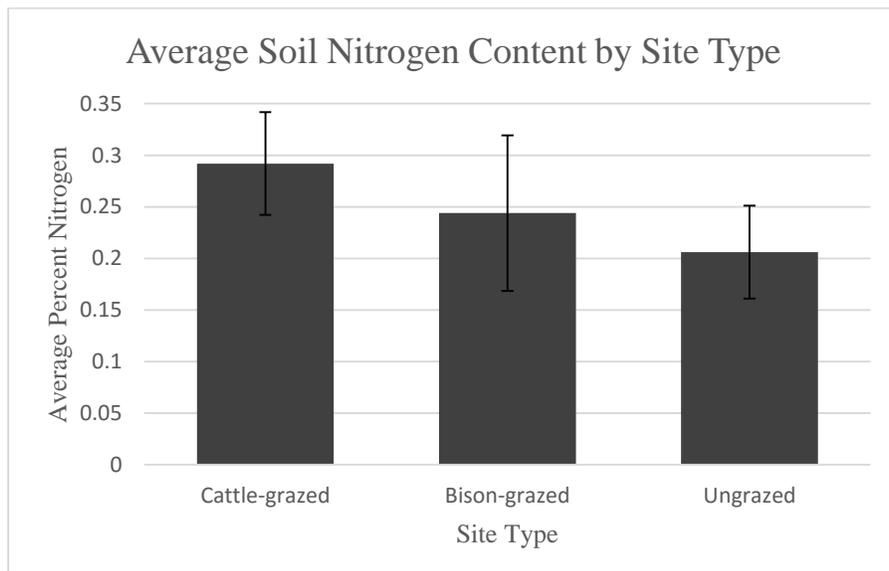


Figure 2. The above figure presents the average amount of soil nitrogen at each site type, as a percentage. Error bars are represented by Standard Error.

Figure 3:

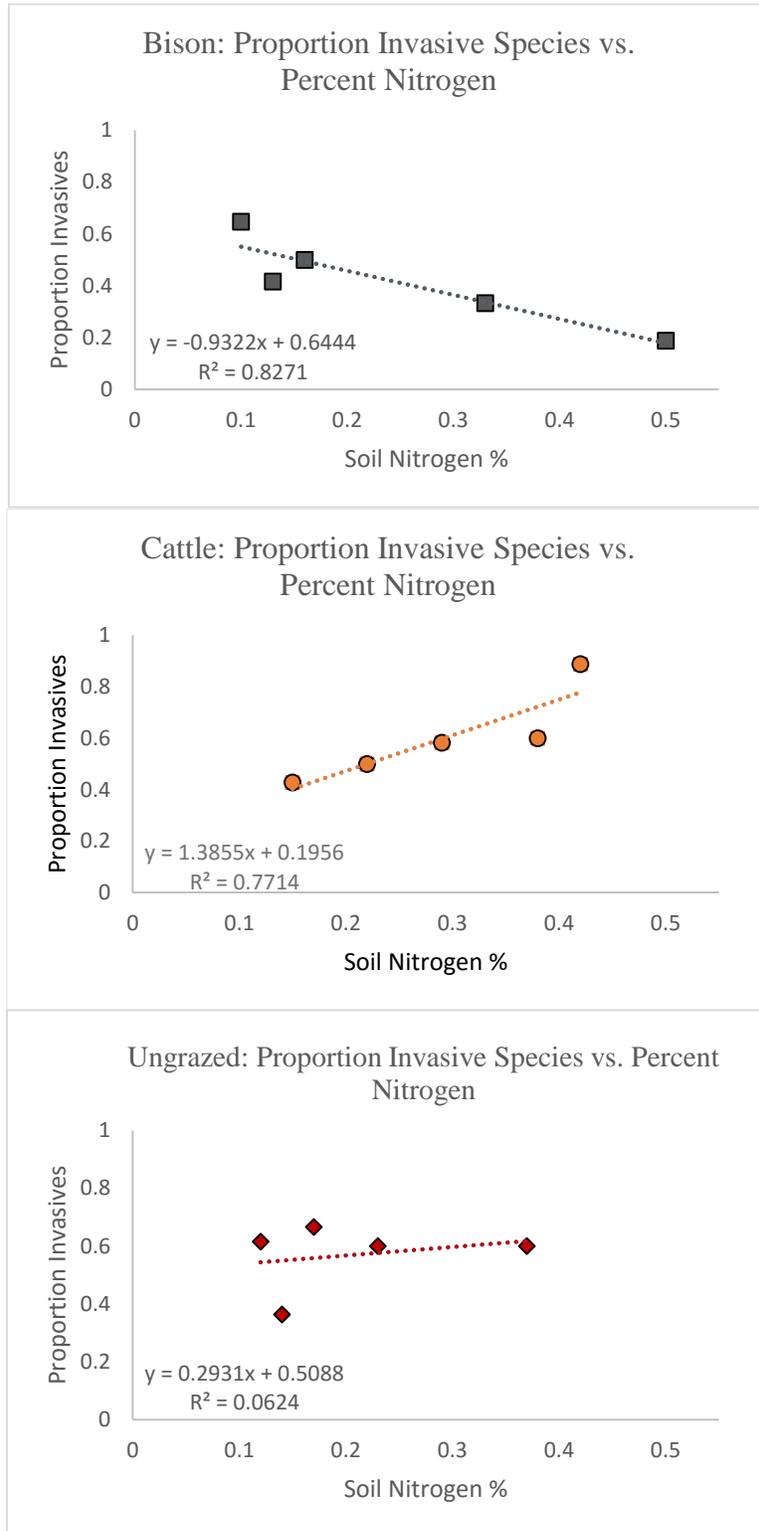


Figure 3. The above three charts present the soil nitrogen (proportion) plotted against invasive species (%) for the three given land types. Cattle ($p=0.050$) and bison ($p=0.032$) grazed land are significant.