EXPLORING VARIATION IN DIVERSITY OF ARTHROPOD COMMUNITIES IN GRASSLANDS OF YELLOWSTONE NATIONAL PARK

by

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DEDICATION

To my community, each of you show up as incredible humans and remind me how many ways there are to share care, respect, and empathy for others, and who have challenged and supported me every step of the way. To my partner who has been here and excited for each milestone I have achieved. And to the land. I am beyond fortunate to live and work in such an incredible place that brings me so much joy, curiosity, and awe each time I go outside. To the indigenous people who have long been stewards of this place, I am grateful to live and learn in these spaces, and aware that this privilege came at the cost of incredible pain and loss to your communities.

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ABSTRACT

Community ecologists have proposed many hypotheses to explain the mechanisms that drive patterns of diversity in plants and animals. For arthropods, understanding community assembly may have important conservation implications, given that this group provides many vital ecosystem services, yet many arthropods are in decline globally. We investigated drivers of arthropod diversity by testing the habitat complexity hypothesis, productivity hypothesis, and intermediate disturbance hypothesis in grasslands in the northern range of Yellowstone National Park. We collected data on vegetation (vegetation cover, litter cover, vegetation height, remotely sensed biomass, and the normalized difference vegetation index) and bison movement as explanatory variables, and sampled arthropods to help us test our hypotheses. We used generalized linear models and multivariate methods to explore patterns of richness and composition of arthropod communities among our sites. We found limited evidence for the habitat complexity hypothesis; richness of predators increased with heterogeneity in litter cover. In contrast, richness of multiple functional groups decreased with heterogeneity in vegetation cover and we did not detect any relationships with heterogeneity in vegetation height. We found evidence supporting the productivity hypothesis among herbivores; richness of herbivores overall and chewing herbivores were positively related to net primary productivity, whereas richness of omnivorous arthropods decreased with increased biomass. Although the intermediate disturbance hypothesis predicts that species richness will be maximized at moderate levels of disturbance, we found the lowest richness of all arthropods and that of multiple functional groups at moderate levels of disturbance. Overall, we found that herbivorous arthropods were more affected by quality and quantity of vegetation, whereas upper-trophic feeders were more affected by habitat complexity. These findings highlight that different functional groups of arthropods are driven by different mechanisms. By considering diversity metrics beyond taxonomic classification, we can gain important insights about arthropods – a diverse, understudied taxa.

CHAPTER ONE

INTRODUCTION TO THESIS

Community assembly theory provides a framework to explore the dominant factors driving variation in species richness and community composition (Bannar-Martin et al. 2018; Myers et al. 2013), with numerous hypotheses proposed to identify the mechanisms that lead to higher biodiversity (Joern and Laws 2013; Mittelbach and Mcgill 2019). Empirical tests of these hypotheses have found that the mechanisms differ by taxa and ecosystem; multiple mechanisms may operate simultaneously, creating interactive effects (Connell 1978; Huston 2014; Joern and Laws 2013; Mena and Medellín 2017; Rogers 1993; Wright 1983). In this thesis, I build on previous research to continue to explore potential factors supporting high biodiversity.

Although biodiversity hotspots often bring to mind tropical rainforests, grasslands also are characterized by extraordinary biodiversity (Anderson 2006; Petermann and Buzhdygan 2021). Grasslands are most well-known for having high plant diversity, supported in part by different types of disturbance, including extremes in temperature and precipitation, fire, and herbivory (Anderson 2006; Petermann and Buzhdygan 2021). These disturbances occur at different scales and frequencies, creating a mosaic across the landscape (Petermann and Buzhdygan 2021). This variation in conditions can in turn support the needs of diverse species, including arthropods (Joern and Laws 2013).

Arthropods are a very speciose taxa and we have sizeable gaps in our understanding about their taxonomy, diets, habitat needs, behavior, and evolution (Dunn 2005; Joern and Laws 2013; Prather et al. 2013; van Klink et al. 2015). We do however, understand that arthropods provide many vital ecosystem services, including pollination, decomposition, nutrient cycling, and food for many other species (van Klink et al. 2015). Given the high diversity, arthropods may exhibit a wide range of responses to ecological conditions (van Klink et al. 2015). Functional traits, such as in life history strategies, size, mobility, trophic level or feeding groups, could provide a unifying framework to reveal patterns in responses and gain insights.

In this thesis, I explored the overarching question: What factors drive diversity in grassland arthropod communities? I specifically focused on temperate grasslands in Yellowstone National Park (YNP) and investigated three common hypotheses for mechanisms driving arthropod community assembly. Yellowstone is an ideal location to investigate processes structuring North American grasslands, as the native megaherbivore, the American bison (*Bison bison*), remains on the landscape, maintaining some of the natural disturbance patterns (Geremia et al. 2019; Knapp et al. 1999). In Chapter 2, I examined support for the habitat complexity and productivity hypotheses (Chesson 1985; Wright 1983) by modelling the relationships between richness of arthropods and different attributes of vegetation structure and primary productivity. The habitat complexity hypothesis suggests that structural heterogeneity creates different conditions, opens different niches, and provides habitat requirements for more types of organisms (Joern and Laws 2013). Alternatively, the productivity hypothesis focuses on the dominant roles of food resources and competition on community composition (Post 2007; Wright 1983). Under this hypothesis, areas with higher productivity have more resources available, potentially increasing the probabilities that more species persist (Joern and Laws 2013; Storch, Bohdalková, and Okie 2018). In Chapter 3, I explored the intermediate disturbance hypothesis, by comparing the arthropod community across a gradient of disturbance by bison. The intermediate disturbance hypothesis (Fox 1979; Joern and Laws 2013; Gao and Carmel 2020) is premised on the idea that moderate levels of disturbance create the most heterogeneous conditions to support needs of more species (Adler et al. 2005; Joern and Laws 2013; van Klink et al. 2015). In both chapters, I consider richness of the overall arthropod community, as well as different functional feeding groups to gain additional insights.

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CHAPTER TWO

VARIATION IN VEGETATION CHARACTERISTICS HAS DIFFERENTIAL EFFECTS ACROSS ARTHROPOD FUNCTIONAL GROUPS

Contribution of Authors and Co-Authors

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Contributions: Implemented the study, collected and analyzed data, wrote manuscript

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Contributions: Helped develop initial study idea, guided study design, assisted in securing funding, helped with data analysis, thoroughly edited manuscript

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Manuscript Information

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Abstract

Mechanisms that drive patterns of diversity are complex and vary by biome and taxa. We were interested in understanding the drivers of arthropod richness – overall and of individual functional groups – in grasslands of Yellowstone National Park. Specifically, we tested two hypotheses proposed to explain patterns of diversity: the habitat complexity and productivity hypotheses. To measure complexity, we collected data on vegetation cover, litter, and height, and calculated the coefficient of variation. To measure productivity, we used remotely sensed biomass and NDVI data. We used generalized linear models and multivariate methods to test our predictions. Richness of multiple functional groups, especially herbivores, decreased as heterogeneity of vegetation cover increased; richness of predators increased with heterogeneity of litter cover. We failed to detect relationships with heterogeneity of vegetation height. Richness of omnivores decreased and herbivores increased with vegetation biomass, whereas richness of chewing herbivores increased with biomass and NDVI. Herbivorous arthropods responded to vegetation quality and quantity, whereas upper trophic groups responded more strongly to complexity, which makes sense given their different life history strategies. The variation in our findings reinforces that diversity is driven by multiple mechanisms, requiring additional information to make reliable predictions.

Implications for Insect Conservation: Arthropods are a highly diverse taxa that require variation in conditions. We found that vegetation characteristics play an important role in diversity of grassland arthropods; incorporating functional traits into our analyses may provide a better understanding of the conditions that nurture communities of high taxonomic and functional diversity.

Introduction

Biodiversity, typically defined as the measure of the number and abundance of species in a given area (DeLong 1996), is a high-profile term in ecology. Despite the importance associated with biodiversity in community ecology, understanding the mechanisms driving variation in biodiversity is still a work in progress (van der Plas 2019). Given that many forces interact to determine the composition of a community, teasing apart some dominant patterns can be challenging (Joern and Laws 2013). Many hypotheses have been proposed to explain why one area may host more species than another, yet tests of these hypotheses often have conflicting results depending on how the study is performed (Mora et al. 2011; Stork 2018), how biodiversity is defined and measured (DeLong 1996), the scale of the study (global to local), and the focal taxa (Joern and Laws 2013). However, despite the disparity in findings, these hypotheses form a framework to design further studies (Bannar-Martin et al. 2018; Joern and Laws 2013).

Community assembly theory focuses on the processes that influence community composition (Bannar-Martin et al. 2018; Myers et al. 2013), namely that local species diversity is highly dependent on the regional species pools, with stochasticity, dispersal, and different abiotic and biotic factors acting as "filters" (Mittelbach and Mcgill 2019). Filters may include structural features, food resources, climatic conditions, predators, or competitors (Leibold, Chase, and Ernest 2017; Mittelbach and Mcgill 2019). These filters therefore are potential mechanisms driving variation in biodiversity, creating testable hypotheses (Joern and Laws 2013; Leibold, Chase, and Ernest 2017). For example, the habitat complexity hypothesis suggests that structural heterogeneity creates different conditions, opens different niches, and provides habitat requirements for more types of organisms (Joern and Laws 2013). Previous work has supported this hypothesis in multiple animal communities including small mammals (Mena and Medellín 2017), macroinvertebrates (O'Connor 1991), and marine invertebrates (Dean and Connell

1987). Other studies have found no, weak, or mixed support for this hypothesis in taxa such as small mammals (Chen et al. 2020), frogs (Carvalho-Rocha, Peres, and Neckel-Oliveira 2021), and fish (Chen et al. 2020). The variation in findings suggests that the scale of measurement, the metric for complexity, and other forces all may influence results (Joern and Laws 2013; Jimenez Martinez, n.d.; Leibold, Chase, and Ernest 2017). Alternatively, the productivity hypothesis focuses on the dominant roles of food resources and competition on community composition (Post 2007; Wright 1983). Under this hypothesis, areas with higher productivity have more resources available, potentially leading to greater abundance of individuals overall, as well as higher probabilities that more species persist (Joern and Laws 2013; Storch, Bohdalková, and Okie 2018). Empirically, there seems to be some support for the productivity hypothesis in plant communities, which is likely due to niche complementarity (Mittelbach and Mcgill 2019; Tilman et al. 2001; Wright 1983). Testing the same hypothesis in animal communities has had less straightforward results (Mittelbach and Mcgill 2019), with medium to strong support in communities of amphibians (Qian et al. 2007), birds (Dillon and Conway 2021), and bats (Threlfall et al. 2011), but little evidence in communities of aquatic zooplankton (Dodson, Arnott, and Cottingham 2000), ants (Sanders et al. 2007), and birds (Dobson et al. 2015). The variation in findings among animal communities, even within the same taxa, again suggests that the primary productivity hypothesis may be context dependent and influenced by other factors (Mittelbach et al. 2001; van der Plas 2019).

Although biodiversity often is quantified in terms of taxonomic richness, there has been a recent shift to consider the diversity of functional traits, or the characteristics of organisms that define their fitness or role (Nock, Vogt, and Beisner 2016). Functional traits can pertain to life history strategies, as well as morphological, structural, phenological, or behavioral features, such as feeding groups (Nock, Vogt, and Beisner 2016). Quantifying functional traits alongside traditional taxonomic metrics may allow us to consider other community characteristics (e.g., niches filled) and gain a deeper understanding about ecosystem processes. For example, focusing on which characteristics lead to greater diversity of detritivores provides important implications for understanding nutrient cycling. These additional insights also may help to shed light on some of the varied support for diversity hypotheses.

Although many diversity studies focus on “biodiversity hotspots” such as tropical rain forests, grasslands also support very high levels of species diversity (Petermann and Buzhdygan 2021). Diverse species can be supported in grasslands, in part, because of high levels of temporal and spatial heterogeneity (Joern and Laws 2013). In grassland systems, drought severity, periodic fire, herbivory, and temperature extremes vary over time – both seasonally and annually (Lauenroth, Burke, and Gutmann 1999; Petermann and Buzhdygan 2021). These forces also create spatial heterogeneity across the landscape, interacting with the local topography, hydrology, soil types, and other features to influence plant establishment and growth (Lauenroth, Burke, and Gutmann 1999; Petermann and Buzhdygan 2021). Due to a long co-evolutionary history with herbivores, grasslands also are characterized by high plant productivity (Hamilton III and Frank 2001). The heterogeneity and productivity of grassland ecosystems mean they can serve as an important study system for examining patterns of diversity.

Grasslands often are associated with large herds of megaherbivores and their predators, however some of the most important and specialized grassland species are the many known and unknown arthropods (Joern and Laws 2013; Petermann and Buzhdygan 2021). Arthropods are essential to many ecosystem processes and services, including pollination and nutrient cycling (van Klink et al. 2015; Whiles and Charlton 2006). Despite their vital roles, we often have large gaps in our knowledge about arthropod communities and the mechanisms driving composition, even in well-studied natural areas (Stork 2018; van Klink et al. 2015; Whiles and Charlton 2006). Due to these gaps and the roles arthropods fill in an ecosystem, we also may be missing important insights about ecosystem functions (Podgaiski et al. 2014; Whiles and Charlton 2006).

We tested the habitat heterogeneity and productivity hypotheses in communities of grassland arthropods in Yellowstone National Park (YNP). In combination, these two hypotheses lead us to expect that areas of high heterogeneity and high productivity also are likely to host more arthropod species (Joern and Laws 2013). We also explored the arthropod community through the lens of functional feeding groups (e.g., herbivores, predators, detritivores) to provide insights about these understudied taxa and their ecological roles (Nock, Vogt, and Beisner 2016).

Many aspects of habitat structure may be important for different taxa. For grassland arthropods, habitat structure is formed primarily by the horizontal cover and vertical height of plants, as well as dead vegetation that accumulate as litter (Lauenroth, Burke, and Gutmann 1999; van Klink et al. 2015), which also will affect temperature and humidity (van Klink et al. 2015). Variation in these characteristics create a mosaic of structural and microclimate conditions that may support greater diversity (Joern and Laws 2013). We predicted that more heterogeneity (complexity) in these components of vegetation structure would result in higher richness of arthropods, specifically arthropods that feed on vegetation or litter.

Food resources in grasslands are primarily comprised of vegetation (e.g., leaf and stem material, pollen, nectar, and seeds), litter (e.g., dead vegetation, dung, and occasional carcasses), and other arthropods; each of these may be preferred food resources for different species of arthropods. In addition, many herbivorous arthropods are host specific and require specific plant species (Stork 2018). Higher plant productivity often is associated with more plant species (Mittelbach et al. 2001; Tilman, Lehman, and Thomson 1997; Tilman et al. 2001), meaning that areas of high productivity may provide diverse resources for more kinds of arthropods and functional traits (Wright 1983). Based on the productivity hypothesis, we predicted that areas with higher productivity in vegetation would result in higher richness of arthropod species overall, as well as richness within each functional feeding group. We also predicted that more litter cover would result in more species of detritivores. Our observational study aimed to explore patterns of diversity that may help inform future research questions that can be addressed in an experimental framework.

Methods

Study Area

Yellowstone National Park is located in the western United States, falling within three states, Idaho, Montana, and Wyoming. Our study took place on the northern third of YNP, commonly known as the northern range (Beyer et al. 2007). The northern range (1,556 km^2) occurs at lower elevations (1600-2200 m) (Singer and Renkin 1995) than the southern portions of the park (2130-2590 m) (Hague 1921), resulting in a lower snowpack and a generally drier environment (Plumb et al. 2009). As a whole, YNP has a short growing season occurring between snowmelt (May) and the onset of the next snowfall (September), although the northern range has a slightly longer snow-free period than the southern portions of the park (Geremia 2014; Singer and Renkin 1995). The northern range includes several significant rivers that inundate numerous wide valleys, creating a mix of grassland types differentiated by plant species that vary in their moisture requirements (Singer and Renkin 1995).

Many of the more mesic grasslands were cultivated as hayfields in the early 20th century (Meagher 1973) and now are primarily dominated by several species of perennial non-native grasses (e.g., Kentucky bluegrass [*Poa pratensis*] and Timothy-grass [*Phleum pratense*], Hamilton III and Frank 2001; Stoughton and Marcus 2000), often with rhizomatous or mat-forming growth forms (Hamilton III and Frank 2001). These mesic grasslands include plant species that grow faster and are less limited by nitrogen and water, and thus have more capacity for regrowth (Frank, Wallen, and White 2016). The drier grasslands are primarily sagebrush steppe dominated by perennial native bunchgrasses (e.g., Sandberg bluegrass [*Poa secunda*], Idaho fescue [*Festuca idahoensis*], and prairie junegrass [*Koeleria* *macrantha*]) (Boccadori et al. 2008) with lower aboveground net primary production (Frank, Wallen, and White 2016). In addition to differences between primary production, each grassland type also has different structural characteristics, such as the amount of bare ground or interspersed shrub cover, that may be preferable to different arthropod species.

Site Selection

We selected study sites that each consisted of an area ranging from 8,000-78,000 m^2 in size, separated by at least 1.6 km to maintain independence. We selected sites representing each grassland type (mesic rhizomatous or drier bunchgrass-dominated) that also had similar annual plant production, vegetation characteristics, temperature, and precipitation, based on remotely sensed data (Landsat8, 30 x 30 m pixels, Xu & Guo, 2014). To make these selections, we first computed annual normalized difference vegetation index (NDVI), maximum NDVI, and the Julian date of peak NDVI between 2013 and 2017 for the raster pixels on the northern range. We excluded forested areas based on an available vegetation layer. We included annual net temperatures and annual average precipitation from Parameter-elevation Regressions on Independent Slopes Model (PRISM) databases for the same years (Daly and Bryant 2013). We used these remotely sensed data and hierarchical clustering to collect subsets of raster pixels into distinct groups. We then used these groupings as a training dataset for a machine learning algorithm to classify all the remaining raster pixels in the northern range into the rhizomatous or bunchgrass-dominated grasslands based on their NDVI value.

We then stratified sites based on the grazing intensity by bison. To categorize grazing intensity, we combined GPS data from all collared bison on the northern range for the summer vegetation growth periods each year (2013 to 2017, 82 total individuals). Based on these data, we calculated utilization distributions with Brownian-Bridge movement models (Kranstauber et al. 2012). Grazing intensity was calculated as the probability of utilization in each raster and sites were stratified based on 3 categories (low, medium, and high). Low grazing was calculated as <90% probability, medium was calculated as 90%-<99%, and high intensity was designated as ≥99%.

We aimed to select 3 sites for each combination of grazing intensity (low, medium, high) and grassland type (rhizomatous or bunchgrass-dominated). We selected 10 sites in the rhizomatous grassland areas (4 high, 3 moderate, and 3 low-intensity grazing), which we sampled in 2021. We selected 8 sites in the bunchgrass-dominated sagebrush steppe (3 high, 2 moderate, and 3 low-intensity grazing), which we sampled in 2022. Our study sites experienced drought conditions in 2021 and an abnormal rain and flooding event in 2022. Any differences we observed between years could result from differences in grassland type, soil moisture, weather conditions, or some combination of these factors.

Timing of Sampling

We used the timing of peak vegetation biomass to inform the timing of our sampling, to align sampling based on when similar vegetation phenology and productivity would occur. We determined peak biomass based on NDVI data averaged over 5 previous years (2016-2020).

Vegetation Sampling

Vegetation Structure We characterized vegetation structure based on horizontal vegetation cover, vegetation height (vertical structure), and litter cover; we sampled these variables one week prior to peak biomass. To characterize horizontal vegetation cover, we selected 6 random locations within each site and photographed these areas with cameras capable of capturing enhanced normalized difference vegetation index (ENDVI) values. Photographs were taken directly overhead and captured a 0.7 x 0.7-m quadrat within the frame. We calculated foliar cover, or the percentage of the quadrat that consisted of live vegetation (Ferreira and Rasband 2012), using the *countcolors*, *colordistance*, and *scatterplot3d* packages in R (Weller 2019; 2021; Ligges, Maechler, and Schnackenberg 2023). We measured vegetation height using a drop disc (Stewart, Bourn, and Thomas 2001) at 20 random locations within each site; we sampled height only during 2022 (i.e., bunchgrass-dominated sites).

We quantified litter cover by sampling a 0.6 x 0.4-m quadrat at 60 random locations within each study site; we assigned a cover class for litter based on Daubenmire (1959). Litter was counted when it was structural (i.e., fecal or vegetation, excluding soil crusts) within the quadrat. Due to the flooding event in 2022, we were able to measure the litter for 3 of the 8 study sites; for the remaining 5 sites, we used data compiled in previous years using the same methods.

To explore our hypotheses about the complexity of vegetation structure, we characterized heterogeneity by computing the coefficient of variation (CV, %) for plant characteristics of interest: vegetation cover, vegetation height, and litter cover, among the sampled locations within each site.

Vegetation Productivity We quantified vegetation productivity using remotely sensed biomass (i.e., amount of plant material) and NDVI (i.e., greenness of plant material). We acquired the biomass data from the Rangeland Analysis Program (RAP). We cropped the rasters to a polygon of each site and used the *terra* package (Hijmans et al. 2024) to extract values for biomass of annual and perennial plants. We calculated mean biomass by year for: all plants, annual plants, and perennial plants for each site (g/m^2).

We used rasters from the MODIS terra satellite (MOD09Q1) to extract summed integrated NDVI (summed INDVI) values (csumNDVImax, Wildlife Move Tools 2024) for each growing season during our sampling periods. We cropped the appropriate rasters (2021 and 2022) to the polygons of the sampled sites and used the *terra* package (Hijmans et al. 2024) to extract the values. Some sites intersected with multiple pixels; when this was the case, we computed the mean of all pixel values for the site.

Arthropod Sampling

We sampled flying and vegetation-dwelling arthropods using vacuum sampling methods (Buffington and Redak 1998) one week prior to peak biomass. We used a vacuum/blower (DeWalt DCBL720B 20V Max Lithium Ion XR, reverse motor) to sample a 0.7 x 0.7-m quadrat for 2 minutes, using a grid pattern to ensure uniform sampling; we repeated this sampling at 5 random locations in each site. We sprayed the sample with ethanol (80% dilution) immediately after collection to reduce predation and stored samples in a freezer for later sorting and identification.

We sorted specimens from plant matter and detritus collected during the sampling process by sifting samples through progressively smaller metal sieves (2 mm [No. 10], 1 mm [No. 18], and 500 µm [No. 35] sizes, U.S.A Standard Test Sieve, ASTM E11 specification) and removing arthropods at each stage. Collected arthropods were sorted into morphospecies based on their visible morphological characteristics (Oliver and Beattie 1996). We assigned a number to each morphospecies to track similarities in communities among sites, much as we would if specimens were identified to species. We identified each arthropod morphospecies to taxonomic order or family depending on which was necessary to determine a functional group. We identified all collected arthropods to a functional group: chewing herbivores, sap-feeding herbivores, pollinators, omnivores, detritivores, predators, parasites, and non-feeders (Johnson and Triplehorn 2004). We classified specimens from the family Formicidae into several morphospecies based on their color, hair, and spines. We grouped all “daddy long-leg” species (order Opiliones) as one morphospecies, due to the difficulty of identification and the condition of those samples. All Orthoptera instars were assigned to one morphospecies due to identification challenges. For members of the order Diptera, we used the functional groups of the larval stage for that family, even though our samples were captured in the adult stage, because Diptera often spend up to 11 months as larva, and only days as adults, making the larval functional group more ecologically meaningful

(McAlpine 1981). Morphospecies that were categorized as non-feeders were adult forms of aquatic macroinvertebrates.

We computed overall richness as the number of morphospecies present per site. We also computed richness for each functional group (chewing herbivores, sap-feeding herbivores, omnivores, detritivores, predators, and parasites). We also computed richness of herbivores overall, combining the chewers, sap-feeders, and pollinators, as well as richness of upper-trophic feeders, which combined predators and parasites.

Statistical Analysis

We used generalized linear models to explore our hypotheses about the influences of vegetation heterogeneity and productivity on overall arthropod richness and richness of each functional group. We selected the appropriate distribution and link function for each response variable. Specifically, we explored Poisson and negative binomial distributions to model our richness counts, each with a log link function. We used a likelihood ratio test to select the distribution that best fit each response. Each generalized linear model was fitted using either the *glm* or the *MASS* package in R (Ripley et al. 2024). We used R version 4.3.3 for all analyses (R Core Team 2021).

We found a high correlation between the CVs for vegetation cover and vegetation height (Pearson's r = -0.78), but low correlation between the CV for vegetation cover and CV for litter (r = 0.33). Based on this, we examined 2 separate regression models for the habitat complexity hypothesis: 1) simple linear regressions with CV of vegetation height as the explanatory variable and 2) multiple linear regressions including CVs for vegetation cover and litter as the explanatory variables. Biomass and summed INDVI were not highly correlated (r = 0.51), so we fit multiple linear regressions with summed yearly annual and perennial biomass and summed INDVI as the respective explanatory variables to evaluate the productivity hypothesis. We explored these models (2 models for heterogeneity and 1 for productivity) for overall arthropod richness, as well as for richness of each functional group. We did not have enough non-feeders or pollinators to analyze as independent functional groups. In results, we present tables of back-transformed coefficients and 95% confidence intervals to represent the multiplicative changes in arthropod richness for every 10% increase in the explanatory variables.

We also explored community composition further, using multivariate methods to retain the identity of the arthropods instead of collapsing these details into a single richness value. We described variation in the composition of the arthropod community as a function of several vegetation variables (heterogeneity [CV] of vegetation cover, heterogeneity of litter cover, mean litter cover, biomass of annuals, biomass of perennials, and summed INDVI) using a transformation-based redundancy analysis (tb-RDA). The tb-RDA combines regression and principal component analysis, allowing us to use multiple vegetation variables to describe variation in the composition arthropod community (Borcard, Gillet, and Legendre 2011). We used a tb-RDA instead of canonical correspondence analysis (CCA), after checking for linearity in the data using a detrended correspondence analysis (Hill 1979; Lepš and Šmilauer 2003). We used the *vegan* package (Oksanen et al. 2024) and performed some post-hoc permutation tests to assess the model fit.

Results

Heterogeneity

We found that arthropod richness changed with habitat complexity, mainly heterogeneity of vegetation cover (Table 1). However, this relationship was consistently negative, contrary to the habitat complexity hypothesis (Fig1). We found that two sites had potentially influential values, so we examined the relationship with and without these sites. Richness of all arthropods, all herbivores, and chewing herbivores all decreased as heterogeneity of vegetation cover increased; evidence of the negative relationship remained with and without these 2 sites (Table 1). We also found evidence of a negative relationship between heterogeneity of vegetation cover and richness of sap-feeding herbivores, detritivores, predators, parasites, and upper-trophic feeders, yet the strength of this relationship was driven by these 2 sites. When we excluded these sites, we found limited evidence of a relationship with sap-feeding herbivores, detritivores, and parasites, whereas we found stronger evidence of a positive relationship with predators and upper-trophic feeders (Table 1). After accounting for heterogeneity of vegetation cover, we found evidence of a relationship between richness and heterogeneity of litter cover for only a few functional groups. Richness of predators and upper-trophic feeders increased with heterogeneity of litter cover (Table 1). For the upper-trophic feeders, this positive relationship was only evident when we excluded the 2 influential sites. We failed to detect a relationship between heterogeneity of vegetation height and richness of arthropods overall or of any functional groups (Table 2).

Productivity

We found support for the productivity hypothesis in just a few functional groups, primarily herbivorous arthropods (Fig2). Herbivore richness increased with plant biomass and richness of chewing herbivores increased with both plant biomass and summed INDVI (Table 3). In contrast, richness of omnivores decreased with plant biomass, after accounting for summed INDVI (Table 3). We failed to find a relationship between either productivity metric and richness of arthropods overall or of other functional groups (i.e., sap-feeders, detritivores, predators, parasites, and the combined upper trophic group) (Table 3).

Arthropod Community

The composition of the arthropod community varied among sites and some (41.4%) of this variation was explained by vegetation covariates. The first axis in the RDA explained 14% of the variation in arthropod composition, which was mainly driven by summed INDVI (Fig3). Summed INDVI explained the most variation (7%) in the model (Table 4); sites sampled in 2021 (mesic rhizomatous grasslands) had higher summed INDVI values (right side of axis 1) than sites sampled in 2022 (drier bunchgrass-dominated, left side of axis 1, Fig3). Other vegetation covariates were weakly correlated with RDA axes (Table 4). We found that individual morphospecies were only weakly correlated (-0.357 to 0.322) with the first RDA axis, suggesting there were no predictable patterns in arthropod morphospecies composition among sampled sites based on the vegetation variables we considered.

Discussion

We found that the drivers of biodiversity, even within one ecosystem and one taxa, are complex and nuanced. Tests of both the habitat complexity and productivity hypotheses produced varying results (Aguirre-Gutiérrez et al. 2017; Batáry et al. 2007; Chen et al. 2020), suggesting that no single set of mechanisms unifies taxa, scales, or environments (Joern and Laws 2013). Our findings are consistent with the literature, Mena and Medellín (2017), for example found that habitat complexity was a better predictor of small mammal diversity than elevation, yet, Marquet (1994) found a positive relationship between small mammal diversity and elevation. Multiple drivers influence community assembly even within the same taxa (Mena and Medellín 2017), so discerning the processes at work can still be quite challenging.

Incorporating functional groups, in addition to overall taxonomic richness, allowed us to consider different relationships based on specific habitat needs and ecosystem functions that can provide insights about important mechanisms. When we examined community composition based on morphospecies richness, we found no predictable patterns in composition, whereas we were able to discern some clearer relationships when we considered functional groups. Given the high diversity among arthropods, even a single order or family can contain species with numerous functional traits (Nock, Vogt, and Beisner 2016). Focusing on those functional groups can allow patterns to emerge that would not otherwise have been recognized based on taxonomic identity (Aguirre-Gutiérrez et al. 2017).

Although we found little evidence of the habitat complexity hypothesis, richness of herbivores did change with heterogeneity of vegetation, albeit counter to our prediction, as richness was highest with low heterogeneity. Richness of herbivores increased with plant biomass, consistent with the productivity hypothesis. In tandem, these findings suggest that for herbivorous arthropods, especially chewing herbivores, the availability and quality of plant forage is more important for presence than variation in habitat structure. Given that the habitat complexity hypothesis is based on the idea that heterogeneous conditions create more types of niche space, and that the productivity hypothesis posits that abundant food resources reduces competition, the herbivorous arthropods in our system may be sorted more strongly along food resource niches rather than structural niche space.

Although functional groups did reveal some important insights to understand patterns of biodiversity in our study, some uncertainty remains. Arthropods are a very diverse group, for which we still lack essential information. Some species may consume only specific species of plants or differ in how much they predate versus scavenge. Many arthropods could be classified into several feeding groups, within and among life stages. Melo, Silva, and Piratelli (2020), in their study on habitat complexity and functional traits of birds, tried to solve a similar dilemma by further separating feeding groups based on percentages of different food types in the diet. For example, they distinguished frugivorous birds from those that ate multiple types of vegetation and omnivorous birds that primarily ate vegetation from those that mainly ate insects. Accounting for variation in feeding strategies, and thus the numbers of niches, did provide additional insights (Melo et al. 2020). However, we lack that knowledge for most arthropod species, and even when we have this information, identifying samples to species can be challenging for certain arthropod groups. We found that richness of predators and the upper trophic feeders increased with heterogeneity of vegetation and litter cover, which suggests that these arthropods may rely on dead and living vegetation to provide needed structure for hunting or as habitat for their prey. Classifying these species based on more detailed information, such as hunting strategies, the degree of prey specialization, and other life history requirements could provide additional insights.

Variation in support for different biodiversity hypotheses also could stem from using different metrics to characterize ecological filters. We considered several variables to characterize habitat complexity and productivity and found mixed results – more support for heterogeneity of cover than heterogeneity of litter or vegetation height and slightly more support for biomass than summed INDVI. Other studies exploring the habitat complexity hypothesis also included vertical and horizontal metrics of vegetation complexity (Aguirre-Gutiérrez et al. 2017; Melo, Silva, and Piratelli 2020; Mena and Medellín 2017), as these aspects of heterogeneity sometimes play different roles in altering microclimate, protection from predators, or providing structure for hunting prey. Although we failed to detect a relationship between heterogeneity of vegetation height and any of our functional groups, we had limited power for these analyses. Some of the metrics we considered also may be coarse proxies for other unmeasured variables with more direct effects. For example, higher plant productivity often is associated with greater plant diversity (Tilman, Lehman, and Thomson 1997; Tilman et al. 2001). Cataloging the identities and diversity of plant species, in addition to measuring plant productivity, could provide a clearer link between food resources and herbivores.

Multiple factors likely interact to create the observed patterns of biodiversity. Many arthropods have short generation times, allowing them to respond rapidly to ecological changes. Our samples represent a single snapshot of these dynamic arthropod communities, which occurred during a drought (2021) and a catastrophic flood (2022). The large differences between sampling years also coincided with sampling different grassland types; this variation was evident in our analysis of community composition. Arthropods are a highly diverse group with differences in life history strategies, mobility, generation times, responses to extreme weather, and other factors, all of which may influence community assembly (Joern and Laws 2013; van Klink et al. 2015). Although we gained some insights about similar patterns within functional groups, when we retained the identities of individual morphospecies in multivariate analyses, we found little evidence of predictable patterns in composition among sites related to our vegetation covariates. These findings could suggest that additional vegetation covariates, as well as non-vegetation covariates (e.g., microclimate), are needed to understand morphospecies-specific needs and patterns of occurrence. Continuing to sample these communities over multiple years and integrating field experiments would provide insights about the degree of dynamism and tease apart influential forces.

Worldwide, habitat for plants and wildlife has declined, in tandem with expanding human populations, such that places identified as biodiversity “hotspots” often attain some degree of conservation protection (Mittermeier et al. 1998). Grasslands support diverse species, but these areas also are often under-protected given their utility for agricultural endeavors (Petermann and Buzhdygan 2021). As a result, grasslands have declined globally, by as much as 90% in some places (Anderson 2006; Petermann and Buzhdygan 2021) Arthropods in these grasslands provide a suite of ecosystem services that benefit both wildlife and humans, yet we still understand little about what drives occurrence and diversity (Joern and Laws 2013; Petermann and Buzhdygan 2021). We found that vegetation characteristics play an important role, especially for herbivorous arthropods, yet continuing to build our mechanistic understanding is essential to conserve species, functional traits, and ecological roles.

Table 1. Estimates, 95% confidence intervals, test statistics, and *P*-values for regression models of arthropod richness as a function of heterogeneity in vegetation cover and heterogeneity of litter cover, *n* = 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022. We used Poisson or negative binomial distributions to model our richness counts, each with a log link function. We used a likelihood ratio test to select the distribution that best fit each response. We found that two sites had potentially influential values, so we examined the relationship with (*n* = 18) and without these sites (*n* = 16); we show both sets of results here. Estimates and confidence intervals are back-transformed and represent the multiplicative changes in arthropod richness for every 10% increase in the explanatory variable.

Richness variable	**Analyses with 18 sites**						**Analyses with 16 Sites**				
	Covariate	**Estimate**	**95% CI**		**z**	***P***	**Estimate**	**95% CI**		**z**	***P***
All arthropods	Cover	0.9146	0.8349	1.0010	-1.8865	0.0067	0.7225	0.5653	0.9205	-2.6497	0.0081
	Litter	1.0235	0.9584	1.0933	0.6820	0.4952	1.0420	0.9754	1.1132	1.2110	0.2261
Herbivores	Cover	0.8665	0.7821	0.9583	-2.7120	0.0067	0.6885	0.5341	0.8842	-2.9640	0.0030
	Litter	0.9950	0.9273	1.0680	-0.1360	0.8919	1.0243	0.9569	1.0965	0.6940	0.4874
Chewers	Cover	0.8950	0.8222	0.9687	-2.6580	0.0079	0.6914	0.5587	0.8503	-3.4470	0.0006
	Litter	0.9912	0.9387	1.0452	-0.3212	0.7480	1.02277	0.9671	1.0800	0.8000	0.4238
Sap-feeders	Cover	0.7021	0.4989	0.9558	-2.2140	0.0268	0.7163	0.03381	1.5217	-0.9110	0.3620
	Litter	1.0495	0.8675	1.2813	0.5020	0.6155	1.0344	0.8426	1.2849	0.3250	0.7450
Upper trophic	Cover	0.9305	0.7870	1.1134	-0.7640	0.4450	0.5248	0.3022	0.9080	-2.5090	0.0121
	Litter	1.1062	0.9670	1.2733	1.4220	0.1550	1.1314	0.9895	1.3020	1.7420	0.0814
Predators	Cover	0.9967	0.8487	1.1792	-0.0370	0.9706	0.5027	0.3042	0.8154	-2.8800	0.0040
	Litter	1.1470	1.0027	1.3181	1.9880	0.0469	1.1910	1.0525	1.3518	2.8060	0.0050
Parasites	Cover	0.6992	0.5020	0.9415	-2.2380	0.0252	0.5788	0.2621	1.2649	-1.4750	0.1400
	Litter	1.0333	0.8671	1.2389	0.3440	0.7308	1.0485	0.8715	1.2722	0.4640	0.6430
Omnivores	Cover	1.0362	0.9167	1.1598	0.5950	0.5520	1.1995	0.8498	1.6724	1.0550	0.2920
	Litter	1.0632	0.9650	1.1673	1.2640	0.2060	1.0468	0.9419	1.1575	0.8720	0.3830
Detritivores	Cover	0.6403	0.3688	1.0449	-1.8390	0.0659	0.7912	0.2844	2.2533	-0.4400	0.6603
	Litter	1.0630	0.8250	1.4105	0.4180	0.6757	1.0228	0.7853	1.3723	0.1470	0.8835

Table 2. Estimates, 95% confidence intervals, test statistics, and *P*-values for regression models of arthropod richness as a function of heterogeneity (coefficient of variation, CV, %) in vegetation height, *n* = 8 sites, northern range of Yellowstone National Park, summer 2022. We used Poisson or negative binomial distributions to model our richness counts, each with a log link function. We used a likelihood ratio test to select the distribution that best fit each response. Estimates and confidence intervals are back-transformed and represent the multiplicative changes in arthropod richness for every 10% increase in the explanatory variable.

Richness variable	**Estimate**	**95% CI**		**z**	***P***
All arthropods	1.0187	0.9353	1.1107	0.44	0.66
Herbivores	1.0146	0.9244	1.1150	0.32	0.75
Chewing herbivores	1.0157	0.9573	1.0761	0.52	0.60
Sap-feeding herbivores	1.0067	0.9086	1.1106	0.13	0.90
Omnivores	0.9558	0.8642	1.1052	-0.91	0.37
Upper trophic feeders	1.0256	0.8406	1.2640	0.27	0.79
Predators	1.0683	0.8810	1.3057	0.71	0.48
Parasites	0.9605	0.7607	1.2232	-0.36	0.72
Detritivores	1.0295	0.9198	1.1471	0.52	0.60

Table 3. Estimates, 95% confidence intervals, test statistics, and *P*-values for regression models of arthropod richness (overall and by functional group) as a function of productivity metrics (yearly biomass of annuals [g/m^2] and summed INDVI), *n* = 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022. We used Poisson or negative binomial distributions to model our richness counts, each with a log link function. We used a likelihood ratio test to select the distribution that best fit each response. Estimates and confidence intervals are back-transformed and represent the multiplicative changes in arthropod richness for every 10-unit change in biomass or summed INDVI.

Richness variable	**Covariate**	**Estimate**	**95% CI**		**Z**	***P***
All arthropods	Biomass	1.0243	0.9196	1.1411	0.44	0.66
	NDVI	1.0595	0.9410	1.1934	0.97	0.34
Herbivores	Biomass	1.1040	0.9835	1.2401	1.68	0.09
	NDVI	1.0393	0.9145	1.1819	0.59	0.55
Chewers	Biomass	1.0740	0.9906	1.1643	1.73	0.08
	NDVI	1.0830	0.9899	1.1838	1.75	0.08
Sap-feeders	Biomass	1.2595	0.9121	1.7467	1.43	0.15
	NDVI	0.8247	0.5676	1.1927	-1.08	0.28
Upper trophic	Biomass	0.9085	0.7230	1.1395	-0.84	0.40
	NDVI	1.1342	0.8851	1.4600	1.01	0.31
Predators	Biomass	0.8477	0.6734	1.0645	-1.44	0.15
	NDVI	1.1744	0.9198	1.5071	1.29	0.20
Parasites	Biomass	1.0241	0.7388	1.4157	0.15	0.89
	NDVI	1.0623	0.7341	1.5454	0.34	0.74
Omnivores	Biomass	0.8567	0.7314	1.0006	-1.94	0.05
	NDVI	0.9704	0.8211	1.1438	-0.36	0.72
Detritivores	Biomass	1.0790	0.6263	1.7979	0.31	0.75
	NDVI	0.8466	0.5022	1.4277	-0.62	0.53

Table 4: Variance, test statistics, and *P*-values from permutation tests for each vegetation (predictor) variable and each axis from a transformation-based redundancy analysis (tb-RDA) of arthropod morphospecies composition and vegetation variables, *n* = 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022. The full RDA model explained sufficient variation ($F_{6,11}$ = 1.30, *P* = 0.0062).

Variable	**Variance**	$F_{1,11}$	***P***
Vegetation covariate			
CV vegetation cover	0.03539	0.9929	0.4309
CV litter cover	0.02930	0.8220	0.8085
Mean litter cover	0.03138	0.8804	0.6677
Biomass of annuals	0.03692	1.0358	0.3538
Biomass of perennials	0.03865	1.0844	0.2864
Summed INDVI	0.07339	2.0589	0.0019
RDA axis			
1	0.09402	2.6376	0.0163
2	0.05867	1.6459	0.1360
3	0.03574	1.0025	0.9917
4	0.03352	0.9404	0.9882
5	0.03011	0.8448	0.9648
6	0.02521	0.7072	0.8628

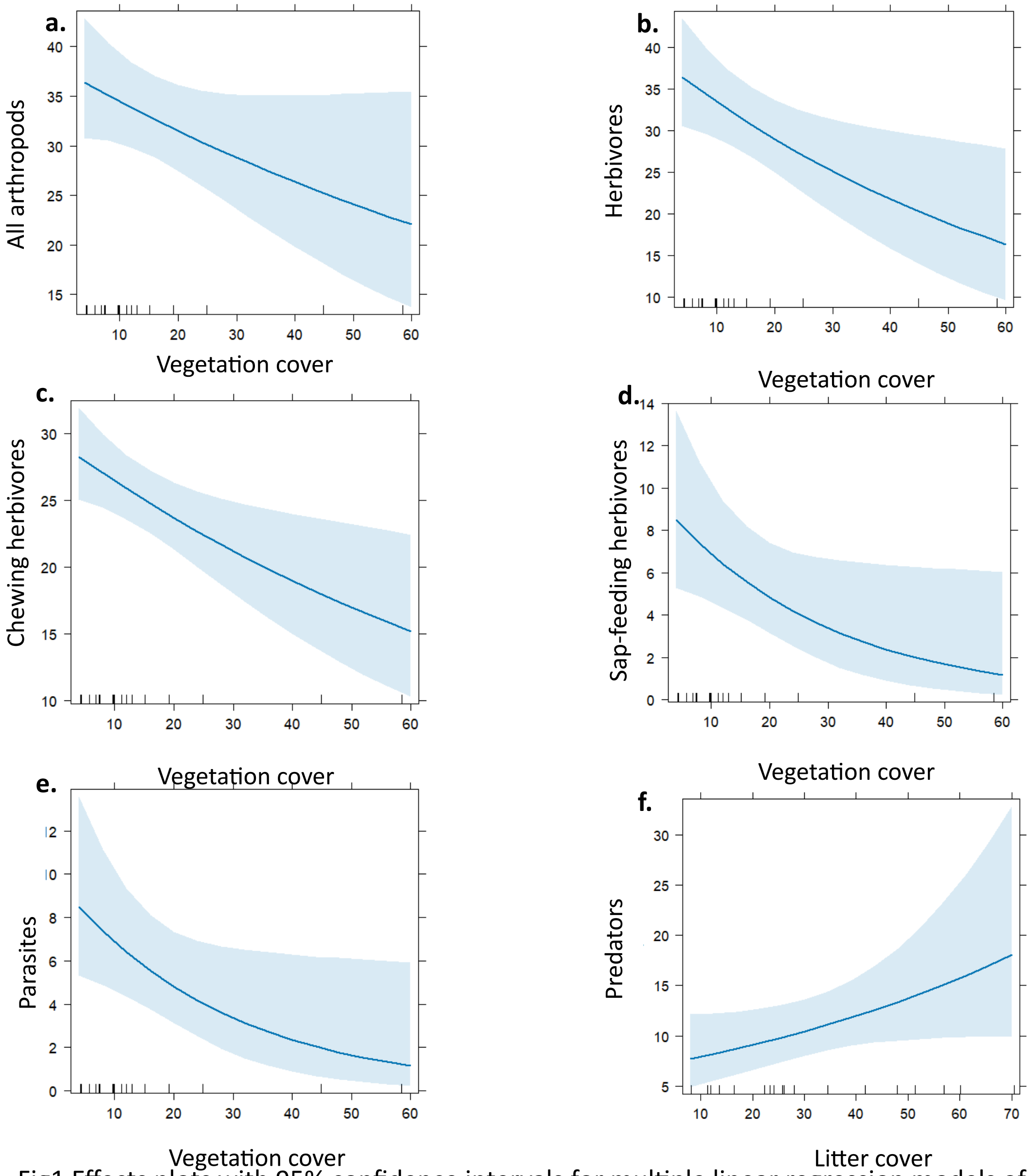

Fig1 Effects plots with 95% confidence intervals for multiple linear regression models of the relationship between morphospecies richness of arthropods and heterogeneity in vegetation cover and litter cover, *n* = 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022. We used Poisson or negative binomial distributions to model our richness counts, each with a log link function. We used a likelihood ratio test to select the distribution that best fit each response. Estimates and confidence intervals represent the multiplicative changes in arthropod richness for every 10% increase in the explanatory variable. Figures show modeled relationships with $P < 0.1$: coefficient of variation of vegetation cover and morphospecies richness of a. all arthropods, b. herbivores, c. chewing herbivores, d. sap-feeding herbivores, and e. parasites, as well as coefficient of variation in litter cover and morphospecies richness of f. predators.

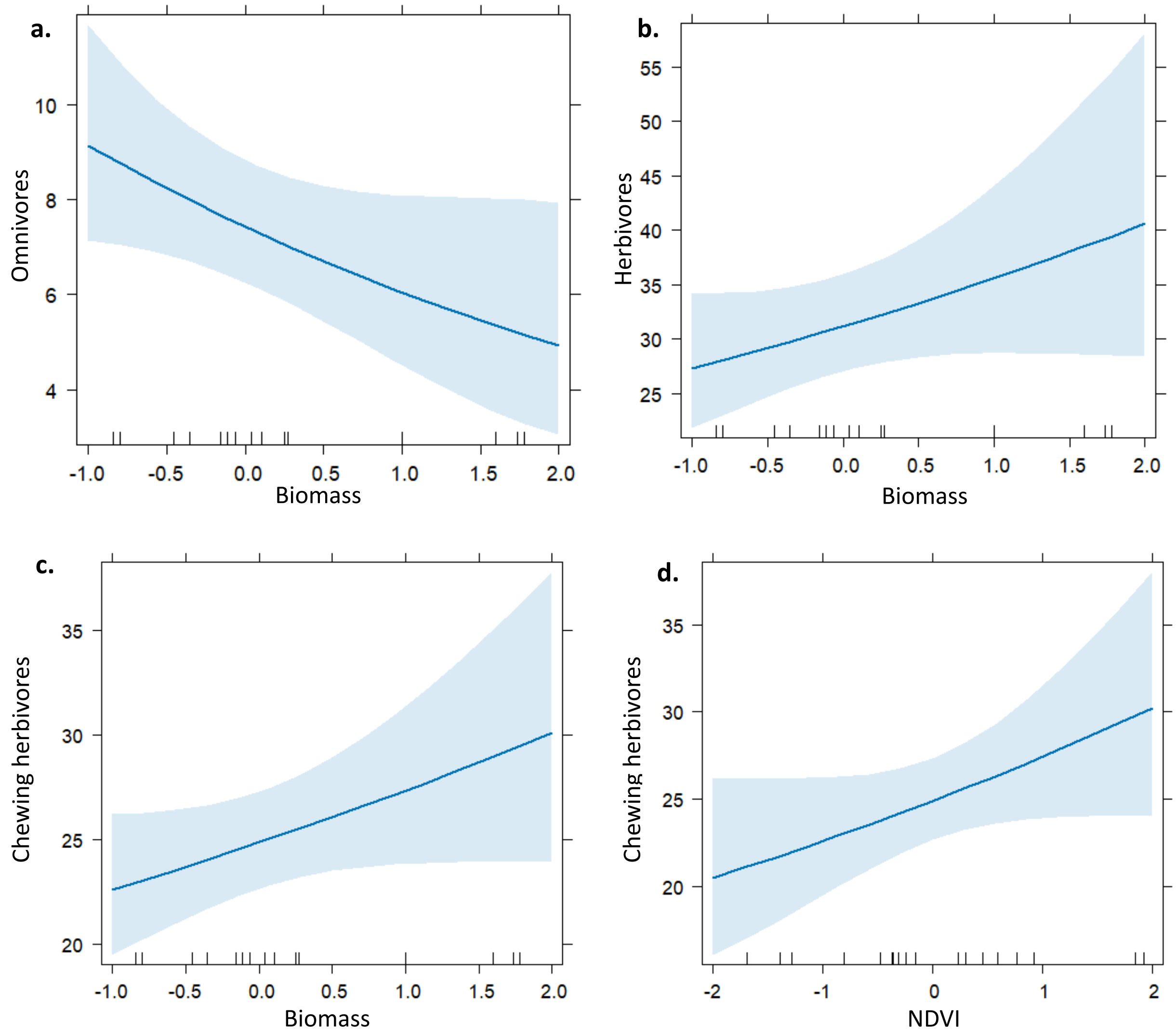

Fig2 Effects plots with 95% confidence intervals for multiple linear regression models of morphospecies richness of arthropods (overall and by functional group) as a function of standardized productivity metrics (yearly biomass of annuals [g/m^2] and summed INDVI), *n* = 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022. We used Poisson or negative binomial distributions to model our richness counts, each with a log link function. We used a likelihood ratio test to select the distribution that best fit each response. Estimates and confidence intervals represent the multiplicative changes in arthropod richness for every 10-unit change in biomass or summed INDVI. Figures show modeled relationships with *P* < 0.1: biomass and morphospecies richness of a. omnivores, b. herbivores, and c. chewing herbivores, as well as summed INDVI and d. chewing herbivores.

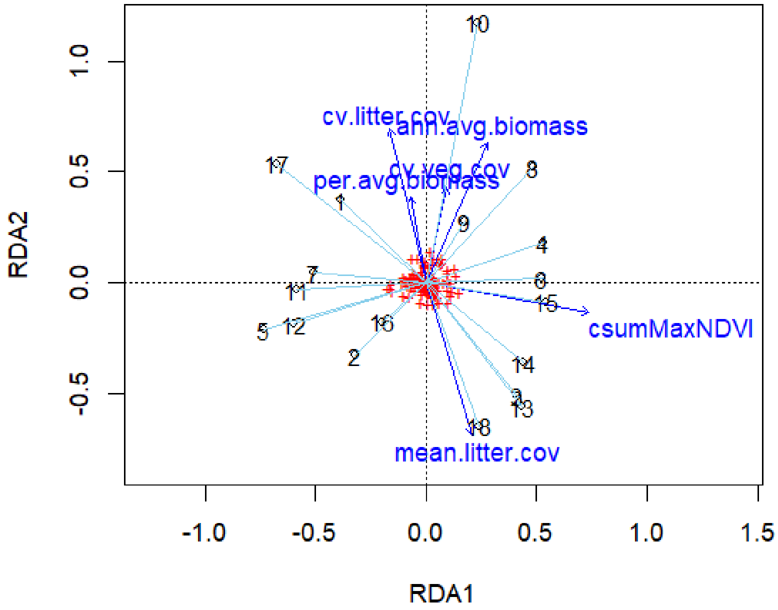

Fig3. Results from a transformation-based redundancy analysis (tb-RDA) of arthropod morphospecies composition and vegetation variables, n = 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022. Sites (numbered in black) are plotted as a function of arthropod composition and correlations with vegetation predictor variables (labeled in blue). We considered the following variables: coefficient of variation (CV) of vegetation cover (cv.veg.cov), CV of litter cover (cv.litter.cov), mean litter cover (mean.litter.cov), yearly biomass (g/m2) of annual vegetation (ann.avg.biomass), yearly biomass (g/m2) of perennial vegetation (per.avg.biomass), summed INDVI (csumMaxNDVI). The length and angle of the arrow express the strength of the relationship; longer arrows and arrows that parallel an axis indicate strong associations. RDA axis 1 explained 14% of the variation in arthropod composition, which was mainly associated with summed INDVI.

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CHAPTER THREE

BUGS AND BISON: EXPLORING THE LINKS BETWEEN GRASSLAND ARTHROPODS AND A NATIVE MEGAHERBIVORE

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Abstract

Historically, American bison (*Bison bison*) were dominant sources of disturbance in North American grasslands. Bison create a range of conditions, which may be an important force driving community composition. We examined the variation in disturbance by bison in relation to arthropod communities in grasslands of Yellowstone National Park, specifically testing the intermediate disturbance hypothesis. We collected arthropods during two summer growing seasons and characterized disturbance intensity using utilization distributions based on GPS data from collared bison. We used generalized linear models and multivariate analyses. Contrary to our predictions, we found the greatest richness of arthropods, detritivores, upper trophic feeders, and parasites in areas with low and high intensities of disturbance, rather than in areas with moderate disturbance. Richness of herbivorous sap-feeding arthropods decreased with the intensity of bison disturbance. Our multivariate analysis suggested a relationship between disturbance intensity and composition of arthropod communities, but this mainly was driven by a few sites. The mosaic of conditions created by bison disturbance plays a role in the composition of arthropod communities. Quantifying exactly how bison are influencing plants and the habitat conditions across the spectrum of disturbance intensity could demonstrate interconnections between megaherbivores, arthropods, and plants.

Implications for insect conservation: Bison disturbance creates differential conditions across the landscape that could support greater arthropod diversity. Conserving migratory grazing patterns and other natural disturbance regimes may have important conservation implications for arthropod communities in grassland systems.

Introduction

Grasslands are an important biome that provide an array of ecosystem services that benefit a wide diversity of species, including humans (Petermann and Buzhdygan 2021). Historically, grasslands comprised as much as 42% of the global land mass (Anderson 2006). Yet as human populations have increased, grasslands have decreased, by as much as 98% in some areas (Anderson 2006; Petermann and Buzhdygan 2021). Different types of grasslands (i.e., savanna, steppe, prairies) have unique features, yet all grasslands have some key characteristics in common (Lauenroth, Burke, and Gutmann 1999; Petermann and Buzhdygan 2021). Grasslands are characterized by the dominance of non-woody vegetation, especially plants in the family Poaceae, seasonal variation in temperature, as well as diverse disturbances, including drought, fire, and herbivory (Lauenroth, Burke, and Gutmann 1999; Petermann and Buzhdygan 2021).

Disturbances could be key drivers of the extraordinary biodiversity that also characterizes grasslands (Anderson 2006; Lauenroth, Burke, and Gutmann 1999; Petermann and Buzhdygan 2021). The intermediate disturbance hypothesis (Fox 1979; Joern and Laws 2013; Gao and Carmel 2020) is premised on the idea that low and high levels of disturbance lead to more homogenous conditions that support fewer species or taxonomic groups, whereas more moderate levels of disturbance create the most heterogeneous conditions to support needs of more species (Adler et al. 2005; Joern and Laws 2013; van Klink et al. 2015). Empirical support for the intermediate disturbance hypothesis has been mixed (Catford et al. 2012; Fox 1979; Schwilk, Keeley, and Bond 1997), which could be in part because there is no standard for what constitutes “intermediate”. However, the hypothesis has provided insights about diversity in certain systems, such as trees in tropical forests (Connell 1978), the effects of invasive plants (Catford et al. 2012), and recovery of coral after hurricanes (Rogers 1993). In grasslands, disturbance from megaherbivores is one of the major sources of disturbance and may be an important force behind community composition (McMillan et al. 2019; Moran 2014; Olff and Ritchie 1998).

Historically, American bison (*Bison bison*) were dominant sources of disturbance in North American grasslands (Freese et al. 2007). Bison numbered in the tens of millions in wild herds across the continent, which contributed to plants developing adaptations to herbivory, such as high capacity for regrowth (Larson et al. 2001; McNaughton 1984; Olff and Ritchie 1998). Bison are aggregate grazers in the summer months, feeding in groups of hundreds or thousands (Geremia et al. 2019). Bison are one of the largest modern ungulates on the continent (Knapp et al. 1999). Based on their size and their aggregate grazing patterns, bison often are deemed ecosystem engineers because of their significant ecosystem influences (Geremia et al. 2019; Knapp et al. 1999; Nickell et al. 2018). As aggregate grazers, bison consume huge amounts of biomass simultaneously in highly productive areas referred to as grazing lawns, where they return repeatedly throughout the growing season (Geremia et al. 2019; Frank et al. 2017; McNaughton 1984). The grazing lawns consist of shorter-statured plants of higher nutritional content that senesce later in the season, compared to nearby areas with less consistent grazing (Geremia et al. 2019; Milchunas et al. 1995). Through different degrees of herbivory and soil disturbance, bison create a range of conditions capable of supporting diverse species, including arthropods (Joern and Laws 2013; Moran 2014; Oertli et al. 2005; van Klink et al. 2015).

Arthropods are a significant source of biodiversity in grasslands (Joern and Laws 2013; Whiles and Charlton 2006), with different functional groups playing diverse roles vital to ecosystem processes (Joern and Laws 2013; Redak 2000; Whiles and Charlton 2006). For example, arthropods provide key food resources for many species, detritivores aid in nutrient cycling, and many plants require arthropods as pollinators (Redak 2000; Whiles and Charlton 2006). Many species of arthropods have short life cycles, and as such, populations often respond quickly to environmental change (Joern and Laws 2013), yet the factors that drive these responses are less clear (Joern and Laws 2013; van Klink et al. 2015). Further, different species and functional groups may differ in the direction and magnitude of their responses to change (Redak 2000), which increases the challenge of discerning general patterns and mechanisms (Joern and Laws 2013).

Megaherbivores may influence arthropods directly through trampling and ingestion, indirectly as herbivory and soil disturbance change characteristics of the soil, nutrient cycling, or plants, or some combination of these effects (van Klink et al. 2015). Influences of megaherbivores on arthropods have been negative, positive, and non-significant, with results differing depending on the megaherbivore, study location, and focal group of arthropods (Batáry et al. 2007; Cully 1999; Moran 2014). Understanding which factors drive this variation in responses is critical for broad ecological insights (Joern and Laws 2013). Previous work often has focused on a single taxon of arthropods (Joern 2005; Spalinger et al. 2012; van Klink et al. 2015) or examined disturbance as a binary factor (e.g., grazed vs. ungrazed, (Cully 1999; Moran 2014), which could limit our ability to distill patterns in responses. Considering functional groups of arthropods and quantifying the intensity of disturbance could add to our understanding and guide future research directions.

Today, bison occupy less than 1% of their historic range (Freese et al. 2007; Geremia et al. 2019) and are reduced to domestically ranched herds and a small percentage of wild bison in conservation herds (Freese et al. 2007; Geremia et al. 2019; Meagher 1986). Although bison are not endangered, typically there are some human-imposed limits on their movements and population growth (Freese et al. 2007). Habitat loss, decreases in population size, and restricted migration has made it difficult to gain insight about the full ecological role of bison (Knapp et al. 1999). However, we are gaining some understanding about the importance of bison in the function and diversity of North American grasslands based on the accumulation of studies on some of these disconnected conservation herds (Frank and

McNaughton 1992; Geremia et al. 2019; Nickell et al. 2018; Ratajczak et al. 2022). The largest conservation herd of bison occurs in Yellowstone National Park (YNP) (Berger and Cain 1999; Geremia et al. 2019). In this system, bison are free ranging and primarily follow their preferred migration paths.

We used an observational study in YNP to examine how variation in disturbance by bison influences arthropod communities. In accordance with the intermediate disturbance hypothesis (Fox 1979; Grime 1973; Joern 2005), we expected that species richness of arthropods – overall and within each functional group – would be maximized when disturbance by bison is at intermediate levels. We completed our work in two different types of grasslands: mesic grasslands dominated by rhizomatous grasses and drier sagebrush-steppe dominated by bunchgrasses; we predicted differences in the composition of the arthropod communities between these types.

Methods

Study Area

Yellowstone National Park occurs in the western United States (Idaho, Montana, and Wyoming) and consists of two distinct areas: the central range and the northern range. The northern range (1,556 km^2) makes up the northern third of YNP (Beyer et al. 2007) and contains lower elevations (1600-2200 m) on average (Singer and Renkin 1995) than the central range (2130-2590 m) (Hague 1921). Lower elevation areas receive less snow, creating a generally drier environment (Plumb et al. 2009). Overall YNP has a short growing season occurring between the primarily snow-free months from May to September; the northern range has a slightly longer snow-free period than the central range (Geremia 2014; Singer and Renkin 1995).

The lower elevation, lower snowpack, and longer snow-free period make the northern range a desirable area for wildlife. Currently, most of the bison population (4000 of roughly 5000 individuals, Geremia 2014) uses the northern range as their primary grazing grounds; we completed our work in the northern range to coincide with these main grazing areas and greatest bison density.

Bison move and graze across wide valleys made up of two primary types of grasslands: rhizomatous mesic grasslands or drier bunchgrass-dominated sagebrush steppe (Frank, Wallen, and White 2016). Many of the more mesic grasslands were cultivated as hayfields in the early 20th century (Meagher 1973) and are primarily dominated by several species of perennial non-native grasses (e.g., Kentucky bluegrass [*Poa pratensis*] and Timothy-grass [*Phleum pratense*], Hamilton III and Frank 2001; Stoughton and Marcus 2000). Plants in these more mesic grasslands often grow faster and are less limited by nitrogen and water, giving them more capacity for regrowth, which experience higher intensities of grazing (Frank, Wallen, and White 2016). The grasses in the sagebrush steppe are primarily native bunchgrasses (e.g., Sandberg bluegrass [*Poa secunda*], Idaho fescue [*Festuca idahoensis*], and prairie junegrass [*Koeleria macrantha*]) (Boccadori et al. 2008). This plant community typically has lower aboveground net primary production than the more mesic grasslands (Frank, Wallen, and White 2016).

Site Selection

We selected study sites (8,000-78,000 m^2 areas) that had similar characteristics, namely annual primary production, temperature, and precipitation, based on remotely sensed data (Xu and Guo 2014). First, we computed annual normalized difference vegetation index (NDVI), maximum NDVI, and the Julian date of peak NDVI for the raster pixels (Landsat8, 30 x 30 m pixels) on the northern range between 2013 and 2017. We excluded forested areas based on an available vegetation layer. We included annual net temperatures and annual average precipitation from Parameter-elevation Regressions on Independent Slopes Model (PRISM) databases for 2013 through 2017 (Daly and Bryant 2013). We used these remotely sensed data and hierarchical clustering to collect subsets of raster pixels into distinct groups. We then used these groupings as a training dataset for a machine learning algorithm to classify all the remaining raster pixels in the northern range into the rhizomatous or bunchgrass-dominated grasslands based on their NDVI value.

After locating areas with similar vegetation characteristics, we stratified sites based on the intensity of disturbance by bison. We combined GPS data from all collared bison on the northern range for summers, representing the vegetation growth period, across five years (2013-2017, 82 total individuals). Based on these data, we calculated utilization distributions with Brownian-Bridge movement models (Kranstauber et al. 2012). We used the probability of utilization in each site as a measure of intensity of disturbance and then stratified site selection based on 3 categories (low, medium, and high intensity). Sites with <90% probability of use was categorized as low intensity, medium intensity was 90-99%, and high intensity was ≥99%.

We aimed to select at least 3 sites for each combination of disturbance intensity (low, medium, high) and grassland type (rhizomatous or bunchgrass-dominated); sites were separated by at least 1.6 km to maintain independence. We selected 18 total sites: 10 sites in the rhizomatous grasslands (4 high, 3 moderate, and 3 low-intensity disturbance by bison) were sampled in 2021 and 8 sites in the bunchgrass-dominated grasslands (3 high, 2 moderate, and 3 low intensity) were sampled in 2022. Our study area experienced drought conditions in 2021 and an abnormal rain and flooding event in 2022. Any differences between years could therefore result from the different grassland types, variation in soil moisture, variation created by weather conditions, or some combination of influences.

Timing of Sampling

We used the timing of peak vegetation biomass to inform the timing of our sampling, to reduce variation based on vegetation phenology and productivity. We determined peak biomass based on NDVI data averaged over 5 previous years.

Arthropods

We sampled flying and vegetation-dwelling arthropods using vacuum sampling methods (Buffington and Redak 1998) one week prior to peak biomass. We used a vacuum/blower (DeWalt DCBL720B 20V Max Lithium Ion XR, reverse motor) to sample a 0.7 x 0.7-m area for 2 minutes, using a grid pattern to ensure uniform sampling; we repeated this sampling at 5 random locations in each site. Immediately after collection, we sprayed the sample with ethanol (80% dilution) to reduce predation and stored samples in a freezer for later sorting and identification.

We sorted specimens from plant matter and detritus using a series of metal sieves (2 mm [No. 10], 1 mm [No. 18], and 500 µm [No. 35] sizes, U.S.A Standard Test Sieve, ASTM E11 specification) and removing arthropods at each stage. Collected arthropods were sorted into morphospecies based on their visible morphological characteristics (Oliver and Beattie 1996). We assigned a number to each morphospecies and identified taxonomic order or family depending on which was necessary to determine a functional group. We identified all collected arthropods to functional group: chewing herbivores, sap-feeding herbivores, pollinators, omnivores, detritivores, predators, parasites, and non-feeders (Johnson and Triplehorn 2004). We grouped all individuals in the family Formicidae into several morphospecies based on their color, hair, and spines. We also lumped all “daddy long-leg” species as Opiliones due to the condition of those samples and difficulty of differentiation. Orthoptera instars were all assigned to one morphospecies due to identification challenges. For members of the order Diptera, we used the functional groups of the larval stage for that family, even though our samples were captured in the adult stage. Diptera often spend up to 11 months as larva, and only days as adults, making the larval functional group more ecologically meaningful (McAlpine 1981). All non-feeders were adult forms of aquatic macroinvertebrates.

We computed overall richness as the number of morphospecies sampled per site. Similarly, we computed richness for each functional group. We also computed richness for a combined group of herbivores – the summed richness of chewers, sap-feeders, and pollinators, and a group of upper trophic feeders – predators and parasites combined. We had low numbers of non-feeders and pollinators, so we did not analyze these functional groups independently.

Disturbance Intensity

To create a continuous measure of disturbance intensity to use in our analyses, we again calculated utilization distributions for bison with Brownian-Bridge movement models (Kranstauber et al. 2012). We used the probability of utilization in each site as a measure of intensity of disturbance by bison. We computed the average utilization distribution values over five years (2013-2017) for each site (*n* = 82 collared bison). We also considered values from utilization distribution models for the specific year of sampling, but these were correlated with the 5-year average (Pearson's r = 0.74). We used the 5-year averages to characterize disturbance intensity in our analyses, as these were computed based on a larger number of GPS points and are more likely to accurately reflect the influences on plant growth patterns over longer time frames, which may have strong relationships with the arthropod communities.

Statistical Analysis

We used generalized linear models to explore support for the intermediate disturbance hypothesis, modelling the relationship between intensity of disturbance by bison and overall arthropod richness, as well as richness of each functional group. We considered both Poisson and negative binomial distributions to model the richness counts, each with a log link function. We selected the distribution that best fit each response based on likelihood ratio tests. We fit models using the *glm* and *MASS* packages (Venables and Ripley 2013) in R (R Core Team, 2021). We centered and scaled the continuous covariate for disturbance intensity. We first explored evidence for a quadratic relationship, as predicted by the intermediate disturbance hypothesis. If we found limited support (i.e., $P > 0.1$), we removed the quadratic term and fit a simple linear relationship. All analyses were completed using R version 4.3.3 (R Core Team, 2021).

Additionally, we explored the composition of the arthropod communities using multivariate methods. We ordinated the arthropod data using a principal component analysis (PCA) with the *vegan*, *factomineR*, and *factoextra* packages (Kassambara and Mundt 2020; Lê, Josse, and Husson 2008; Oksanen et al. 2024). We calculated the mean eigenvalues for all axes and retained axes with eigenvalues greater than the mean. To understand the potential influence of bison disturbance on the arthropod community, we explored correlations of each principal component axis with disturbance intensity. For any axes that were highly correlated ($r \geq |0.6|$), we modeled the relationship using linear regression and explored the identities of any arthropods strongly associated ($r \geq |0.6|$) with that principal component.

Results

Richness of some arthropod groups changed based on the degree of disturbance by bison (Table 1). We found evidence of a quadratic relationship for richness of all arthropods, detritivores, parasites, and the combined upper-trophic group (Table 1). However, these relationships were opposite of that predicted by the intermediate disturbance hypothesis, as we found the lowest arthropod richness at moderate levels of disturbance by bison (Fig1). Richness of sap-feeders decreased linearly with increased disturbance, but we failed to detect relationships for other functional groups (Table 1).

Arthropod composition varied among our sampled sites. Some of this variation was associated with disturbance by bison, but also was likely related to differences between the two grassland types and years of sampling. The first principal component separated arthropod communities in the bunchgrass-dominated sites we sampled in 2022 from the rhizomatous grasslands sampled in 2021 (Fig2); this axis explained 14.2% of the variation in arthropod composition. The second principal component (PC2) explained 9.8% of the variation and was associated with bison disturbance (r = -0.64, Table 2, Fig3). Two sites with low intensity disturbance were potentially influential in this relationship (Fig2 a). These two sites were geographically distant from each other, represented both grassland types, and were sampled in different years. Most of the arthropod morphospecies (12%, 23 morphospecies) correlated with PC2 occurred solely in one of these two sites (Table 2). Of these species, 52% were herbivores, specifically chewing herbivores (39%), and 26% were predators. Hemiptera (all herbivores) and Diptera (various functional groups) comprised most of these species (30% and 17.4%, respectively). We also explored variation in composition of the arthropod community without these two sites, creating a new PCA (n = 16 sites, Fig2 b). Most of the variation was again explained by grassland type/sampling year; the first axis explained 15.1% of the variation (Fig2 b). However, no axes from this second PCA were strongly correlated (all correlations ≤ |0.5|) with disturbance intensity.

Discussion

Disturbance is a clear driver in grasslands, given that many grassland species have adaptations to fire, herbivory, and drought (Anderson 2006; Petermann and Buzhdygan 2021). These disturbances operate at different frequencies, intensities, return intervals, and spatial scales creating conditions that support diverse species (Adler et al. 2005; Anderson 2006; Davis et al. 2014; Lytle 2001). We found evidence that disturbance by bison influenced arthropods, but insights differed based on functional group, reflecting different needs among arthropod groups (Joern 2005; Nock, Vogt, and Beisner 2016; Podgaiski et al. 2014).

Other studies focused on relationships between large herbivores and arthropods also have found variation in responses that could be, in part, attributable to the diversity of habitat requirements and functional traits (reviewed in van Klink et al. 2015). van Klink et al. (2015) reviewed 141 studies focused on large herbivores and arthropods and found that the most common trend was a negative relationship, although they mainly focused on linear relationships. We found a negative linear relationship between richness of sap-feeding herbivores and intensity of disturbance by bison which could suggest that the plants these arthropods feed on were more prevalent with less herbivory and trampling by bison. Batáry et al. (2007) found that higher levels of grazing had a negative effect on the richness of generalist herbivorous beetles in grasslands but limited effects on specialist herbivorous beetles. One explanation for these somewhat conflicting results is that the generalist species were more reliant on heterogeneity and increased grazing created more homogeneous conditions, whereas the specialists relied on plant species that were not reduced with grazing (Batáry et al. 2007). Including detailed functional traits when exploring the relationships between disturbance and arthropod communities will be essential for understanding complex responses.

Although theory suggests that moderate disturbance increases the chances that more types of species will find their preferred niche conditions, empirical evidence for the unimodal relationship predicted under the intermediate disturbance hypothesis has been inconsistent (Fox 1979; Podgaiski et al. 2014; Schwilk, Keeley, and Bond 1997). Collins and Barber (1986) found evidence of a unimodal relationship between grazing and plant diversity, yet the highest diversity occurred in areas with light to moderate grazing, with interacting influences of the presence of wallows and fire. In our case, we found evidence of a curvilinear relationship for arthropod richness overall, as well as richness of detritivores, parasites, and the upper trophic group, yet richness of each was lowest at intermediate levels of disturbance. These departures from our predictions may be due to multiple mechanisms. Bison may influence habitat conditions in different ways across the spectrum of disturbance intensity (Knapp et al. 1999). Detritivores may benefit from accumulation of plant litter where disturbance by bison is lower but also could consume dung litter where bison spend more time. Different species of parasites may be capitalizing on different hosts in areas with low and high disturbance intensity (van Klink et al. 2015). Arthropod predators vary in their hunting strategies, with some that require dense vegetation for hiding and stalking prey and others that need lower cover and bare ground that may be more likely in areas with higher intensity disturbance (Joern and Laws 2013; van Klink et al. 2015). We found that some arthropod morphospecies occurred only at a single site, suggesting that species' preferred conditions could be spatially limited, and that a mosaic of conditions also could be created at larger spatial scales than our individual study sites. Additionally, future work will likely find further relationships by including functional traits based on life history attributes that we did not define; for example some specialist species may require specific conditions related to either high or low intensity of disturbance. Although we postulated that moderate disturbance may provide heterogenous conditions that could support arthropods that prefer the ends of the disturbance spectrum, moderate levels of disturbance may instead create marginal conditions for these species. Further explorations of the specific habitat requirements of arthropod groups, as well as the actual conditions created along the spectrum of disturbance intensity provide an excellent platform to generate future research questions.

Bison, and other megaherbivores, may influence the character of a site through herbivory, trampling, soil disturbance, and even defecation (Olff and Ritchie 1998; van Klink et al. 2015); each of these influences could create different conditions for arthropods and other species. We used movement data to make inferences about the intensity of disturbance by bison; yet these data do not distinguish what the animals were doing in these locations. Other studies have included information about wallow prevalence, litter composition (plant material versus dung), vegetation height, or vegetation species composition to parse out these direct and indirect effects (Collins and Barber 1986; Nickell et al. 2018; Olff and Ritchie 1998; van Klink et al. 2015). Manipulative experiments that combine exclosures, simulated grazing (e.g., clipping vegetation), and natural bison disturbance may be necessary to clarify the separate and interactive influences of movement patterns, herbivory and soil disturbance. Additionally, we did not account for variation in timing, frequency, or return intervals of these grazers (Petermann and Buzhdygan 2021; Podgaiski et al. 2014; van Klink et al. 2015). All these factors could have different influences on the arthropod community depending on their alignment with patterns of growth and reproduction in arthropod species.

Disturbances such as fire or grazing often are referenced as creating a mosaic of conditions on the landscape that benefit many species (Joern 2005). We predicted that diversity would be maximized by moderate intensities of disturbance but we did not find this to be true at the scale of our sites. We found some morphospecies in just one or a few sites, which could suggest that this mosaic of conditions occurs at a larger spatial scale. As grasslands have decreased in size, many of the disturbance regimes that characterized these systems also have been lost or severely altered (Anderson 2006; Petermann and Buzhdygan 2021). Efforts to conserve these imperiled ecosystems also must consider maintaining or restoring ecological processes, including the natural migration paths and grazing patterns for native herbivores such as bison, to retain floral and faunal diversity.

Table 1: Estimates, standard errors, test statistics and *P*-values for all regressions between arthropod richness and intensity of disturbance by bison, 18 sites, northern range, Yellowstone National Park, summers 2021 and 2022. We first explored evidence for quadratic relationships; when quadratic terms were not significant, we used simple linear regression.

Richness Term	**Covariate**	**Estimate**	**Std Error**	**z**	***P***
All arthropods	Bison use	-0.0421	0.0599	-0.70	0.48
	Bison use^2	0.1618	0.0891	1.82	0.07
Detritivore	Bison use	-0.1919	0.2194	-0.87	0.38
	Bison use^2	0.8864	0.3514	2.52	0.01
Upper trophic	Bison use	0.0196	0.1258	0.16	0.88
	Bison use^2	0.3148	0.1869	1.68	0.09
Parasites	Bison use	0.0504	0.1650	0.31	0.76
	Bison use^2	0.6402	0.2580	2.48	0.01
Predators	Bison use	-0.0262	0.1394	-0.19	0.85
Herbivores	Bison use	-0.0785	0.0764	-1.03	0.30
Chewers	Bison use	-0.0110	0.0483	-0.23	0.82
Sap-feeders	Bison use	-0.3768	0.1703	-2.21	0.03
Omnivores	Bison use	-0.0270	0.0878	-0.31	0.76

Table 2: Taxonomic order and feeding group of arthropod morphospecies most associated (r ≥ |0.6|) with the second axis (Dim2) of a principal component analysis, along with correlations and the number of sites where the morphospecies was collected, 18 total sites, northern range, Yellowstone National Park, summers 2021 and 2022. The second axis (Dim2) was negatively correlated with intensity of bison disturbance (Figure 2 A).

Order	Functional group	Correlation	# sites
Diptera	Sap-feeder	0.6416	1
	Chewer	0.6416	1
	Predator	0.6416	1
	Predator	0.6416	1
Lepidoptera	Chewer	0.6416	1
	Chewer	0.6416	1
	Chewer	0.6416	1
Coleoptera	Chewer	0.6416	1
	Chewer	0.6416	1
Araneae	Predator	0.6416	1
Acari	Parasitic	0.6416	1
Isopoda	Detritivore	0.6416	1
Diptera	Predator	0.6101	1
	Detritivore	0.6101	1
	Detritivore	0.6101	1
Hemiptera	Sap-feeder	0.6101	1
	Sap-feeder	0.6101	1
	Sap-feeder	0.6101	1
	Chewer	0.6101	1
Araneae	Predator	0.6101	1
	Predator	0.6101	1
Hymenoptera	Parasitic	0.6101	1
Coleoptera	Chewer	0.6101	1
Trichoptera	Non-feeder	-0.6138	11

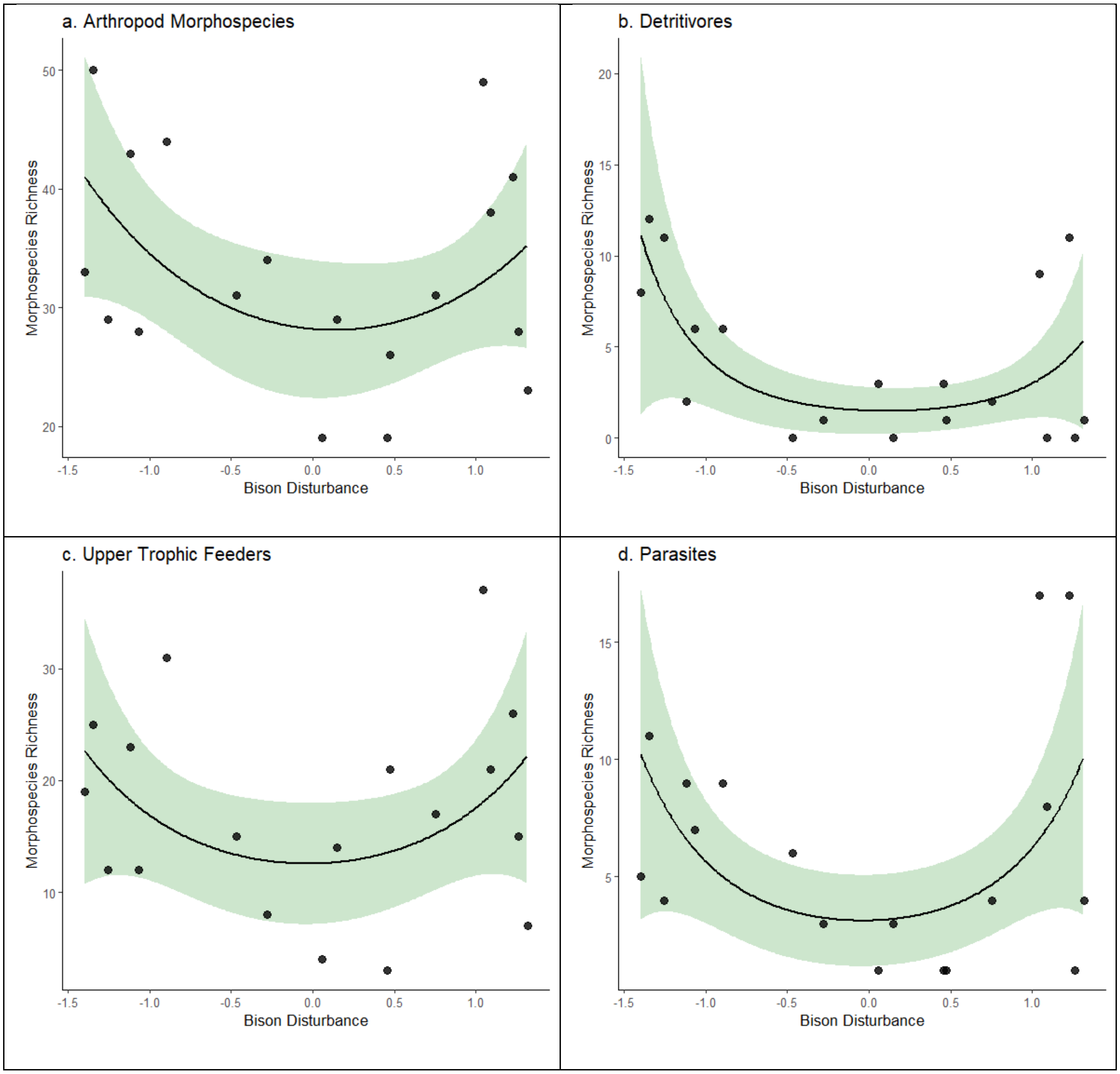

Fig1 Quadratic relationships (and 95% confidence intervals) between richness of: a) all arthropod morphospecies, b) detritivores, c) upper trophic feeders, and d) parasites and the intensity of disturbance by bison, 18 sites, northern range, Yellowstone National Park, summers 2021 and 2022. We quantified disturbance intensity based on Brownian-Bridge model utilization distribution values of probability of bison use); these values were standardized for analysis and plotting.

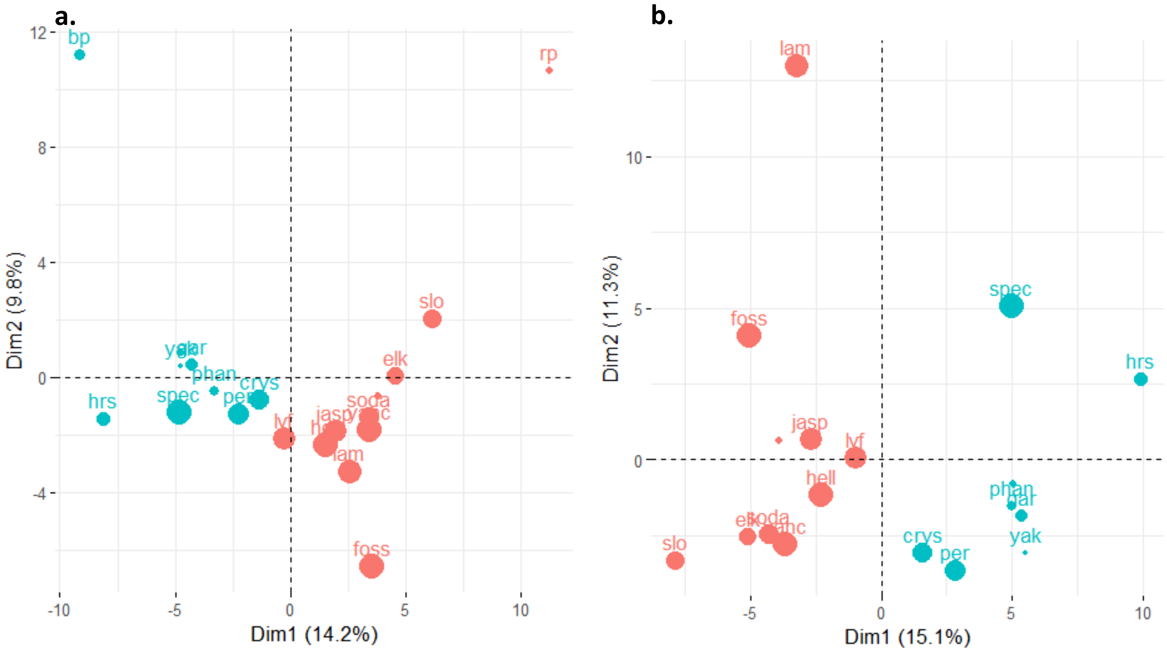

Fig2 Variation in the composition of the arthropod community, based on the first two axes of a principal component analysis (PCA) based on: a) all 18 sites and b) 16 sites, northern range, Yellowstone National Park, summers 2021 and 2022. Points are colored based on grassland type and sampling year (blue: mesic grasslands sampled in 2021, red: xeric grasslands sampled in 2022). Points are sized based on a measure of the intensity of disturbance by bison, from low intensity (smaller dots) to high intensity (larger dots). In both PCAs, the first principal component (Dim1) separated sites based on grassland type and sampling year; PC1 explained 14.2% of the variation in a and 15.1% of the variation in b. In a, the second principal component (Dim2) explained 9.8% and was correlated with a measure of the intensity of disturbance by bison. Given that 2 sites with low intensity disturbance (“bp” and “rp”) seemed influential in this relationship, we redid the PCA without these sites (b); Dim2 now explained 11.3% and was no longer correlated with disturbance intensity.

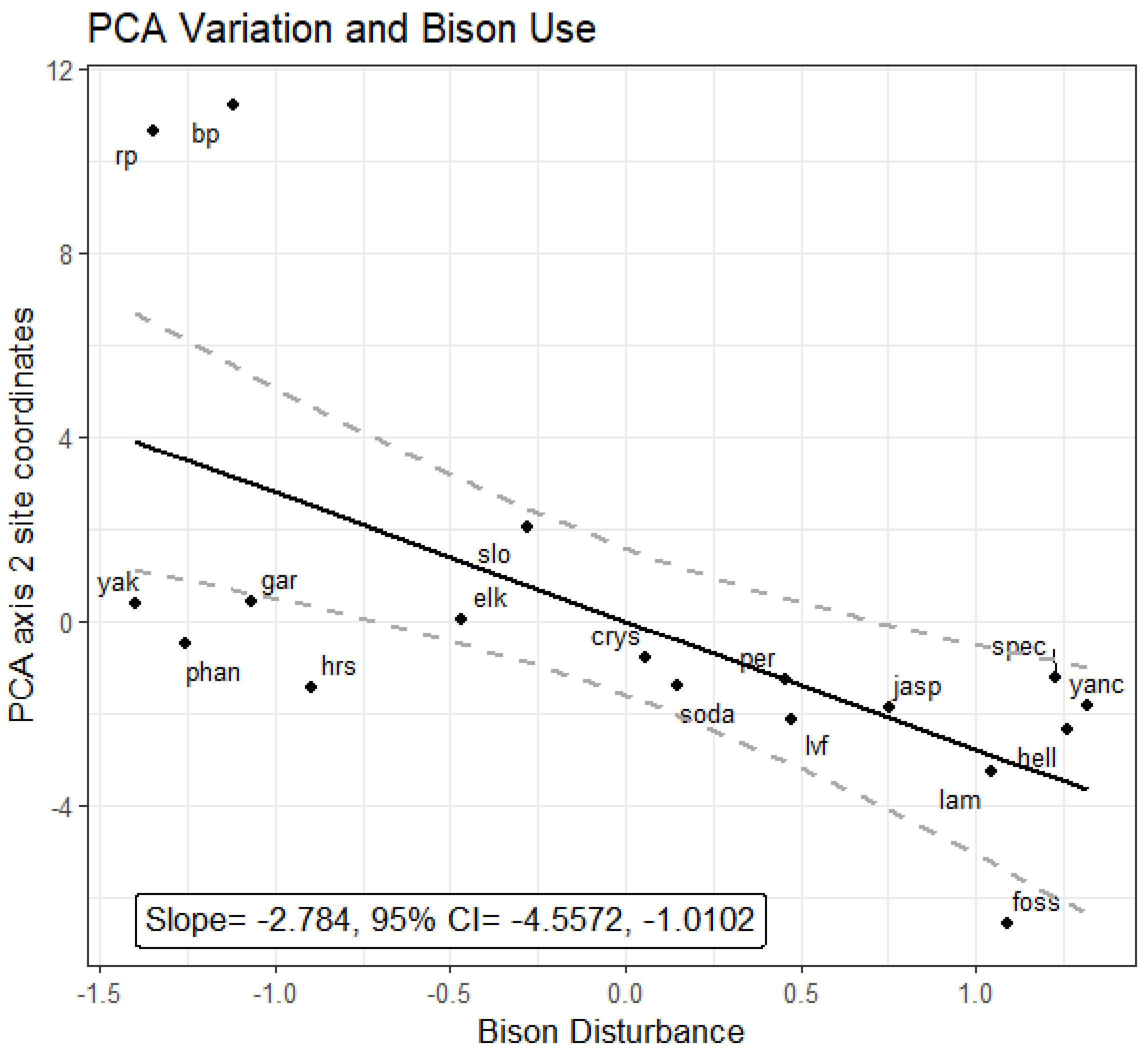

Fig3 Relationship (and 95% CI) between arthropod composition (based on the second axis of a principal component analysis) and intensity of disturbance by bison (standardized Brownian-Bridge utilization distribution values), 18 sites, northern range of Yellowstone National Park, summers 2021 and 2022.

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CHAPTER FOUR

CONCLUSION OF THESIS

Many different drivers may work in concert to shape community composition (Joern and Laws 2013; Mittelbach and Mcgill 2019). Each of these may act directly, indirectly, or interactively to create more niches and reduce competition (Coops et al. 2019; Joern and Laws 2013; Milchunas et al. 1995; Wang, Tang, and Fang 2009). The challenge in investigating mechanisms of community assembly is distinguishing among the disparate forces that may be operating on different taxa.

In this thesis, I found the above pattern of complexity reflected; the degree of support for each hypothesis differed and varied by functional group. Yet, simultaneously examining several hypotheses in the same system provided some unique observations that would have been missed by focusing on a singular mechanism. For example, we found that herbivores had a negative relationship with habitat complexity, but a positive relationship with plant productivity, and we did not detect a relationship with bison disturbance. These collective findings suggest that vegetation quantity and quality, rather than variability, are particularly important to herbivorous arthropods. Including functional traits of our sampled arthropods also helped to reveal some important patterns. For example, we found that although richness of herbivores declined with increased habitat complexity, richness of predators increased. In concert, these findings make a lot of biological sense; herbivores are more directly impacted by the amount and quality of vegetation as a food source, whereas predators are more likely to be impacted by the structural traits of the vegetation to support their hunting strategy (e.g., web-spinning spiders (Laws and Joern 2013; van Klink et al. 2015).

The findings in this thesis contribute to our knowledge about biodiversity drivers and highlight avenues for future research. Given that many arthropods could be classified into several feeding groups, and have a variety of diverse life history strategies, adding more detail about functional traits would likely provide additional insights into the mechanisms driving diversity (Nock, Vogt, and Beisner 2016). Information about hunting strategies, distinguishing between generalist and specialist feeders, phenology, and reproductive strategies could help us understand the niche dimensions of different groups (Batáry et al. 2007; Laws and Joern 2013; Moran 2014). Combining this with additional details characterizing the disturbance created by megaherbivores, such as wallow presence, litter composition, and vegetation composition could demonstrate interconnections between megaherbivores, arthropods, and plants (Collins and Barber 1986; van Klink et al. 2015). Sampling over longer periods to characterize temporal variation would build on our snapshot of the arthropod community and assist in parsing out climatic influences (Laws and Joern 2013; Moran 2014; Nickell et al. 2018).

This research represents the first comprehensive survey of arthropod communities in the grasslands of Yellowstone National Park. Although many questions remain, this thesis research supports the idea that a variety of conditions, including productive vegetation, 3-dimensional habitat complexity, and natural disturbance regimes, are required to support the different needs of a variety of organisms (Báldi 2008; Chesson 1985; Collins and Barber 1986; Mittelbach et al. 2001). Although grasslands have declined worldwide, there is a current recognition that these biomes are important to protect (Anderson 2006; Knapp et al. 1999; Petermann and Buzhdygan 2021). The more we understand the conditions that lead to greater diversity in grasslands, we can better support those conditions through conservation and management actions.

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