

HERBIVOROUS INSECT AND PLANT COMMUNITIES RESPOND IN COMPLEX WAYS
TO RAINFALL MANIPULATION IN AN OAK SAVANNA GRASSLAND

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Abstract

Changes in precipitation due to climate change will have consequences for plant and herbivore communities alike. Multiple hypotheses exist to explain how changes in plant diversity and productivity may cause changes in herbivorous insect community composition. However, the effects of water availability on the relationships between plant and herbivore communities are less well understood. For my M.Sc. thesis, I used a long-term rainfall manipulation experiment in a remnant patch of Garry oak (*Quercus garryana*) savanna to examine how plant community composition and productivity have responded to changing levels of precipitation over a 5-year period. This highly endangered ecosystem is predicted to experience significantly wetter springs and drier summers by 2080. I also investigated plant-mediated, indirect effects of manipulated precipitation on the diversity and abundance of herbivores, drawing on multiple hypotheses that describe the relationships between the composition of plant and herbivore communities. I found that plant productivity increased significantly with increasing growing season soil moisture. Plant productivity was also influenced by plant diversity, with plant productivity increasing with increasing plant diversity but only in drier plots, highlighting a context dependent effect. Further, I found that the effects of soil moisture on the herbivore community were mediated by plant productivity. Herbivore abundance decreased with increasing plant productivity, refuting the more individuals hypothesis. This indirect effect of soil moisture was in addition to a significant negative effect of soil moisture directly on herbivore diversity. The results of this study show that drought will result in significant decreases in plant productivity in this ecosystem and both direct and indirect impacts on the composition of the herbivore community. This study provides valuable insight into the effects of climate change on a highly endangered ecosystem and how future changes in precipitation with climate change will effect plant and herbivore communities.

Lay Summary

The objective of this study was to examine how plant and herbivorous insect communities respond to changes in rainfall. Plants and the insects that eat them interact in many ways, and research shows that these interactions can shift when resource availability is altered. I used a rainfall manipulation experiment to change the amount of water available to plants and insects in a highly endangered Pacific Northwest oak savanna, where spring rainfall is predicted to increase while summer rainfall is predicted to decrease. The results of this study show that drought will result in decreases in the productivity of plants in this ecosystem, and that water availability will have direct and indirect impacts on the composition of the insect community. This research contributes to our greater understanding of how climate change will affect plant and insect communities in this region and provides insight into how and why these effects may occur.

Preface

This thesis is original, unpublished work by the author, Lauren J. Smith. Guidance and supervision for this work was provided by Dr. Jennifer L. Williams (University of British Columbia, Geography). Plant community data was collected by many former and current members of the Williams Lab between 2015-2021, including Jennifer L. Williams, Jenna Loesberg, Piper Battersby, Sophie Duncan, Deirdre Loughnan, Jens Johnson, Hailey Bloom, and Charlotte Trowbridge. All data analysis and insect data collections were done in 2020 and 2021 by Lauren J. Smith. Insect identification was done in collaboration with Erin McHugh. Access to the Cowichan Garry Oak Preserve was approved and provided by the Nature Conservancy of Canada.

Portions of this work were presented at the Ecological Society of America Conference (virtual, August 2021).

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List of Symbols

D: Simpson's diversity index

H_h: Shannon diversity index for the herbivore community, calculated using morphospecies

H_p: Shannon diversity index for the plant community

List of Abbreviations

CGOP: Cowichan Garry Oak Preserve

SEM: Structural equation model

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Dedication

This work is dedicated to my parents. Mom and Dad, you constantly inspire me, and I am endlessly grateful for your support and encouragement, especially through everything that has happened in the last year. I love you both so much and thank you for everything.

Chapter 1: Introduction

Changes in precipitation due to climate change will have consequences for plant and herbivorous insect communities alike. Plant species diversity and plant productivity can have significant effects on the composition of herbivorous insect communities, as herbivores rely on and sometimes specialize on specific plants for food and shelter, and plant-herbivore interactions can also have significant impacts on the overall composition and function of plant communities (Root, 1973; Tilman et al., 1996; Siemann et al., 1998; Siemann, 1998; Haddad et al., 2009; Haddad et al., 2011; Liebhold et al., 2018). However, the effects of changes in abiotic factors such as water availability on plant and herbivore communities are less well understood. As primary consumers, herbivores play an important role in the transfer of energy and nutrients from the bottom of the trophic pyramid to higher trophic levels; therefore, it is important to understand the effects of water availability on these underlying relationships to understand how future changes in plant communities may result in changes to herbivore communities.

Primary productivity has been shown to be higher in more diverse plant communities (Naeem et al., 1995; Siemann et al., 1998; Tilman et al., 1997; Tilman, 2001; Cardinale et al., 2007).

However, the underlying mechanisms, such as niche complementarity and sampling effects, are still highly debated and often vary between different types of ecosystems (Hooper et al., 2005).

Importantly, altered resource availability can change the interactions between plant productivity and diversity (Mulder et al., 2001), adding further uncertainty to how the underlying mechanisms behave. Introducing manipulated precipitation to an ecosystem alters resource availability which may shift the predicted plant diversity-productivity relationship (Mulder et al., 2001; Alon & Sternberg, 2019) by affecting the types and overall all diversity of species that can thrive in that

ecosystem and by shifting competition within and among species (Napier et al., 2016), or by shifting the ability for species to produce new biomass (Hsiao, 1973). For example, one study found no relationship between species richness and biomass under control conditions; however, under drought conditions plant productivity was higher in more species rich communities, and they attributed this to facilitative interactions between species (Mulder et al., 2001). In contrast, other studies have found significant decreases in plant productivity under drought conditions, but no shift in the diversity-productivity relationship (Craven et al., 2016). Dominant functional groups or species may shift from year to year or even within single growing season resulting in differences in diversity-productivity relationships if species evenness shifts dramatically. Shifts in functional diversity may also have important impacts on herbivores if dominant resources are more or less palatable to the herbivores present in the community.

Plant diversity and plant productivity significantly influence herbivore abundance and diversity across many ecosystems. Changes in the herbivore community may arise from changes in plant diversity, plant productivity, or a combination of those factors, all of which may affect the quality and quantity of resources available for herbivores (Borer et al., 2012). While it is generally accepted that more productive and diverse plant communities support a more diverse herbivore community (Root, 1973; Tilman et al., 1996; Siemann et al., 1998; Siemann 1998; Haddad et al., 2009; Haddad et al., 2011; Liebhold et al., 2018), there are a myriad of potential interactions between these two trophic levels (Borer et al., 2012; Prather et al., 2020) and with the abiotic environment. Plant-herbivore interactions may be directly or indirectly affected by changes in water availability, leading to complex ways that water availability can affect this network of interactions. Direct effects of water availability on the herbivore community include

effects on herbivore behavior and physiology, which ultimately may limit which species are able to persist in a particular location (Awmack & Leather, 2002; Jamieson et al., 2012). On the other hand, indirect effects include plant-mediated effects on the herbivore community resulting from changes in plant diversity and plant productivity (Barnett & Facey, 2016). By altering the quality and/or quantity of plant resources, water availability has the potential to influence the interactions between plant and herbivore communities, to alter the diversity and abundance of herbivores, or to have impacts on herbivore performance and/or fecundity (Awmack & Leather, 2002). These shifts in resource availability have the potential to affect herbivores differently throughout the growing season as water availability and dominant plant functional groups shift.

Within the herbivore community, feeding groups, or guilds, may be affected differently by changes in water availability. Two of the broad feeding guilds that are recognized for herbivorous insects are “sap-feeding,” those that feed on the water-based phloem, xylem, and mesophyll of plants, and “chewing,” those that eat foliage, bore or mine into leaves and stems, or form galls (Huberty & Denno, 2004). Because of these differences in feeding behavior, guilds may respond differently to changes in water availability. For example, drought can have a negative effect on sap-feeding guilds but not on chewing guilds (Huberty & Denno, 2004). Given these bottom-up effects, predicted changes in water availability due to climate change will have consequences for plant and herbivore communities alike.

Multiple hypotheses exist to explain how changes in plant diversity and plant productivity may cause changes in herbivore community composition (Figure 1). For example, the resource heterogeneity hypothesis predicts that arthropod diversity will increase with increasing plant

diversity because there is a wider spectrum of resources and niches available for consumers (Hutchinson, 1959; Borer et al., 2012; Prather et al., 2020). In contrast, the resource concentration hypothesis predicts that herbivore abundance increases when plant diversity is low because particular resources are more abundant, which increases the abundance of arthropods that consume those concentrated resources (Root, 1973; Haddad et al., 2001; Haddad et al., 2009). Several studies have explored these effects of plant diversity on arthropod diversity, with some showing support for the resource concentration hypothesis (Kéry et al., 2001; Otway et al., 2005) and for the resource heterogeneity hypothesis (Murdoch et al., 1972; Siemann et al., 1998; Uchida & Ushimaru, 2014). However, many empirical studies have found no direct relationship between arthropod diversity and plant diversity (Koricheva et al., 2000; Borer et al., 2012; Prather et al., 2020), and instead find that other factors, such as producer productivity, are driving arthropod diversity (Borer et al. 2012, Prather et al. 2020).

A third hypothesis, the more individuals hypothesis (Srivastava & Lawton, 1998), predicts that increased plant productivity (or producer biomass) will increase herbivore abundance by increasing the quantity of resources (Joern & Laws, 2013; Hertzog et al., 2016), and this increase in herbivore abundance will lead to an increase in herbivore diversity because a higher total number of individuals can support a higher number of species (Storch et al., 2018; Figure 1). A meta-analysis of studies testing the more individuals hypothesis found that just over half of the experimental and observational studies on invertebrate taxa supported the more individuals hypothesis, while the rest showed little to no support (Storch et al., 2018). For example, both ant density and species richness increase with increasing plant productivity, particularly at small scales (Kaspari et al., 2000; Kaspari et al., 2003). Some studies support the first part of the more

individuals hypothesis that insect diversity or richness increases with increased insect abundance, but find conflicting (Prather et al., 2020) or no support (Uchida & Ushimaru, 2014) for the prediction that insect abundance increases with plant productivity. Other studies have found no support (Brändle et al., 2001; Haddad et al., 2009). Collectively, these three hypotheses (Figure 1) illustrate how various mechanisms could drive interactions between the plant and herbivore communities but results from across a suite of studies vary quite significantly.

Although many studies have examined plant-insect interactions in grassland ecosystems, the majority take place in tall-grass prairies. Even within similar ecosystem types (e.g. grasslands), changes in plant productivity due to manipulated rainfall regimes can differ in both direction and magnitude (Heisler-White et al., 2009). For example, studies have shown that tall grass prairie plants decreased in plant productivity in response to less frequent (but more severe) rainfall events, while plants in mixed-grass prairie and semi-arid steppe sites increased in plant productivity (Heisler-White et al., 2009; Wilcox et al., 2017; Korell et al., 2021). In this study, I examined the effect of manipulated (increased or decreased) rainfall on plant and herbivorous insect communities in a remnant patch of Garry oak savanna in the Pacific Northwest, where average annual net primary productivity is relatively low compared to other types of North American grasslands (Grace et al., 2007). Garry oak savanna is a highly threatened ecosystem with only 5% of its original distribution remaining in Canada, and is characterized by an open canopy and a grass- and forb-dominated understory (Fuchs, 2001; Natural Resources Conservation Service, 2017). Annual precipitation in this area is predicted to significantly increase with climate change, primarily in the winter and spring, while summer precipitation is predicted to decrease dramatically (Cowichan Valley Regional District, 2017), and it is important

to explore how these shifts in precipitation affect this ecosystem. In contrast to other studies that directly manipulate plant species diversity and/or richness, it is also valuable to study plant-insect interactions in natural systems where the plant community composition has not been modified by seeding or planting, in order to learn more about how these mechanisms behave in natural systems. Studying these mechanisms and interactions in the Garry oak savanna will further contribute to our understanding of how diversity-productivity relationships may vary across ecosystems and in the face of climate change.

I used a long-term rainfall manipulation experiment, with treatments that either increase or decrease rainfall, to explore how the plant and herbivore communities in the Garry oak savanna ecosystem respond to changes in rainfall. First, I examined how plant community composition and productivity have responded to increased or decreased precipitation over 6 years (2016-2021). I predicted that drought treatments would result in decreased soil moisture, decreased plant diversity, and decreased plant productivity, and the converse for the irrigated treatments. In addition, I predicted that an increase in plant diversity would result in an increase in plant productivity. Alternatively, decreased diversity may result in increased plant productivity if a few species with high productivity dominate, decreasing the evenness of the community.

Second, I investigated plant-mediated effects of manipulated precipitation on the diversity and abundance of herbivores and explored the factors that drive the assemblage of herbivores in an oak savanna ecosystem throughout the growing season. I predicted that increased precipitation would lead to an increase in the diversity and abundance of herbivores, if plant diversity and plant productivity responded positively to added precipitation, thus increasing the types of

resources available (resource heterogeneity hypothesis and more individuals hypothesis). Alternatively, increased precipitation may lead to a high abundance or concentration of certain plant resources if some plant species competitively exclude others, lowering plant diversity (Napier et al., 2016) and leading to an increase in the abundance of certain herbivores (resource concentration hypothesis).

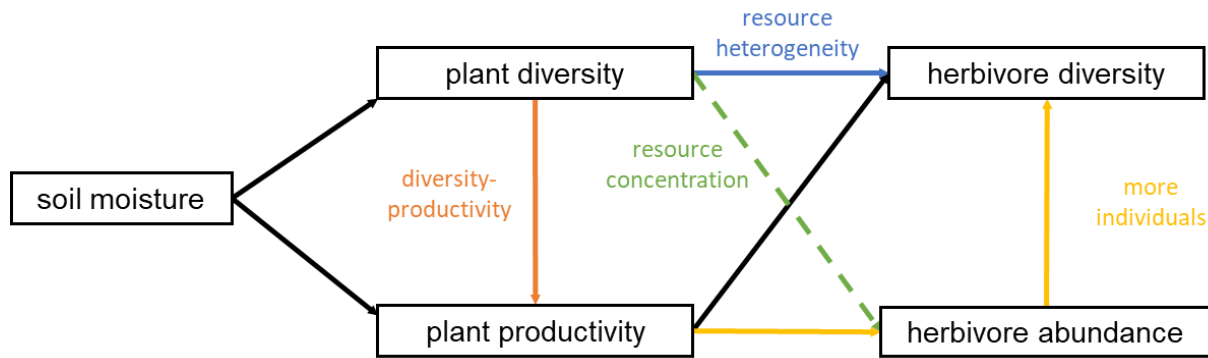


Figure 1 Diagram of interactions between water availability, the plant community, and the herbivore community as described by the hypotheses discussed above. The dashed line represents a negative relationship and solid lines represent positive relationships.

Chapter 2: Methods

2.1 Study site

This study took place in a remnant patch of Garry oak savanna at the Cowichan Garry Oak Preserve (CGOP) in Duncan, British Columbia. This site lies on the traditional Coast Salish territories and on the lands of the Cowichan tribes (Fuchs, 2001), and is currently managed by the Nature Conservancy of Canada. Garry oak savanna is a threatened ecosystem; it ranges from the southeastern portion of Vancouver Island to Northern California, however less than 5% of the original distribution of Garry oak savanna remains in Canada (Fuchs, 2001; MacDougall et al., 2004; Lea, 2006; Costanzo et al., 2011). Threats facing this ecosystem include habitat loss and fragmentation, conifer encroachment (primarily *Pseudotsuga menziesii*), fire suppression, and invasion of exotic species (Fuchs, 2001; Dunwiddie & Bakker, 2011). Garry oak savanna generally is associated with a Mediterranean-like climate, and the Cowichan Valley where the CGOP is located exhibits a warmer and drier climate than surrounding areas on Vancouver Island (MacDougall & Turkington, 2006; Vellend et al., 2008; Bjorkman & Vellend, 2010). The average annual precipitation in the Cowichan Valley is approximately ~1100mm/year, with most falling from mid-fall to mid-spring (Ziter & MacDougall, 2013; Figure 12). Annual precipitation is predicted to increase by 11% by 2080, increasing primarily in spring and winter; however, summer precipitation is predicted to decline by 26% by 2080 (Cowichan Valley Regional District, 2017).

Quercus garryana (Garry oak or Oregon white oak) is the dominant tree species in this ecosystem. The understory is characterized by annual and perennial forbs and grasses, both native and introduced (MacDougall et al., 2004; MacDougall & Turkington, 2006). First Nations

people maintained this ecosystem by periodically burning the understory, and they harvested numerous species for food, including *Allium acuminatum*, *Allium cernuum*, *Brodiaea coronaria*, *Fritillaria lanceolata*, *Camassia quamash*, and *Camassia leichtlinii* (Fuchs, 2001; Bjorkman & Vellend, 2010). The Garry oak savanna ecosystem is home to nearly 700 species of plants (61 of which are listed as endangered or at risk), 454 of which are associated with the Garry oak savanna in British Columbia (MacDougall et al., 2006). Across seven remnant patches in the Cowichan Valley researchers have recorded an average plant species richness of 53 species per site (MacDougall et al., 2006). Earlier inventories estimate that there are approximately 800 species of arthropods associated with Garry oak savanna (Evans, 1985), with 17 arthropod species listed as at risk in British Columbia (Fuchs, 2001).

2.2 Rainfall manipulation experiment

The rainfall manipulation experiment consists of 15 2 x 2 m plots: 5 control, 5 drought, and 5 irrigated. The experiment was designed following the International Drought Experiment (IDE) protocol (Knapp et al., 2017). To simulate drought conditions, 3 x 3 m shelters were constructed (in 2015) over the drought plots. The shelters are made out of wooden frames with corrugated plastic that intercepts 50% of the total incoming precipitation (corresponding to a 100-year drought in this system). The collected rainfall was then used to water the irrigated plots through a passive drip irrigation system, doubling the precipitation over each irrigated plot. To further evaluate the potential for increased spring precipitation in Garry oak savanna, extra water was added to the irrigated plots during the growing season (April 8th – June 16th) in 2021. Sixty liters of extra water was added to the five irrigated plots twice per week (three times per week when air temperatures were above 20°C) through the passive drip irrigation system over a 24-hour

period; this equated to approximately 15 mm/m² (60 mm total over each 4 m² plot) of additional precipitation for each plot during the 2021 growing season. Soil moisture data (volumetric water content, m³/m³) were collected hourly year-round in each plot using Decagon soil moisture probes. Hourly weather data, including precipitation, were also collected year-round at an on-site HOBO U30 weather station.

2.3 Plant data collection

To assess plant community composition, percent cover surveys were conducted at peak diversity (approximately mid-May) in a 1 x 1 m permanent sub-plot of each plot in each year starting in 2015. We identified all of the species present in each plot, then estimated percent cover of each species to the nearest 1%, following the Nutrient Network protocol (Borer et al., 2014). Species identification was done using a species list compiled for the site by a former graduate student and with reference to *Flora of the Pacific Northwest: An Illustrated Manual* (Hitchcock et al., 1976). To assess annual net above-ground primary productivity, I used above-ground biomass as a proxy for plant productivity in this study (Scurlock et al., 2002). Above-ground biomass was collected at peak biomass each year (approximately mid-June) by destructively clipping all plant material at ground level in a 20 x 100 cm section of a permanent biomass subplot in each plot. Each year, biomass was collected from a different 20 x 100 cm section of the subplot to avoid sampling from the same area that was sampled in the year prior. After collection, biomass was sorted by functional group (grasses, forbs, shrubs, bryophytes, and dead material) and dried at 60°C for 48 hours, and then each functional group was weighed separately (Borer et al., 2014). In contrast to Nutrient Network protocol, all aboveground shrub biomass was collected in 2015-2019, including some secondary productivity and previous year's woody material. Using

samples retained from 2017 and 2019, it was estimated that the actual annual net aboveground biomass of shrubs was about 50% of the total biomass collected. To adjust for this inconsistency, shrub biomass in 2015, 2016, and 2018 was divided by 2 in any plot where shrub biomass was greater than 5 g/m². Moss biomass was removed from analyses of productivity in this study because of inconsistent collection methods from year to year. All dead biomass (corresponding to previous year's productivity) was also excluded.

2.4 Insect sampling

I collected insects twice in 2020 and three times in 2021. Initially, I planned to sample insects three times during the growing season (early, mid, and late growing season) in both years, along with additional plant community composition surveys corresponding with each insect sample. However, due to COVID-19 restrictions I was only able to sample twice in June 2020, once at peak biomass and once at the end of June. In the analyses, I used only the insect sample from mid-June 2020, since I was not able to resurvey plants again at the end of June. In 2021, I sampled three times: end of April (early growing season), mid-May (mid-growing season, peak diversity), and in mid-June (late-growing season, peak biomass), and I resurveyed plant community composition at each of these time periods. The sample periods are referred to as late 2020, early 2021, mid 2021, and late 2021.

I collected insects using a backpack aspirator (modified and sold by BioQuip Products) and sampled a 1 x 2 m area on the south side of each plot for two minutes by evenly sweeping the nozzle of the aspirator across the plot. I chose to use vacuum sampling because this method has been shown to be more effective than other common sampling methods, such as sweep netting, in

sampling certain orders of arthropods including Diptera, Hymenoptera, and Hemiptera (Buffington & Redak, 1998). Additionally, vacuum sampling is often less destructive to vegetation than sweep netting (Buffington & Redak, 1998), which is important because the study site is in a sensitive ecosystem. After collection, I transferred the insects into plastic bags containing a small amount of ethyl acetate and stored them on ice until processing. In the lab, I transferred insects to vials containing 70% ethanol for storage before and after identification. I identified all insects to order and family, and for herbivorous families, I identified individuals to morphospecies within each family if possible. I used *How to Know the Insects* (Bland & Jaques, 1978) and *A Field Guide to Insects: America North of Mexico* (Borror & White, 1970) for identification of order and family, and morphospecies were classified by distinct visual characteristics. I also classified each family of herbivores by feeding guild (i.e. sap-feeding, chewing, nectar/pollen; Table 1) using *American Insects: A Handbook of the Insects of America North of Mexico* (Arnett Jr., 2000).

2.5 Analysis

2.5.1 Soil moisture

To quantify soil moisture during the growing seasons of 2016-2021, I calculated the average soil moisture (m^3/m^3) in each plot from April 1st-June 15th in each year. Missing data were filled in using simple linear regressions based on highly correlated plots of the same treatment (Figure 12). In 2019, data were missing for all plots during a portion of the growing season due to battery failure, so the averages for 2019 were calculated using only the existing data and missing data were not interpolated. To assess the effects of soil moisture on plant-herbivore interactions in

2020 and 2021, I calculated the average soil moisture for each plot in the two weeks prior to each sampling period (Prather et al., 2020).

2.5.2 Plants and insects

I calculated plant species richness, Shannon diversity (H_p), and Simpson's diversity (D) using the *vegan* package in R (Oksanen et al., 2020). Both the Shannon diversity and Simpson's diversity indices incorporate the richness and abundance of species (Morris et al., 2014). The Shannon index is more sensitive to changes in species richness, so I used also the Simpson's index to assess shifts in evenness, as it gives more weight to common species compared to rare ones and provides more information about the dominance of one or a few species in a community compared to Shannon diversity (Shannon, 1948; Simpson, 1949; Smith & Grassle, 1997; Morris et al., 2014). Each plant species was also categorized by growth form (forb, graminoid, shrub, or tree). Biomass ($\text{g}/0.2 \text{ m}^2$) was multiplied by 0.2 to convert the values to g/m^2 . For the herbivore community, I calculated herbivore diversity (H_h , Shannon diversity using morphospecies), herbivore abundance, and abundance of sap-feeding and chewing herbivores. Abundances of both feeding guilds were log-transformed.

2.5.3 Models

All analyses were conducted using R 4.0.3 (R Development Core Team, 2020). I was not able to use pre-treatment data from 2015 due to lack of soil moisture data, and I excluded Plot 15 in 2016 due to a broken soil moisture sensor. To assess the effects of treatment and soil moisture on the plant community from 2016-2021, I used linear mixed effects models (*nlme* package; Pinheiro et al., 2021), with plot as a random effect to account for repeated measures (Table 2). I

log-transformed total productivity and grass productivity and log+1 transformed forb productivity to meet normality assumptions. I included treatment and year as categorical variables and all other variables as continuous. The response variables plant diversity (H_p), plant productivity, percent cover of grasses, productivity of grasses, percent cover of forbs, and productivity of forbs were regressed on treatment and soil moisture separately, and plant diversity was included as a predictor variable for plant productivity, based on *a priori* hypotheses Figure 1 (Table 2). Treatment was not a significant predictor in any model and did not improve model fits (AIC), so none of the models with treatment as a predictor variable were selected (Table 2). I used *emmeans* (*emmeans* package; Lenth, 2021) to perform Tukey post hoc comparisons of the response variables, and I used *emtrends* (*emmeans* package; Lenth, 2021) to compare marginal slopes in models where there was a significant interaction between predictor variables.

To assess the indirect effects of treatment and soil moisture on plant-herbivore interactions, I used a piecewise structural equation model (*piecewiseSEM* package; Lefcheck, 2016). The structural equation model (SEM) is composed of five linear mixed effects models (Table 3) with plot as a random effect in each model to account for repeated measures. For the structural equation model, each model was selected based on the pathways hypothesized in the *a priori* model in Figure 1, and non-significant pathways were not removed. Plant productivity did not need to be log-transformed to meet normality assumptions using only 2020 and 2021 data. Treatment was not included as a predictor for soil moisture in the SEM because there was no significant effect of treatment on soil moisture. Tests of directed separation (or d-separation tests) indicated that pathways between soil moisture and herbivore abundance and herbivore

diversity (H_h) were significant (Shipley, 2013; Lefcheck, 2016), so soil moisture was added as a predictor variable in the models for herbivore diversity and herbivore abundance. This made the SEM a fully saturated model, meaning that I could not calculate any goodness of fit measures, however it is reasonable to continue evaluating a fully saturated model if there are significant pathways present and the amount of variance explained by the individual models is relatively high (Lefcheck, 2016; Table 3). The indirect effects in this network are quantified by multiplying the coefficients of connecting pathways, and total effects are quantified by summing the coefficients of the direct and indirect effect.

Due to limited sample size, I was unable to use multigroup analysis to compare the SEM pathways across the growing season. Instead, used linear mixed effects models to explore how herbivore diversity (H_h), herbivore abundance, and abundance of two main feeding guilds (sap-feeding and chewing) differed in response to plant productivity and plant diversity throughout the growing season in 2021 and between the late growing season in 2020 and 2021. To compare herbivore diversity (H_h) and herbivore abundance across the growing season, I added sample period as a predictor variable to the herbivore diversity (H_h) and herbivore abundance models used in the SEM (Table 3) and tested the interaction of sample period with all of the predictor variables; non-significant interactions were removed (Table 4). To compare late growing season of 2020 to 2021, I used the same process with year as a predictor variable instead of sample period. I used additional linear mixed effects models for abundance of the two main feeding guilds that included plant diversity (H_p), plant productivity, and sample period or year as predictors (Table 4).

Chapter 3: Results

3.1 Average daily soil moisture during growing season

Overall, average daily soil moisture during the growing season from 2016-2021 was 6% higher in the irrigated treatment and 0.6% lower in the drought treatment than in the control, but these differences were not significant (treatment: $F_{2,12} = 0.98$, $P = 0.40$; Figure 13). The effect of treatment on soil moisture also did not vary significantly across years (treatment x year: $F_{10,59} = 1.61$, $P = 0.12$). Average daily soil moisture varied across years ($F_{5,59} = 34.59$, $P = <0.0001$; Figure 2a) and was generally correlated with total growing season precipitation. Total precipitation ranged from 38.4 mm (in 2016) to 183.1 mm (in 2017) (Figure 2b). On average, 2016 had the lowest soil moisture across all plots with an average of $0.117 \text{ m}^3/\text{m}^3$ and had the lowest total precipitation during the growing season (Figure 2). However, while 2020 had the highest soil moisture across all plots with an average of $0.211 \text{ m}^3/\text{m}^3$, nearly two times higher than 2016 (Figure 2a), it did not have the highest precipitation. While 2017 had similar but slightly lower soil moisture than 2020, precipitation was highest in 2017 (183.1 mm), almost 45% higher than in 2020 (130.1 mm) (Figure 2b).

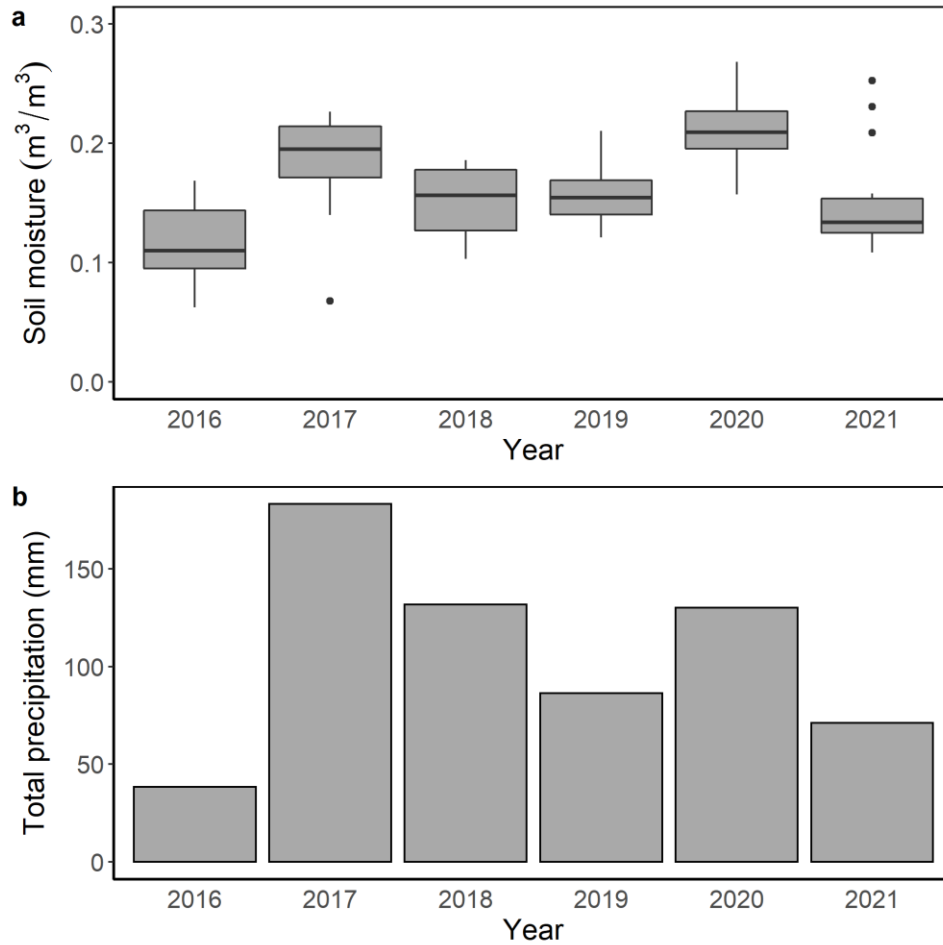


Figure 2 (a) Average daily soil moisture averaged across all 15 plots during the growing season (April 1st – June 15th). Boxes represent the interquartile range for each year with the median indicated by the line in the middle of each box; whiskers show the minimum and maximum values in each year. (b) Bar plot of total precipitation during the growing season (April 1st – June 15th) for each year.

3.2 Plant productivity response to rainfall manipulation & soil moisture

Plant productivity did not vary significantly by rainfall treatment ($F_{2,12} = 1.04$, $P = 0.38$; Figure 14**Error! Reference source not found.**d), and thus treatment was excluded from subsequent models and soil moisture was used as the predictor instead. On average, plant productivity was higher in plots with higher soil moisture ($F_{1,61} = 13.28$, $P = 0.0006$; Figure 3). Although year on its own was not a significant predictor of plant productivity ($F_{5,61} = 1.35$, $P = 0.26$; Figure 4d),

the effect of soil moisture depended on year (year x soil moisture: $F_{5,61} = 7.44$, $P < 0.0001$; Figure 3). In the first two years (2016 and 2017), plant productivity declined as soil moisture increased, and then in the most recent four years, the pattern reversed, and plots with higher soil moisture had greater plant productivity (Figure 3).

In contrast to my hypothesis that plant productivity would increase with increasing plant diversity (H_p), I did not find a significant main effect of plant diversity (H_p) on plant productivity ($F_{1,61} = 0.20$, $P = 0.66$). However, the effect of plant diversity (H_p) on plant productivity weakly depended on soil moisture (soil moisture x H_p : $F_{1,61} = 2.04$, $P = 0.16$), such that when soil moisture is high, increased plant diversity (H_p) results in lower plant productivity and vice versa, but at low soil moisture, increased plant diversity (H_p) results in slightly higher plant productivity (Figure 5).

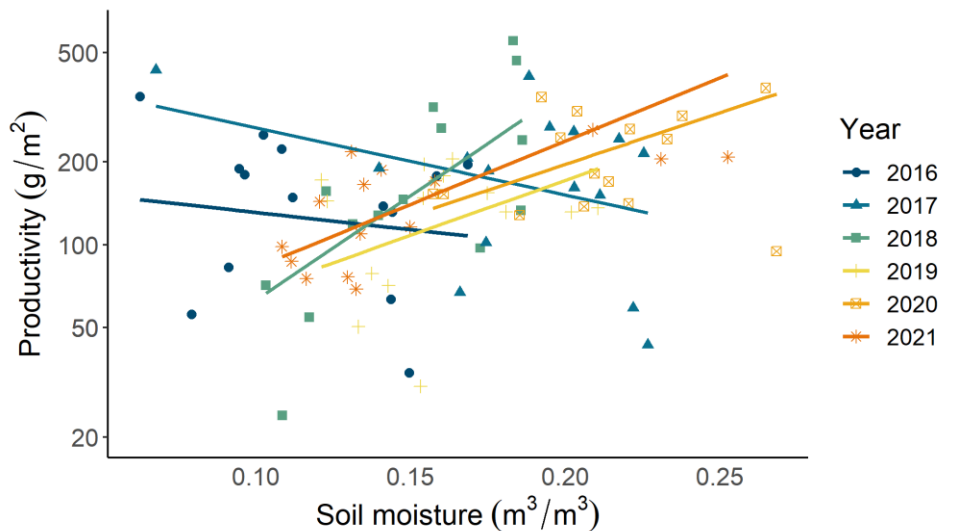


Figure 3 Effects of soil moisture on plant productivity in each year. Lines are based on estimates from the linear mixed effects model.

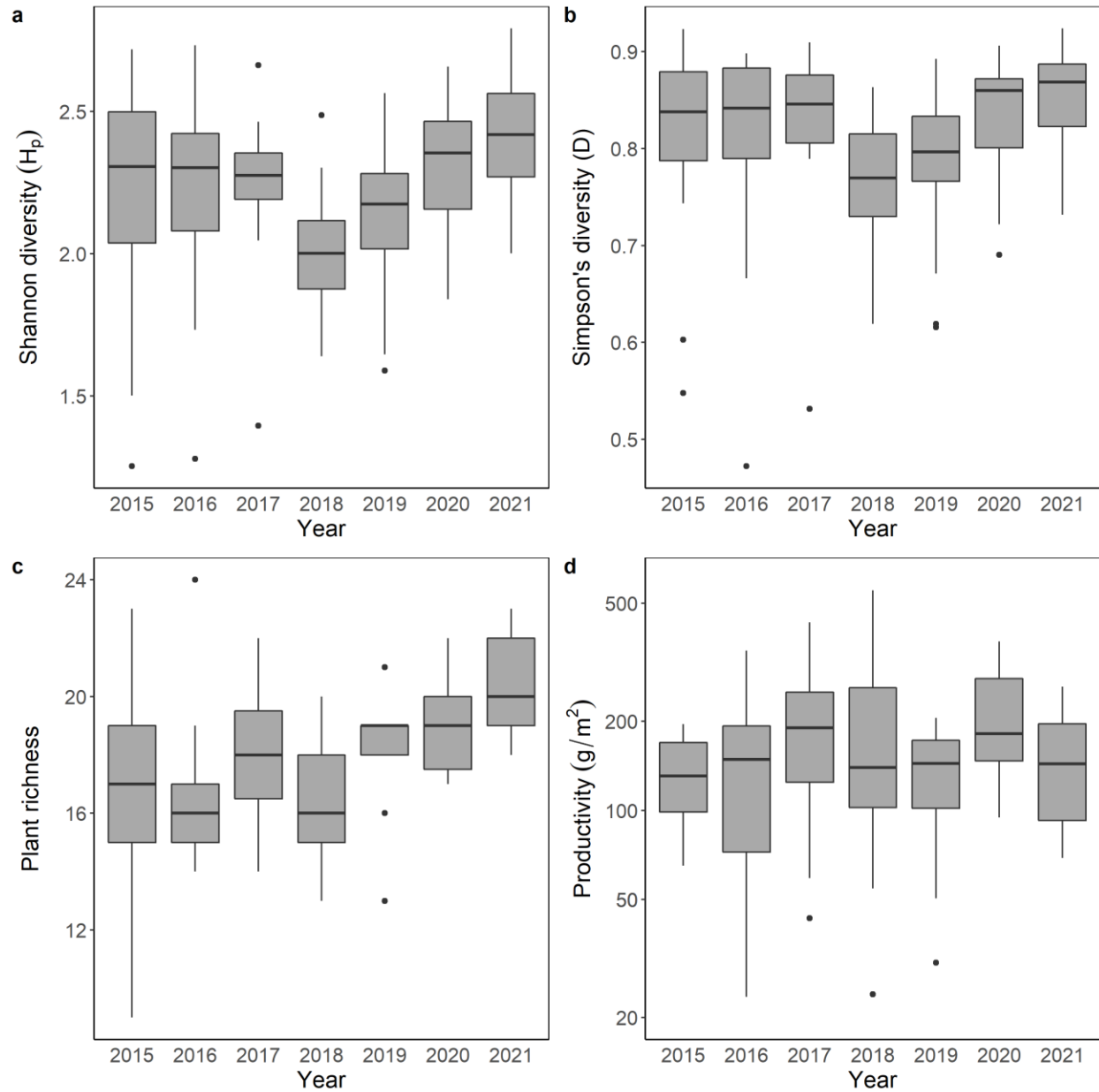


Figure 4 Average Shannon diversity (H_p) (a), Simpson's diversity (D) (b), plant richness (c), and plant productivity (d) across all plots in each year. Boxes represent the interquartile range for each year with the median indicated by the line in the middle of each box; whiskers show the minimum and maximum values in each year.

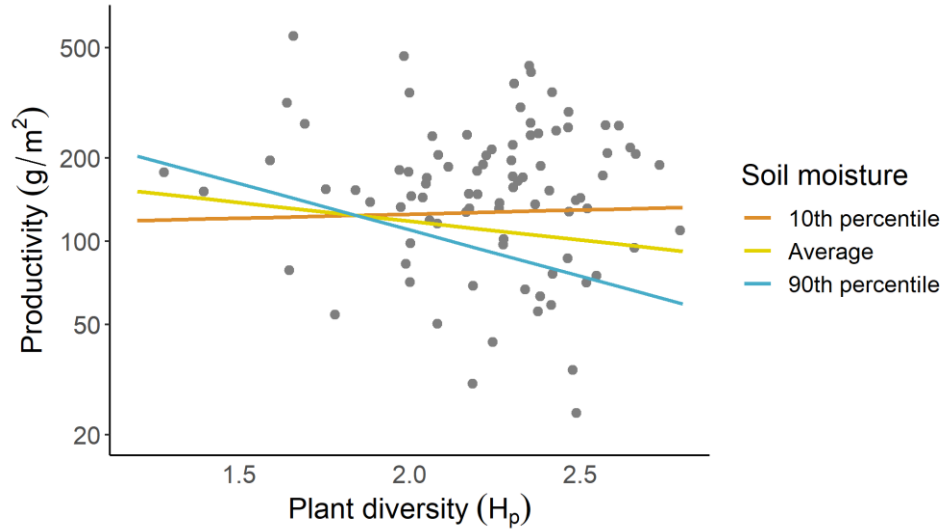


Figure 5 Predicted effect of plant diversity (H_p) on plant productivity at low soil moisture (orange; 10th percentile), average soil moisture (yellow), and high soil moisture (blue; 90th percentile). Points are the measured values of plant diversity (H_p) and plant productivity for each plot in each year.

3.3 Plant diversity response to rainfall manipulation & soil moisture

Since 2016, 74 plant species have been observed in the experiment, with an average of 17.9 species per plot from 2016-2021 (Figure 14c). Plant diversity (H_p and D) and plant richness did not vary by watering treatment (H_p : $F_{2,12} = 0.17$, $P = 0.85$; D : $F_{2,12} = 0.26$, $P = 0.77$; richness: $F_{2,12} = 0.69$, $P = 0.52$; Figure 14a-c), therefore treatment was excluded from subsequent models, and soil moisture was used as the predictor variable instead.

Soil moisture did not have a significant effect on plant diversity (H_p and D) or plant richness (H_p : $F_{1,68} = 0.035$, $P = 0.85$, Figure 6a; D : $F_{1,68} = 0.025$, $P = 0.88$, Figure 6b; richness: $F_{1,68} = 0.88$, $P = 0.35$), and the effect of soil moisture on any of these metrics did not depend on year (NS interactions; Figure 6). However, plant diversity (H_p and D) and plant richness varied significantly from year to year (H_p : $F_{5,68} = 7.17$, $P < 0.0001$; D : $F_{5,68} = 4.11$, $P = 0.003$; richness:

$F_{5,68} = 11.65$, $P < 0.0001$; Figure 4a-c). Marginal mean plant diversity was highest in 2021 (2.41) while lowest in 2018 (2.01) (Figure 4a), and overall there was a 6% increase in plant diversity (H_p) from 2016 to 2021, but this increase was not significant ($P = 0.49$; Figure 4a). Marginal mean plant species richness increased from 16.4 to 20.2 species (23%) from 2016 to 2021 ($P < 0.0001$; Figure 4c). Pairwise contrasts of Simpson's diversity (D) by year indicate little overall change in evenness between most years. However, from 2018 to 2021, there was a significant increase in Simpson's diversity (D) from 0.77 to 0.85 ($P = 0.004$), indicating that since 2018 the plots have become slightly more even and less dominated by one or a few species.

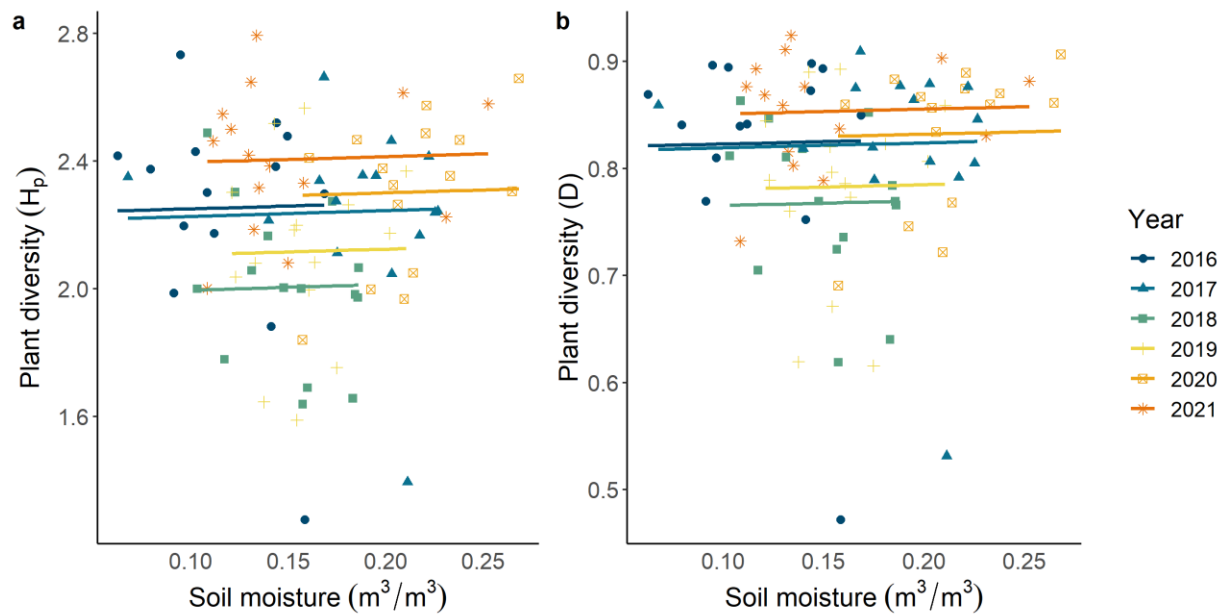


Figure 6 Effects of soil moisture on plant diversity, H_p (a) and D (b) in each year. Lines are based on predictions from linear mixed effects models.

3.4 Forb and graminoid response to rainfall manipulation & soil moisture

Overall, wetter plots had higher percent cover and productivity of grasses. While grass cover and productivity did not respond to watering treatments (cover: $F_{2,12} = 0.014$, $P = 0.99$, productivity: $F_{2,12} = 0.052$, $P = 0.95$; Figure 15), grass cover increasing significantly with increasing soil moisture ($F_{1,68} = 4.65$, $P = 0.035$; Figure 7a) and grass productivity responded significantly but the magnitude and direction of the response was dependent on year ($F_{5,68} = 4.44$, $P = 0.0016$; Figure 7b). Grass cover also varied significantly from year to year ($F_{5,68} = 16.74$, $P < 0.0001$), ranging from 23.7% in 2018 to 50.6% in 2021. Marginal mean grass cover in 2021 was approximately 69% higher than in 2016 ($P < 0.0001$). In 2021, marginal mean grass cover increased by approximately 2000% from the early to late growing season.

Forb cover and productivity also did not respond to the watering treatments (cover: $F_{2,12} = 0.35$, $P = 0.71$; productivity: $F_{2,12} = 1.88$, $P = 0.20$; Figure 16). However, forb productivity was significantly greater in plots with higher soil moisture ($F_{1,68} = 19.65$, $P < 0.0001$, Figure 7d). Forb cover had only a weak positive, but non-significant response, to soil moisture ($F_{1,68} = 1.78$, $P = 0.19$; Figure 7c). Forb cover and productivity varied significantly by year (cover: $F_{5,68} = 5.76$, $P = 0.0002$; productivity: $F_{5,68} = 2.54$, $P = 0.037$; Figure 7c,d), and marginal mean forb cover per plot increased by 47.4% from 2016 to 2021 ($P = 0.027$), ranging from 37.1% in 2016 to 56.3% in 2017. Marginal mean forb productivity increased from 2.85 g/m² in 2016 to 3.27 g/m² in 2021, but this increase was not significant ($P = 0.77$). In 2021, forb cover did not respond significantly to soil moisture ($F_{1,27} = 2.14$, $P = 0.15$) and did not vary significantly throughout the growing season ($F_{2,27} = 1.46$, $P = 0.25$).

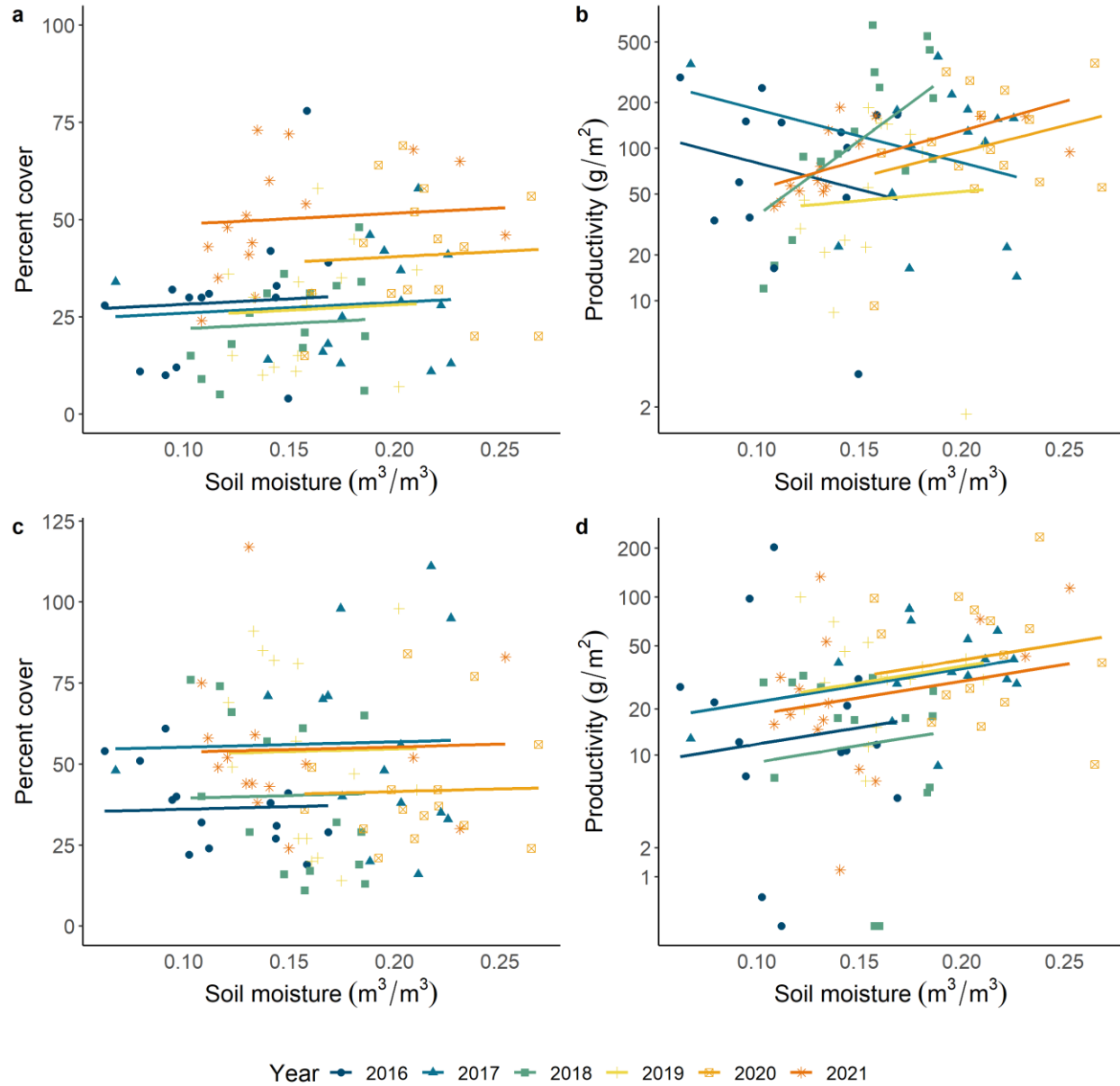


Figure 7 Percent cover and productivity of grasses (a, b) and forbs (c, d) against soil moisture in each year. Lines are based on predictions from linear mixed effects models.

3.5 Herbivore community response to soil moisture

I collected a total of 17,409 insects, and 3,260 were herbivorous insects (637 from 2020 and 2,623 from 2021) from 24 families and 40 morphospecies (Table 1); one set of insect samples (containing 1366 herbivores) was excluded from analysis because I was unable to resurvey the plant community at the time of sampling. On average, diversity was 3% lower in drought plots and 1% lower in irrigated plots compared to the control plots, although these differences were not significant (Figure 17a). Abundance per plot ranged from 9 to 174 individuals. Abundance was 4% lower in drought plots and 19% lower in irrigated plots than control plots, but these differences were also not significant (Figure 17b). Treatment also did not have a significant effect on the average soil moisture two weeks prior to sampling, so treatment was excluded from the structural equation model and only soil moisture was used in the models.

In contrast to my initial hypothesized network of interactions, soil moisture had a significant negative direct effect on herbivore diversity (H_h ; $P = 0.012$; Figure 8, Figure 9a) and a marginally significant positive effect on herbivore abundance ($P = 0.051$; Figure 8, Figure 9b), as indicated by tests of directed separation (*piecewiseSEM*, Lefcheck, 2016). The presence of these direct effects indicates that the effects of soil moisture on the herbivore community are only partially mediated by the plant community.

My results show that the effects of soil moisture on herbivore abundance is partially mediated by plant productivity, but not plant diversity (H_p) (Figure 8). Similar to the above analyses (see *Plant productivity response to rainfall manipulation & soil moisture*) across all years of the experiment, wetter plots had higher plant productivity in 2020 and 2021 ($P = 0.001$), and plant

diversity (H_p) did not differ significantly between wetter and drier plots ($P = 0.21$; Figure 8). In contrast to my previous analysis and in agreement with my initial predictions, plant diversity (H_p) had a marginally positive effect on plant productivity in 2020 and 2021 ($P = 0.08$, Figure 8). Following the effect of soil moisture on plant productivity, herbivore abundance decreased significantly in response to increased soil moisture ($P = 0.01$, Figure 8), indicating that plots with higher plant productivity had lower abundance of herbivores. Herbivore abundance did not respond significantly to plant diversity (H_p) ($P = 0.44$, Figure 8), and herbivore diversity (H_h) was not significantly related to either plant diversity or plant productivity (H_p : $P = 0.13$; productivity: $P = 0.13$; Figure 8). Herbivore abundance did not have a significant effect on herbivore diversity ($P = 0.17$, Figure 8). The magnitude of the direct effects of soil moisture on herbivore abundance and herbivore diversity (H_h) were much greater than the total indirect effects via plant productivity (Figure 8).

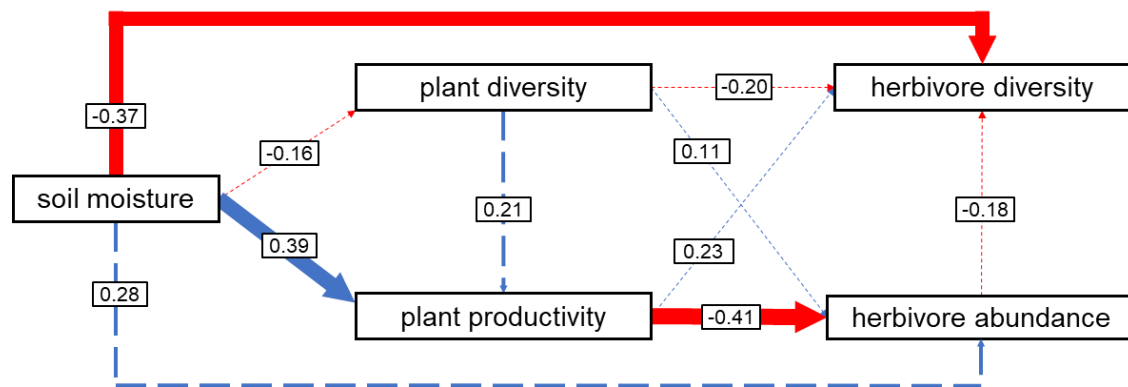


Figure 8 Piecewise structural equation model to assess effects of soil moisture on the plant and herbivore communities. Estimated standardized path coefficients are shown in boxes overlapping the corresponding pathway. Solid arrows represent significant pathways ($p \leq 0.05$), and the width of the arrow corresponds to strength of the effect. Thick dashed arrows represent marginally significant pathways ($p \leq 0.1$). Thin dashed arrows represent non-significant pathways ($p > 0.1$). Red and blue correspond to negative and positive effects, respectively.

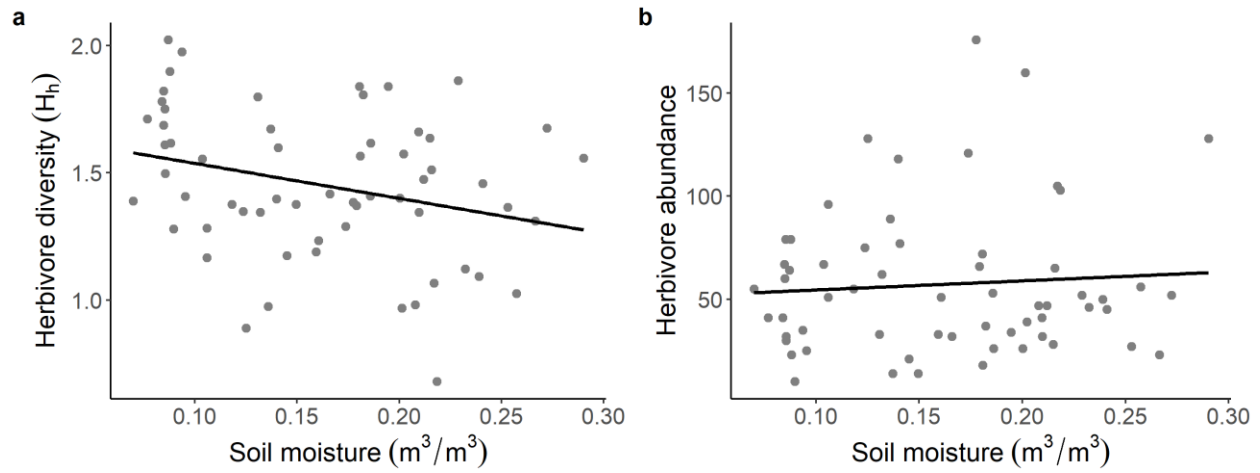


Figure 9 Direct effect of soil moisture on herbivore diversity (H_h) (a) and herbivore abundance (b). Lines are based on predictions from linear mixed effects models.

Herbivore diversity (H_h) varied significantly across the 2021 growing season ($F_{2,25} = 9.68$, $P = 0.0008$; Figure 10a) and was significantly greater in the late growing season compared to early and mid-growing season, increasing by approximately 36% from mid-April (early) to mid-June (late) (Figure 10a). Herbivore diversity (H_h) in the late growing season also differed significantly between 2020 and 2021 ($F_{1,10} = 5.26$, $P = 0.044$, Figure 10a) and was 17% greater in the late growing season of 2021 than in 2020. Herbivore abundance, however, did not vary significantly across the growing season in 2021 ($F_{2,26} = 0.69$, $P = 0.51$) and was only marginally greater in the late growing season of 2021 than in 2020 ($F_{1,11} = 3.65$, $P = 0.08$; Figure 10b).

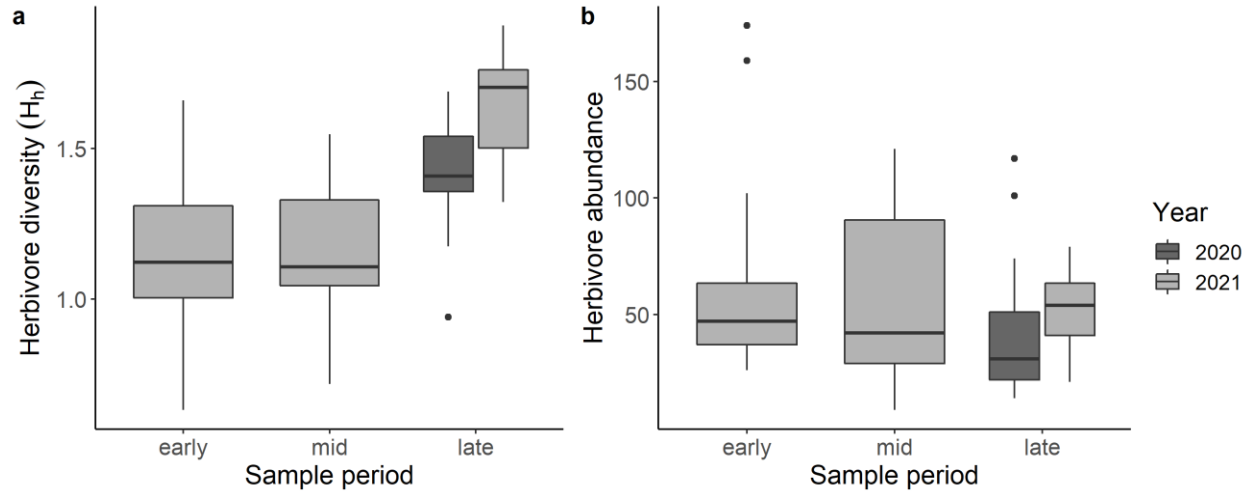


Figure 10 Average herbivore diversity (H_h) (a) and abundance (b) in each sample period, averaged across all 15 plots. Boxes represent the interquartile range for each sample period with the median indicated by the line in the middle of each box; whiskers show the minimum and maximum values in each sample period.

Abundance of chewing and sap-feeding herbivores did not respond significantly to soil moisture and did not vary significantly across the growing season. Nectar and pollen feeding herbivores made up less than 7% of herbivores in any plot during any sampling period, so I focused on chewing and sap-feeding herbivores. Abundance of both feeding guilds did also not respond to increased or decreased plant productivity (chewing: $F_{1,13} = 1.88$, $P = 0.19$; sap-feeding: $F_{1,13} = 0.96$, $P = 0.35$). Sap-feeding herbivore abundance responded to changes in plant diversity, although the direction and magnitude of this response varied across the growing season (diversity x sampling period: $F_{2,25} = 4.09$, $P = 0.029$), such that abundance increased with greater plant diversity in the early and late-growing season but decreased in the mid-growing season (Figure 11a). Chewing herbivore abundance did not respond significantly to plant diversity ($F_{2,27} = 1.48$, $P = 0.23$) and did not vary significantly across the growing season (Figure 11b).

Abundance of sap-feeding herbivores was not significantly different between late 2020 and late

2021 ($F_{1,12} = 0.079$, $P = 0.78$), but chewing herbivore abundance was significantly greater in late 2021 than in late 2020 ($F_{1,12} = 8.21$, $P = 0.014$).

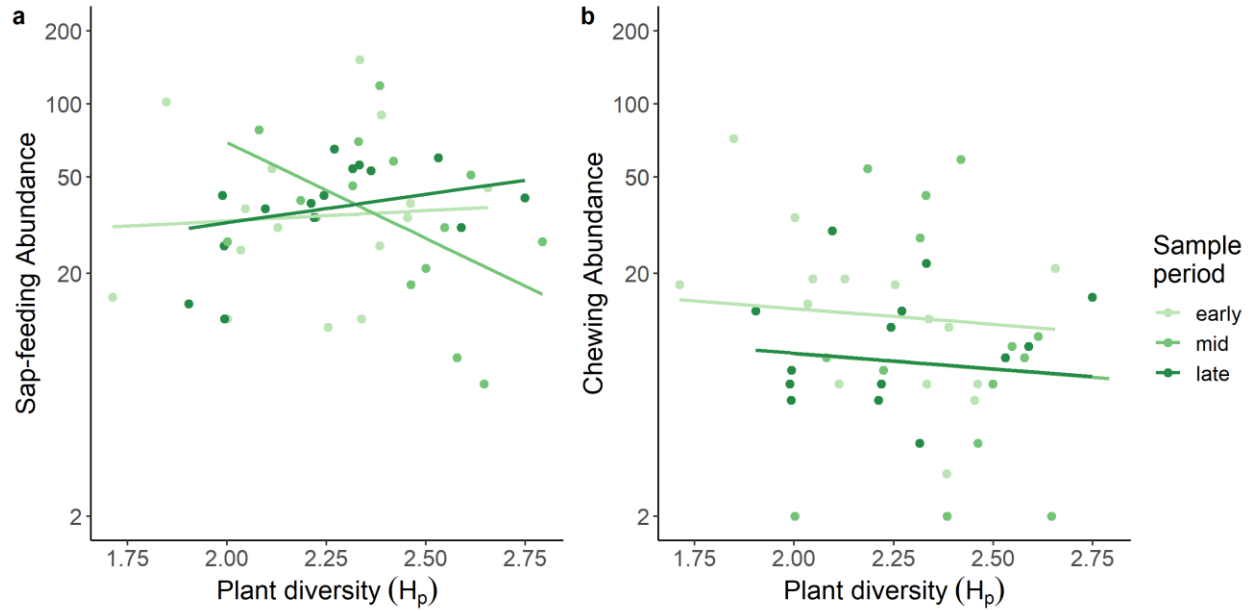


Figure 11 Effect of plant diversity (H_p) on abundance of sap-feeding (a) and chewing (b) herbivores in each sampling period in 2021. Lines are based on predictions from linear mixed effects models.

Chapter 4: Discussion

Plant and herbivore communities may change in multiple ways in response to altered precipitation with climate change, and rainfall manipulation experiments provide an important opportunity to examine how these communities respond to changes in precipitation. After six years, I found that plant productivity, but not plant diversity, responded significantly to changes in soil moisture in a Pacific Northwest oak-savanna, and that changes in water availability led to shifts in the diversity-productivity relationship in this system. These changes in plant productivity translated to significant indirect effects on herbivore community composition in addition to direct negative effects of increased soil moisture on herbivore diversity and herbivore abundance.

4.1 Plant productivity, but not diversity, respond significantly to soil moisture

In support of my predictions, soil moisture had a significant positive effect on plant productivity (Figure 3). This result is in line with many previous studies that have shown that higher precipitation and higher soil moisture will lead to increased plant productivity (Wu et al., 2011; Sala et al., 2012; Zhu et al., 2014; Deng et al., 2016; Wilcox et al., 2017; Ma et al., 2020; Korell et al., 2021) and the converse, that decreased soil moisture will lead to decreased plant productivity (Wu et al., 2011; Craven et al., 2016; Ma et al., 2020). Mechanistically, it is expected that where soil moisture is limiting, increasing soil moisture directly allows plants to increase primary production, and soil moisture can also affect the amount of nutrients that are accessible in the soil, affecting the plants' ability to produce new biomass (Deng et al., 2016).

In addition to increased water availability leading to greater plant productivity, increased plant diversity and richness are hypothesized to contribute to higher plant productivity due to niche complementarity and sampling effects (Naeem et al., 1995; Siemann et al., 1998; Tilman et al., 1997; Tilman, 2001; Cardinale et al., 2007; Craven et al., 2016; Hertzog et al., 2016), but this is still a highly debated topic and results are varied (Hooper et al., 2005). Some studies show a negative or no relationship between plant diversity and plant productivity due to factors such as competitive interactions and disturbance (Hooper et al., 2005; Grace et al., 2007; Cardinale et al., 2007). Other studies have shown that altered resource availability may cause shifts in the diversity-productivity relationship, such that drought can result in a change in the direction and strength of the diversity-productivity relationship (Mulder et al., 2001; Alon & Sternberg, 2019; Ma et al., 2020). In this experiment, I found support for the context dependency of this relationship. Plant diversity had a negative effect on plant productivity at high soil moisture, but a slightly positive effect on plant productivity at low soil moisture (Figure 5), thus providing evidence that changes in resource availability shift the diversity-productivity relationship in this system.

Sensitivity of plant communities to soil moisture and precipitation can vary based the assemblage of plants that are present in ecosystems and across ecosystem types due to differing climate factors (Grace et al., 2007; Hooper et al., 2005; Sala et al., 2012; Wilcox et al., 2017; Brun et al., 2019; Lei et al., 2020). Plant productivity in drier, arid and semi-arid ecosystems tends to be more sensitive to increases in precipitation than wetter ones (Sala et al., 2012; Wilcox et al., 2017), and ecosystems may be more sensitive during years when the growing season is particularly dry (Lozano-Parra et al., 2018). With an average annual precipitation of 1100mm,

plant productivity at our site is likely less sensitive to changes in precipitation than drier arid savanna or grassland ecosystems (Wilcox et al., 2017). The diversity-productivity relationship can also depend on the functional groups of plants present (Hooper et al., 2005; Grace et al., 2007; Brun et al., 2019), and since calculations of plant diversity do not consider the identity of species, some information is lost about the life history and growth form of species. For example, if grass species are more likely to successfully colonize with increasing water availability (McGinnies, 1960; Fay & Schultz, 2009), some highly productive grass species may contribute more to plant productivity than some forb species, resulting in increased diversity due to increased richness, as well as increased plant productivity. However, grasses may competitively exclude other species and decrease evenness of the community (Brun et al., 2019), resulting in a decrease in diversity but an increase in plant productivity. In agreement with other studies that have looked at how functional diversity and plant productivity respond to changes in rainfall (Zavaleta et al., 2003; Suttle et al., 2007; Zhu et al., 2014), my results show a positive relationship between soil moisture and grass cover and productivity in most years (Figure 7a,b), suggesting that plots are becoming grassier where soil moisture is high, resulting in higher plant productivity. However, wet plots were not significantly more or less diverse than drier plots in our experiment, contrary to our initial predictions (Zavaleta et al., 2003; Deng et al., 2016). Forb cover and productivity also increased with increasing soil moisture (Figure 7c,d), so the evenness of the plots did not change much with changing soil moisture, which is also supported by the fact that changes in soil moisture did not cause significant changes in Simpson's diversity (Figure 6b).

Not only did the plant community respond to changes in soil moisture, but I also observed substantial variation in diversity, and richness from year to year, and directional changes in plant richness through time (Figure 4a-c). There are a number of potential explanations for this variation. Changes in diversity from year to year could be due to changes in plant richness or to changes in evenness, and my results show changes in both. I found significant increases in species richness from the beginning of the experiment to the present, and the Simpson's diversity index (D) indicates that plots have become more slightly even and less dominated by one or a few species through time, both of which would contribute to the overall increase in plant diversity. Another contribution to diversity may be that we may have improved at identifying species, in addition to some species being too small to detect and/or identify correctly in some years. I also expect variation in plant life histories to contribute to some of the year-to-year variation in productivity, diversity, and richness. Annual species may go locally extinct, newly colonize plots, or emerge from the seedbank depending both on chance and on environmental conditions. Perennial species may increase or decrease in productivity from year to year depending on how much energy individuals allocate to growth or reproduction and how long-lived they are (Gulmon et al., 1983; Mooney et al., 1986; Lundgren & Des Marais, 2020), particularly some clumping perennial grasses such as *Dactylis glomerata* at the study site. In perennial species, it is generally accepted that individuals tend to grow larger each year, and as perennial species get larger, they have more resources to grow larger the next year (Baden et al., 2021), so that the effects of increasing or decreasing resources such as precipitation should accumulate over time. Finally, annual variability in precipitation (which varied two-fold across the duration of this experiment) may contribute to year to year variation in plant diversity and richness (Suttle et al., 2007, Joern & Laws, 2013), and it may take a significant amount of time

for consistent changes in the plant community to occur following rainfall manipulations, so the first years of an experiment like this one is likely to show a lot of variability (Evans et al., 2011).

4.2 Herbivore community responded to direct & indirect effects of soil moisture

My results show that herbivore diversity increased throughout the growing season and that indirect effects of soil moisture via plant productivity played a role in determining the composition of herbivore communities. Plant diversity did not have a significant effect on herbivore abundance or herbivore diversity (Figure 8), contradicting the resource concentration hypothesis and the resource heterogeneity hypothesis. Plant productivity did have a significant effect on herbivore abundance, which, based on the more individuals hypothesis, I predicted would be a positive effect (Srivastava & Lawton, 1998). However, my results contradict the predictions of the more individuals hypothesis – herbivore abundance decreased with increasing plant productivity and herbivore abundance had no significant effect on herbivore diversity (Figure 8). While many studies do find a positive correlation between insect abundance and plant productivity (e.g. Siemann, 1998, Kaspari et al., 2000; Kaspari et al., 2003; Borer et al., 2012; Hertzog et al., 2016), another recent study also found that insect abundance decreased with increasing plant productivity, although the reason for this negative relationship remains unclear (Prather et al., 2020). Other studies have found no support or contradictory results to the more individuals hypothesis (Currie et al., 2004; Haddad et al., 2009), and a recent meta-analysis shows that the relationships predicted by the hypothesis may be much weaker in ectothermic taxa, including insects, compared to many endothermic taxa (Storch et al., 2018).

In this study, herbivore abundance may have decreased in response to increased plant productivity due to reduction of preferred resources throughout the growing season. With increasing grass cover (which is positively correlated with grass productivity from year to year) during the growing season, herbivore abundance may have decreased because grasses can be lower quality and less palatable resources for many herbivores (Lenhart et al., 2015). Habitat complexity is also often reduced when grasses are the dominant functional group (Hertzog et al. 2016). Further, herbivores are expected to respond strongly to changes in forb cover and productivity because forbs, particularly legumes because of their high nitrogen content, tend to be higher quality and more palatable (Haddad et al., 2001; Rzanny & Voigt, 2012; Hertzog et al., 2016); however, there was no significant change in forb cover throughout the growing season in this study.

Alternatively, sap-feeding and chewing herbivores tend to respond differently to changes in plant productivity when plants are water stressed, resulting in more concentrated and elevated levels of nutrients, particularly nitrogen, in water stressed plants (Huberty & Denno, 2004). Changes in resource quantity and quality could potentially contribute to the effects of plant productivity on herbivore abundance. Sap-feeding herbivores typically responding negatively to water stress in plants while chewing herbivores often have both positive and negative response to water stressed plants (Huberty & Denno, 2004). In this study, the negative relationship between plant productivity and herbivore abundance does not track with decreases in either of the main feeding guilds. With decreasing plant productivity as soil moisture decreases (creating water stressed plants), my results suggest that neither feeding guild have a significant response to water stressed plants in this system. Instead, abundance of sap-feeding herbivores responded differently to

changes in plant diversity throughout the growing season, potentially reflecting shifts in palatable or preferred resources.

In contrast to many other studies that show increased herbivore diversity with increased herbivore abundance (Siemann, 1998; Haddad et al., 2001; Borer et al., 2012; Prather et al., 2020), my results show no significant effect of herbivore abundance on herbivore diversity. Additionally, despite the indirect reduction in herbivore diversity due to decreased soil moisture throughout the growing season, herbivore diversity increased throughout the growing season. It is difficult to disentangle the mechanisms behind the increase in herbivore diversity throughout the growing season that I observed due to limited sample size. A change in herbivore abundance may not have been enough to cause a significant change in diversity through the growing season if the evenness of the herbivore community also did not shift significantly. Alternatively, the direct negative effect of soil moisture on herbivore diversity, likely outweighed the total indirect effects via plant productivity and herbivore abundance, such that herbivore diversity responded positively to decreased soil moisture throughout the growing season.

4.3 Limitations and future directions

Contrary to my predictions, there was no significant effect of rainfall treatment on soil moisture, plant diversity, richness, plant productivity, or on the herbivore community. The lack of a treatment effect is not unexpected and is likely due to other factors that affect the amount of water accessible to plant and herbivore communities or how well the treatments affected soil moisture (Evans et al., 2011; Vicca et al., 2012). Many factors can affect soil capacity for water storage across space and time including soil depth and type, soil chemistry, microbes, air and soil

temperature, and profile of plot (Brady and Weil, 2002; Beier et al., 2012; Vicca et al., 2012; Zavaleta et al., 2003). At the study site, soil depth, texture, and tree cover can vary substantially over short distances, such that differences in these factors between plots also influence soil moisture in our experiment, leading to inconsistent effects of drought or irrigation treatments across plots. For example, some plots are very rocky with shallow soils, while others have deeper and less rocky soils, and others have trees nearby that create more shade. When the experiment was established, trenches were not dug around each plot, so plots are not hydrologically isolated from the areas around them potentially reducing the effects of the treatments. Finally, the soil moisture probes are only located in one place in the plot and at one depth, so soil moisture measurements may not be representative of the entire plot or rooting area (Vicca et al., 2012).

The lack of rainfall treatment effect may also be attributed to a delayed response of the plant or herbivore community to this experiment; the length of time since the beginning of the treatments is important to consider in rainfall manipulation experiments. Research from other long-term precipitation experiments shows that there is often a delay in the plant community response to treatments, and it may take more than 6 years for consistent and significant changes to start occurring (Evans et al., 2011; Griffin-Nolan et al., 2019). Some studies also suggest that lagged effects of soil moisture may influence plant and herbivore community composition. For example, Zhu et al. (2014) found herbivore abundance was lowest in the most productive year of their study, but high rainfall and high biomass led to more oviposition and thus higher herbivore abundance in the following year. Although I did not have enough data to include it in my analyses here, it is important to consider lagged effects of precipitation and soil moisture on the plant and herbivore communities community (Sala et al., 2012; Zhu et al., 2014). For example, if

lagged effects are common, this suggests that while abundance of herbivores responded negatively to increased plant productivity in 2021, high plant productivity in 2021 could lead to a higher abundance of herbivore in 2022.

Additionally, the significant effect of the treatments on soil moisture in 2021 suggest that the magnitude of initial treatments may not have been great enough to result in a significant change in soil moisture. Timing and strength of rainfall manipulation can also affect the magnitude of the response of the plant and/or herbivore communities (Suttle et al., 2007). For example, in a California grassland study, additional rainfall in spring had significantly larger effects on plant productivity than when additional rainfall was during the rainy winter season, suggesting that responses to water availability may shift throughout the growing season (Suttle et al., 2007).

Going forward, with continued added water to the irrigated treatments, this experiment may lead to more significant treatment effects on the plant and herbivore communities and the ability to further disentangle the underlying mechanisms. Long-term rainfall manipulation experiments in general could benefit from examining the effects of water availability on plant and herbivore communities at multiple points throughout the growing season because it will provide further insight into how changes in precipitation will affect these communities.

Chapter 5: Conclusion

Changes in precipitation with climate change will have significant consequences for plant and insect communities, and while this is a generally accepted consequence of climate change, there is little consensus about how and at what magnitude these effects will occur across ecosystems. This rainfall manipulation experiment provides an opportunity to examine these relationships in an endangered oak-savanna ecosystem that falls outside the typical ecosystems that many similar studies take place in, where plant productivity is low despite having relatively high annual rainfall, and springs are predicted to become wetter and summers drier. My M.Sc. thesis shows that both decreases and increases in precipitation will have significant impacts on plant productivity and the dominant plant functional groups in this system. In this study, I show that direct effects outweigh the plant-mediated effects of water availability, but also that these productivity-mediated effects of soil moisture will translate to significant negative effects on herbivore abundance. Here I also show preliminary evidence that the interactions between the plant and herbivore community may shift throughout the growing season with shifting water availability. However, further research is needed to disentangle how increased and decreased precipitation in the spring and summer, respectively, will translate to effects on the herbivore community throughout the growing season. This study provides valuable insight into the effects of climate change on this highly endangered ecosystem and contributes to our greater understanding of how changes in precipitation will affect plant and herbivore communities and the interactions between them.

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Appendices

Appendix A Average daily soil moisture in each year and in each treatment

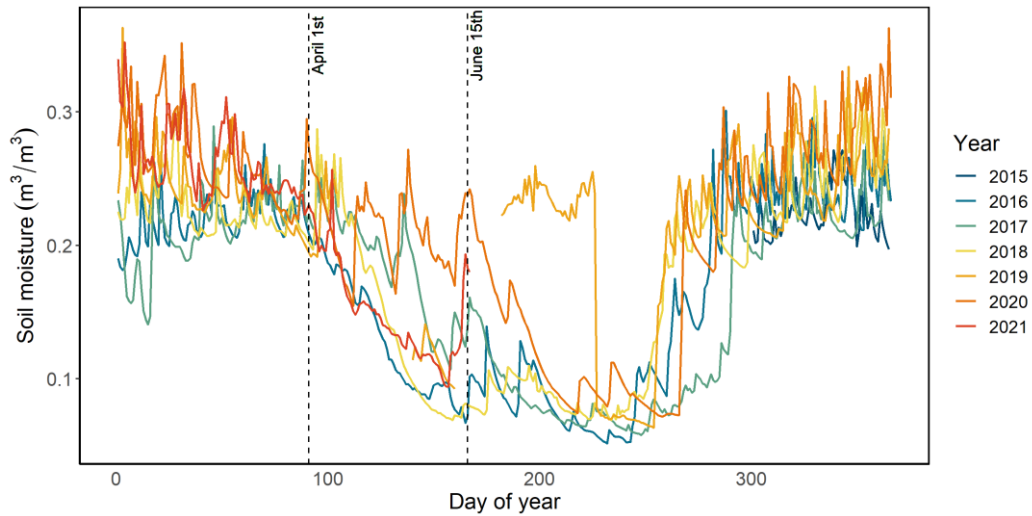


Figure 12 Average daily soil moisture (averaged across all 15 plots) in each year. Dashed vertical lines represent the growing season period between April 1st (Day 91) to June 15th (Day 166) that was used for analyses. Data collection began in October 2015, and here is displayed through June 15, 2021.

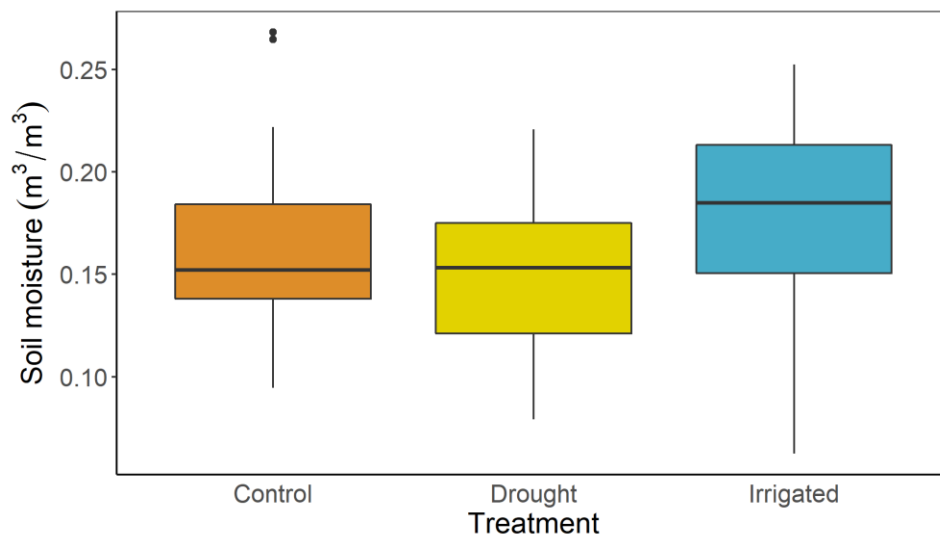


Figure 13 Average daily growing season soil moisture (April 1st – June 15th) in each treatment across all years.

Appendix B Herbivore classification

Table 1 Classification of herbivores by feeding type and total abundance of each family. Families were classified using *American Insects: A Handbook of the Insects of America North of Mexico* (Arnett Jr., 2000).

Feeding Type	Order	Family	n
sap-feeding	Hemiptera	Aleyrodidae	8
	Hemiptera	Aphididae	1708
	Hemiptera	Berytidae	46
	Hemiptera	Cercopidae	45
	Hemiptera	Cicadellidae	1511
	Hemiptera	Lygaeidae	1
	Hemiptera	Miridae	38
	Hemiptera	Pentatomidae	2
	Hemiptera	Pseudococcidae	54
	Hemiptera	Psyllidae	16
	Hemiptera	Unknown	7
	Hemiptera	Tingidae	1
	Trombidiformes	Tetranychidae	376
chewing	Coleoptera	Scolytidae	2
	Lepidoptera	Gelechiidae (larvae)	1
	Lepidoptera	Saturniidae (larvae)	1
	Lepidoptera	Unknown (larvae)	22
	Orthoptera	Acrididae	12
	Thysanoptera	Thripidae	762
nectar/pollen	Diptera	Agromyzidae (adult)	1
	Diptera	Bombyliidae	1
	Diptera	Lonchopteridae	2
	Hymenoptera	Halictidae	1
	Lepidoptera	Coleophoridae (adult)	8

Appendix C Models

Table 2 Components of models that were chosen for each response variable. Marginal r-squared values represent the proportion of the variance of model is explained by the fixed effects, and conditional r-squared values represent the proportion is explained by the fixed and random effects.

Underlined models are best fitting models.

Response	Fixed effects	Random effect	AIC	Marginal R-squared	Conditional R-squared
<u>soil moisture</u>	<u>year</u>	<u>plot</u>	<u>-382.34</u>	<u>0.44</u>	<u>0.77</u>
soil moisture	year + treatment	plot	-380.89	0.49	0.77
<u>plant diversity (H_p)</u>	<u>soil moisture + year</u>	<u>plot</u>	<u>6.59</u>	<u>0.20</u>	<u>0.55</u>
plant diversity (H _p)	treatment + year	plot	8.26	0.21	0.55
<u>plant diversity (D)</u>	<u>soil moisture + year</u>	<u>plot</u>	<u>-207.66</u>	<u>0.32</u>	<u>0.51</u>
plant diversity (D)	treatment + year	plot	-206.21	0.14	0.51
<u>plant richness</u>	<u>soil moisture + year</u>	<u>plot</u>	<u>375.85</u>	<u>0.32</u>	<u>0.57</u>
plant richness	treatment + year	plot	377.35	0.33	0.58
<u>log(plant productivity)</u>	<u>H_p * soil moisture + soil moisture * year</u>	<u>plot</u>	<u>137.07</u>	<u>0.34</u>	<u>0.67</u>
log(plant productivity)	H _p + treatment + year	plot	162.54	0.15	0.45
<u>% grass cover</u>	<u>soil moisture + year</u>	<u>plot</u>	<u>698.47</u>	<u>0.30</u>	<u>0.73</u>
% grass cover	treatment + year	plot	700.80	0.29	0.73
<u>log(grass productivity)</u>	<u>soil moisture * year</u>	<u>plot</u>	<u>229.22</u>	<u>0.19</u>	<u>0.66</u>
log(grass productivity)	treatment * year	plot	244.14	0.081	0.56
<u>% forb cover</u>	<u>soil moisture + year</u>	<u>plot</u>	<u>765.67</u>	<u>0.11</u>	<u>0.70</u>
% forb cover	treatment + year	plot	766.95	0.15	0.70
<u>log(forb productivity + 1)</u>	<u>soil moisture + year</u>	<u>plot</u>	<u>244.09</u>	<u>0.20</u>	<u>0.52</u>
log(forb productivity + 1)	treatment + year	plot	244.12	0.27	0.48

Table 3 Table of component models for the piecewiseSEM and the marginal and conditional R-squared values for each model. Predictor variables where selected based the *a priori* model in Figure 1. Soil moisture was added as a predictor for herbivore diversity (H_h) and herbivore abundance based on tests of directed separation (Lefcheck, 2016).

Response	Fixed effects	Random effect	Marginal R-squared	Conditional R-squared
herbivore diversity (H_h)	herbivore abundance + H_p + plant productivity + soil moisture	plot	0.18	0.18
herbivore abundance	H_p + plant productivity + soil moisture	plot	0.14	0.36
plant productivity	soil moisture + H_p	plot	0.20	0.44
plant diversity (H_p)	soil moisture	plot	0.02	0.33

Table 4 Table of exploratory models for the herbivore community comparing across sampling period in 2021 (sample period added as fixed effect) and comparing the late growing season in 2020 and 2021 (year added as fixed effect). Marginal and conditional R-squared values are reported for each model.

Response	Fixed effects	Random effect	Marginal R-squared	Conditional R-squared
<i>Using only data from 2021 to compare across the growing season</i>				
herbivore diversity (H_h)	herbivore abundance + H_p + plant productivity + soil moisture + sample period	plot	0.53	0.59
herbivore abundance	H_p + plant productivity + soil moisture + sample period	plot	0.04	0.47
log(sap-feeding abundance)	plant productivity + H_p + sample period + H_p * sample period	plot	0.17	0.51
log(chewing abundance)	plant productivity + H_p + sample period	plot	0.07	0.60
% grass cover	soil moisture + sample period	plot	0.80	0.87
% forb cover	soil moisture + sample period	plot	0.081	0.49
<i>Using only data from late 2020 and late 2021 to compare across years</i>				
herbivore diversity (H_h)	herbivore abundance + H_p + plant productivity + soil moisture + year	plot	0.30	0.30
herbivore abundance	H_p + plant productivity + soil moisture + year	plot	0.55	0.56
log(sap-feeding abundance)	plant productivity + H_p + year	plot	0.31	0.31
log(chewing abundance + 1)	plant productivity + H_p + year	plot	0.31	0.51
% grass cover	soil moisture + year	plot	0.44	0.72
% forb cover	soil moisture + year	plot	0.36	0.77

Appendix D Plant community composition metrics in each treatment in each year

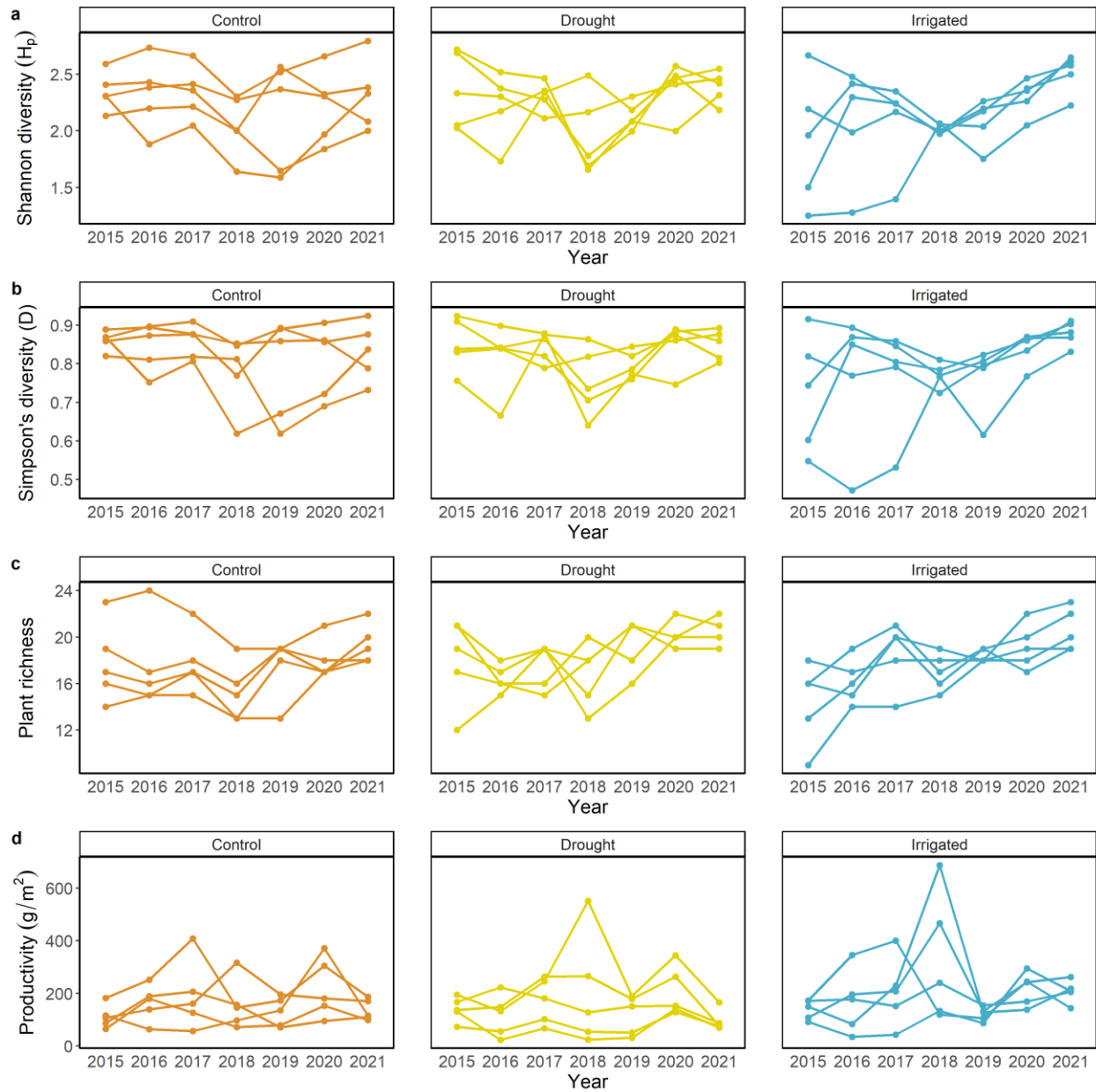


Figure 14 Shannon diversity (H_p) (a), Simpson's diversity (D) (b), plant richness (c), and productivity (g/m^2) (d) in each year in each treatment. Each line represents a single plot, color corresponds to treatment.

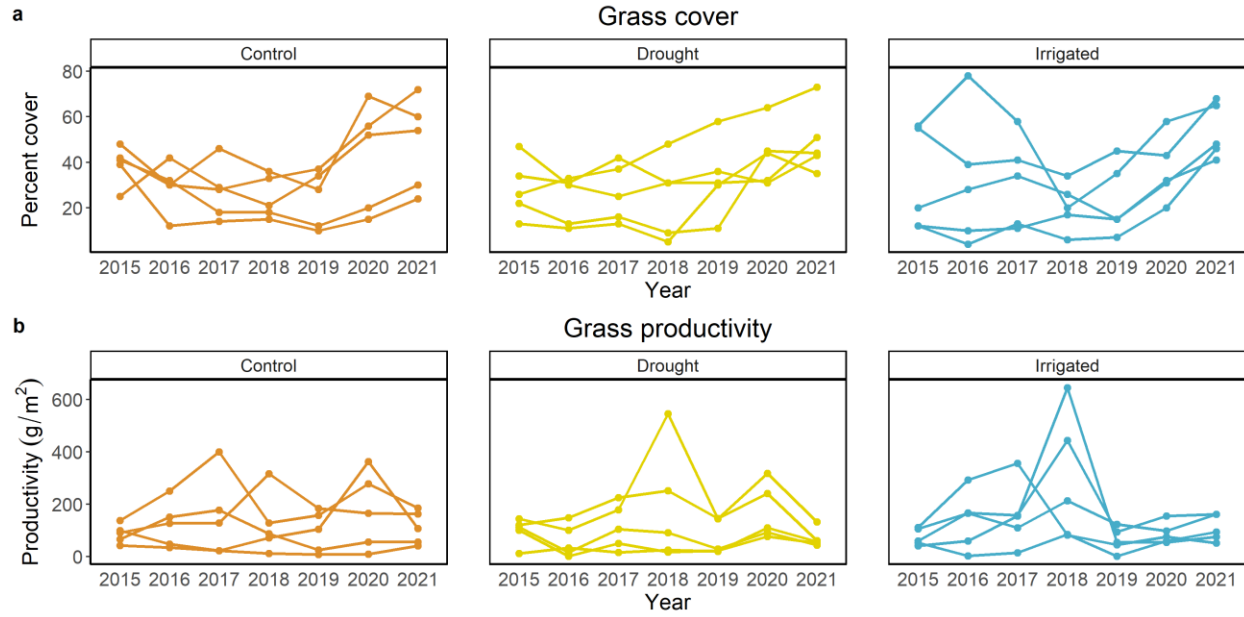


Figure 15 Percent cover (a) and productivity (g/m^2) (b) of grasses and forbs in each treatment in each year in each treatment.

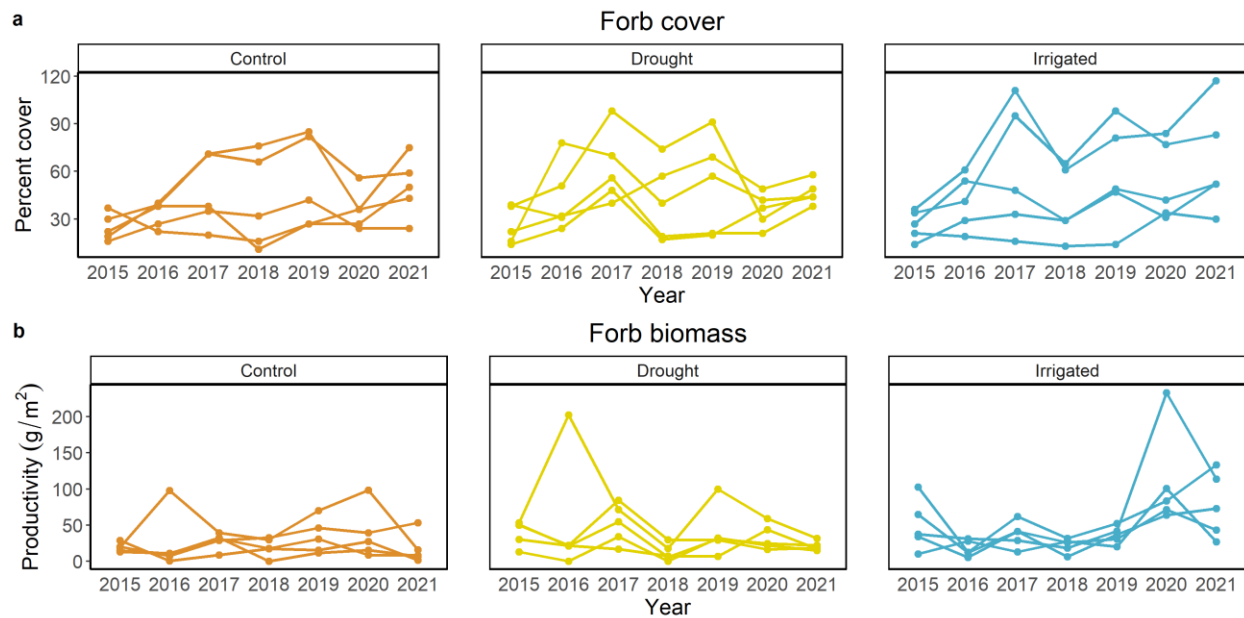


Figure 16 Percent cover (a) and productivity (g/m^2) (b) of forbs in each treatment in each year in each treatment.

Appendix E Diversity, abundance, and richness of herbivore in each treatment

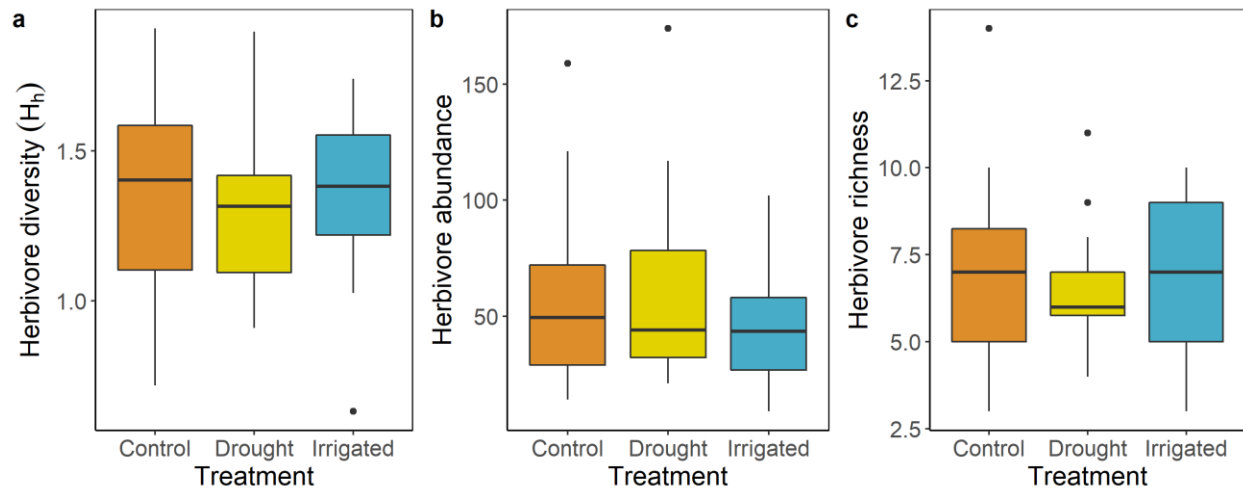


Figure 17 Diversity (H_h) (a), abundance (b), and richness (c) of herbivores in each treatment (averaged across sampling period in 2020 and 2021).