

MANN, WILLIAM T. M.S. NUTRIENT DEPOSITION AND DROUGHT EFFECTS ON ARTHROPOD HERBIVORE DAMAGE IN LONGLEAF PINE SAVANNA UNDERSTORY. (2024)

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Herbivory, a key ecosystem process, ensures the cycling of energy and nutrients. A particularly important driver of grassland and savanna dynamics, nearly a third of plant production moves up the food web by herbivory. Arthropod herbivores account for the majority of herbivory in some grassland systems. Worldwide arthropod abundance and biodiversity are being lost at alarming rates in what is known as the insect apocalypse.

Longleaf pine (LLP) savanna, once expansive throughout the southeastern United States, is now critically threatened, with only 4% of the historical range remaining. Over 900 plant and animal species reside in its understory, making this one of the most diverse systems in the world. The LLP tree is lauded as ‘the tree that built the South’, making the LLP savanna historically and ecologically valuable. Increased drought occurrence and nutrient deposition threaten restoration and conservation success in LLP savannas, among other global change factors.

My research aims to understand how nutrient deposition and drought will interact to affect herbivory. I utilize an existing long-term (4 years total) drought and nutrient experiment in a healthy, mesic LLP savanna in the Sandhills Gamelands of North Carolina (Richmond County). I aim to (1) Quantify the impact of global change on herbivore damage in four dominant understory plant species and determine how herbivore damage changes through time across two timescales; and (2) Explore various mechanisms’ effects on the magnitude of herbivore damage.

Arthropods are a significant component of most ecosystems; understanding the roles they play – especially under global change – and how these roles may differ in the future will help land managers prepare for the changes to come.

NUTRIENT DEPOSITION AND DROUGHT EFFECTS ON ARTHROPOD HERBIVORE  
DAMAGE IN LONGLEAF PINE SAVANNA UNDERSTORY

by

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## CHAPTER I: THESIS INTRODUCTION

### Introduction

#### Herbivory

**Herbivory, a key ecosystem process present across nearly all ecosystems, impacts nutrient cycling, ensures energy transfer up food webs, and alters community dynamics.**

Herbivory is a particularly important driver of grassland and savanna dynamics with these systems supporting nearly all of the world's mega-herbivore biomass (Gibson, 2009). Herbivory by large vertebrates (e.g., bison, cattle, zebra) has been shown to reduce the abundance of palatable dominant species, increasing diversity by allowing less competitive species to increase in abundance (Olf & Ritchie 1998; Koerner, et al. 2018; Hyvarinen, et al. 2021; Staver, et al 2021). The effect of mega-herbivores on grassland community dynamics has been well studied with numerous meta-analyses summarizing decades of herbivore exclusion studies (Bakker, et al. 2015; Koerner, et al. 2018; Price, et al. 2022). While grasslands are known for their charismatic megafauna, **insect herbivores (Figure 1) can account for the majority of herbivory in many grassland systems** (An, et al. 2014; Harpole, et al. 2016; Schowalter, 2016). The effect of insect herbivores and pollinators, particularly the ecosystem processes they perform, can be equally as important (Argawal & Maron 2022).



**Figure 1: Common leaf chewer (order Hymenoptera) in longleaf pine savanna. Photo Credit: W. Mann**



Arthropod herbivores, when outbreaks occur, can have devastating effects on plant communities causing the death of certain individuals; however, lower continuous levels are more common and present throughout most ecosystems. Plant-insect herbivore interactions are nearly ubiquitous across the plant kingdom (Robinson, et al. 2023), and large amounts of literature document the negative effects of insect herbivores on plant performance (Hawkes & Sullivan 2001; Lawrence, et al. 2003; Barton & Koricheva 2010; Takahashi & Yamauchi 2010; Jia, et al. 2018; Martinez-Swatson, et al. 2020). Understanding arthropod herbivory and the role it plays in structuring ecosystems is critical, especially as the current ‘insect apocalypse’ unfolds (Cardoso, et al. 2020; Goulson 2021). The ‘insect apocalypse’, as it has been coined, is a series of anthropogenic effects responsible for a **worldwide 1-2% annual decline in insect abundance** (Wagner, et al. 2021), such as pollution, deforestation, and disturbance disruption. Ecosystem services like pollination, waste management, and nutrient cycling (Welti, et al. 2020), are often maintained by arthropod herbivores. In the absence of arthropods, these vital processes come undone.

**Figure 2: Sandhill Gamelands longleaf pine (LLP) savanna (2023) in south-central North Carolina.**



### ***Longleaf Pine Savannas & Controls Of Herbivore Damage***

The relationship between arthropod herbivory and the environment is especially important in the LLP savanna system (**Fig. 2**) as insects are major herbivores (Van Lear, et al. 2005). Most grazing is performed by small vertebrates such as Sherman’s fox squirrel and the gopher tortoise (Van Lear, et al. 2005). The LLP savanna once covered large portions of the southeastern United States (US), covering the coastal plains of the Carolinas, Georgia, Florida, Alabama, Mississippi, and Louisiana spanning ~90 million acres. Through much of the LLP savanna reign, large herbivores roamed this area, even huge herds of bison up until the 1400s (Martin, et al. 2022). Sadly, the LLP savanna is now among the most critically threatened ecosystems with 5.2 million acres remaining much of which has been restored (Oswalt, et al. 2012), and nearly all large grazing herbivores lost (Engstrom, 1993). The plant community of the LLP savanna yields an incredible amount of biodiversity, from forbs, legumes, and woody species (Frost 1993; Oswalt et al. 2012; Porter et al. 2013; McIntyre et al. 2018). With high plant diversity in the understory and diversity rivaling rainforests at small spatial scales, the LLP savanna is of high ecological importance (Frost 1993; Oswalt, et al. 2012; Porter, et al. 2013).

Additionally, the LLP tree provides economic importance, with this ecosystem having the potential to be a multi-use landscape benefiting both economic and conservation goals.

Restoration has been largely successful in the overstory monoculture (**Fig. 2** overstory tree); however, restoring the understory (**Fig. 2** low herbaceous layer) has proved more complex and requires further focus. Plant-insect herbivore interactions likely play a strong role in structuring both plant and insect communities in this biodiversity hotspot (Orrock, et al. 2023).

Herbivore damage varies across a landscape and even among individuals (Castagneyrol, et al. 2014; Turcotte, et al. 2014; Robinson, et al. 2023). Robinson, et al. (2023) found that most herbivory in a community is found on very few individuals, usually contingent on phylogenetic distance and plant size. In a high-diversity community, there is typically low mean herbivory across all populations. Chemical defenses diversify with phylogenetic distance, making it energetically costly to herbivore multiple species. Comparing understory and overstory: Small size makes plants less likely to experience a herbivore damage event. Tree populations typically contain a smaller variability of herbivore damage, while understory plants tend to have very little or very high amounts of herbivore damage (Robinson, et al. 2023).

The variation seen across plant patches (or plots) is likely driven by three main components: 1) plant community composition and abundance, 2) plant nutrient content, and 3) insect community composition and abundance. Arthropod herbivores rely on the plant community to supply their food source and often their habitat for reproduction. Plant communities control herbivore damage directly by altering the food supply and nutritional value of leaves. The plant nutrient content of soil directly impacts the plant community and indirectly impacts the arthropod community. Enrichment of soil, either through nutrient additions or nutrient deposition, will determine what plants take root (Shan, et al. 2022). The nutritional

quality of plant forage can have a massive impact on herbivore damage, and plant nutritional quality varies with plant species identity and with changes in an individual's (or population) leaf tissue nutrient content. To meet requirements for survival, growth, and reproduction, herbivores can feed in a couple of ways. First, compensatory feeding happens when herbivores increase their intake of low to medium-quality forage, to meet performance requirements. This is often the default feeding strategy for many arthropods (Lavoie & Oberhauser 2004). Conversely, selective feeding occurs when herbivores feed on a lower amount of forage that is of much higher quality. While compensatory feeding is more common, selective feeding frequently yields higher levels of arthropod performance, and therefore, abundance (La Pierre and Smith, Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems 2016). Plant nutrient content affects both plant and herbivore biomass, strongly predicting herbivore and predatory arthropod taxon richness (Lu, et al. 2022). Lastly, high biodiversity within the plant community often reflects high biodiversity in the arthropod community (Haddad, et al. 2009; Dinnage, et al. 2012). Hosting 900 endemic plant and animal species, LLP savanna also hosts high phylogenetic diversity (Levey, et al. 2016; Sheehan & Klepzig 2021; Pau, et al. 2023).

This diversity presents itself in the many herbivores that exist in the LLP savanna range, including the previously mentioned Sherman's fox squirrel, a vertebrate granivore. Arthropod herbivores, while not as destructive as vertebrate herbivores, do contribute to the evenness of herbivore damage across the landscape (Levey, et al. 2016). Many arthropod herbivores in LLP savanna, in particular, tend to be chewing or sucking folivores like grasshoppers or beetles. However, crickets and ants can be granivores, and nectarivorous pollinators like bees and butterflies are common (Sheehan & Klepzig 2021). More diverse assemblages of arthropods

could lead to higher levels of herbivore damage due to niche partitioning (McArthur 1957, 1958), with different species occupying different niches, allowing a resource to be more fully utilized.

### ***Global Change And Herbivory***

In the last century, the natural world has been thrown out of balance with the onset of the Anthropocene. With the rise of greenhouse gas emissions, global mean temperatures are rising and the hydrological cycle is intensifying, leading to more extreme and more frequent weather events, such as drought and hurricanes (Harris, et al. 2006; Hoover, Knapp and Smith 2014; Young, et al. 2021; Sohail, et al. 2022) Simultaneously the amount of N in the Nitrogen cycle has doubled (Fowler, et al. 2013) and P mobilization between land and water has tripled (Yuan, et al. 2018). Previously mentioned climatic factors and previous degradation of the LLP savanna leaves this system especially sensitive to anthropogenic change. Thus, water and nutrient availability changes could have large consequences for this system, including altering herbivory through changes in plant or arthropod composition or plant nutrient content.

While it has been shown that more diverse ecosystems may show greater resilience to drought events (Craine, et al. 2013), recent literature suggests that many studies greatly underestimate the intensity of such events (Smith et al., 2024). Naumann et al. (2018) project that rare, 1-in-100-year drought events may occur as often as every two-to-five years. A 60% decrease in Aboveground Net Primary Product (ANPP) was found to occur in a global experiment under these desiccation events (Smith et al. 2024). Similarly in a site-based experimental drought, grassland production was reduced by as much as 50% in a semi-arid Mongolian grassland (Luo, et al. 2021), with plant species richness decreasing (by 45%) only upon a secondary drought (Luo, et al. 2022). Grassland may maintain resilience (ability to

rebound post drought) for a time, but successive drought events will greatly depreciate the plant community in a short time (Luo, et al. 2021). Drought has shown to reduce nutrient content of leaves (Bista et al. 2018; M. R. Smith et al. 2019; Sitters et al. 2020), reduce the effectiveness of the nutrient-acquiring properties of roots (Bista et al. 2018, 2020), and limit leaf nutrients in barley crops (Bista, et al. 2020). Water stress makes for harsher growing conditions, leading to a decrease in yield and nutrient content.

Huberty & Denno (2004) found that regardless of arthropod feeding guild, host plants display lower arthropod populations under water stress. Under such pressure, chewing arthropods, who must chew through more concentrated allochemicals, tended to avoid water-stressed host plants, locally decreasing their abundance (Huberty & Denno, 2004). Sap-feeding arthropods capitalize on more concentrated xylem and phloem, enriched with nitrogen, ignoring plant surface chemical defense. Both feeding guilds show better performance under acute water stress (Huberty & Denno, 2004; Walter et al., 2011; Jactel et al., 2011), due to decreased plant defense capability. Hosting a plethora of arthropod and plant species, grasslands are arenas where these complex arthropod-plant interactions can be studied in full, now under pressure from global change factors.

Grasslands around the globe are widely known to be nutrient-limited (Vitousek & Howarth, 1991; LeBauer & Treseder 2008; Harpole et al., 2011), often times being most limited by nitrogen (Vitousek & Howarth, 1991). Double the amount of N has been mobilized over the last century (Fowler et al., 2013), resulting in greater N deposition in many ecosystems (Niu et al., 2017). Formerly-limited systems are likely undergoing changes in the plant community as a previously limiting resource becomes available. For example, fast-growing species that capitalize off the added N may come to dominate, eliminating a great deal of biodiversity and resilience to

extreme climate events (Welti, et al. 2017; Muehleisen, et al. 2023). Typically LLP savanna is a nitrogen-limited system (Prior, S.A. et al. 1997), as it burns frequently, volatilizing nitrogen back into the atmosphere. As predicted for grasslands as a whole, nutrient deposition is likely to give rise to fast-growing understory grasses and lead to a loss of native plant species (You, et al. 2017; Muehleisen, et al. 2023).

Historically, the LLP savanna has hosted a number of leguminous forbs such as *Chamaecrista nictitans* and *Lespedeza* species. These legume species are incredibly important to the savanna through their symbioses with various strains of nodulating rhizobia (Ferguson, et al. 2019). These symbioses allow for the fixing of nitrogen into the soil into bioavailable fuel for legumes and their neighbors (Grelen & Duval, 1966). In an ecosystem that burns frequently, this is invaluable to community function. N-limited conditions of the LLP savanna make the symbiosis an evolutionary advantage, allowing for the continued establishment of these species. As the ambient N increases in the LLP savanna due to N deposition, these symbioses, and consequently, the legume species, will become more redundant. Enrichment of nitrogen may lead to the loss of legumes, a vital source of biodiversity and high-quality forage. Thus arthropods may be forced to consume lower-quality forage and thus increase herbivory rates, leading to a smaller, less diverse arthropod community.

Plant community phenology and insect ontogeny are incredibly important to ecosystem function and health. Variations in nutrient availability caused by global change may have a significant effect on the timing of leaf senescence and the sink-source transition, which, in turn, will affect arthropod foraging and morphology (Coleman, 1986; Hochuli, 2001; Yu et al., 2015; Piao et al., 2019). In response to alterations in nutrient content and plant species shifts, the arthropod community may also change. This shift in arthropod communities may lag behind

changes seen at the plant level, leading to a second wave of change in herbivore damage levels. Various feeding guilds and feeding strategies are employed by arthropod herbivores, making arthropod community composition important for understanding herbivore damage. It is hypothesized that feeding strategies will also change in response to community nutrient change. In an N-enriched environment, individual plants could increase in leaf nutrient content and biomass, allowing arthropods to select for a higher nutrient class of food (Behmer and Joern 2008). These more selective feeding strategies allow for greater nutrient intake against energy expenditure, potentially causing arthropod populations to surge. While rates of herbivory will decrease, the number of arthropods allows total ecosystem herbivory to remain roughly the same (La Pierre and Smith 2016).

Many arthropods change forms as they grow, and they are intrinsically tied to the plant host species around them, often timing pupa emergence with leaf susceptibility to herbivory (Coleman 1986). If nutritional shifts in the LLP savanna allow for changes in plant community phenology (Dinnage, et al. 2012) through the earlier emergence of leaves and defensive chemicals, there could be phenological shift in arthropod herbivores. Alternatively, due to shifting plant ontogeny, there could be a major loss of arthropod diversity, leading to a major impact on herbivore damage in the already depreciated LLP savanna ecosystem. Jones and Despland, 2006, found that if emergence of caterpillars is delayed, folivore performance decreases due the effect of leaf age and defense on high-quality food availability. Walter et al., 2011, fed droughted plant material to caterpillars, who were have longer larval and pupa stages. Understanding this interaction may help us understand how arthropod populations may be affected by these changes, and how seasonality may play an important role in the relationship between arthropods and plants.



In a world of ubiquitous global change and multiple co-occurring effects, it is more likely for dual stressors to occur, leading to potentially greater changes in a plant community (Komatsu et al. 2019), yielding greater changes to arthropod herbivores and herbivore damage in the community. Under the dual stressors of nutrient deposition and drought, the LLP ecosystem is in a precarious position. With higher soil N, opportunistic annual species may take up ground cover once occupied by legumes or forb species, reducing community biodiversity. Increased frequency and severity of drought may strip away plant and arthropod biodiversity, leaving the LLP savanna community devoid of the resilience it needs to withstand successional, extreme drought events or other GCFs. These dual events may produce a vastly different ecosystem than is currently present. In an already imperiled position, the LLP savanna is more susceptible to change now than ever. If we do not seek to understand how these changes may impact the LLP savanna, we stand no hope of fortifying it against increasing global change.

### **Objectives And Significance**

My research aims to understand how global change will affect a key disturbance in herbaceous-dominated systems – herbivory. Shifts in herbivore damage could be caused by (1) shifts in the arthropod community, (2) shifts in the plant community, or (3) shifts in plant nutrient content. To understand how global change will impact herbivory and then what the mechanism of change is, I will use a pre-existing manipulative field experiment that simulates drought and nutrient deposition in the LLP savanna of the Sandhill Gamelands (Hoffman, NC).

My two objectives are:

1. Quantify drought and nutrient addition impact on herbivore damage in four dominant understory plant species and determine how herbivore damage changes across years as well as throughout a single growing season

2. Explore various mechanism's effects on the magnitude of herbivore damage (i.e., changes in (1) plant communities or biomass, (2) changes in plant nutrient content, and (3) changes in arthropod communities or biomass)

I hypothesize that both drought and nutrient additions will decrease herbivore damage in early years, but increases in later years. The opposite trends will be due to changes in the mechanisms, with the early years of treatments seeing a decrease in damage due to increases in plant nutrient content, whereas in later years, damage increases will be due to changes in the plant community towards plants of lower quality.

Changes in an ecosystem will have different effects on all organisms within it. As the effects of human impact in the Anthropocene actualize, so too will restoration of the LLP savanna become more difficult. As so much of the historic range of this ecosystem has been devastated, we cannot rely merely on conserving what remains. Instead, the LLP savanna must be restored and prepared to survive in a changing world. This restored savanna might be more sensitive to global change drivers like drought and nutrient deposition making it further susceptible to other changes like invasion. Understanding how herbivore damage will change is critical as all anthropogenic and natural disturbances are likely to interact in key ways and with feedback.

## **Methods**

### **Site Description**

This research took place in the Sandhill Gamelands (Hoffman, NC). The Sandhills region of North Carolina has a Mean Annual Temperature (MAT) of 61.8°F and a Mean Annual Precipitation (MAP) of 46.7 inches, measured from a station ~14 miles from the site. This region of the LLP savanna ecosystem range is mesic sandhills, with well-drained, sandy soil. The

grassland understory is dominated by *Aristida stricta*, *Schizachyrium scoparium*, and *Pteridium aquilinum*, along with numerous forbs and legumes. The Gamelands are burned periodically, every 2 to 5 years. The last burn (and only burn during data collection) on this site took place in 2020.

### **Experimental Design**

This pre-existing experiment is part of two global networks with common experimental set up. The Nutrient Network (NutNet) is a globally distributed experiment addressing relationships between plants and nutrients. In the NutNet plots, nitrogen, potassium, and phosphorous are added ( $10\text{g/m}^2$ ) in full factorial (8 total treatments) to simulate extreme nutrient deposition and alleviate resource limitations. The experiment has an  $n=3$  per treatment, leading to 24 total plots. The Drought-Net Research Coordination Network (Drought-Net) is a global network of researchers seeking to assess terrestrial ecosystem sensitivity and response to drought. Rainout shelters are erected for 5 months yearly, excluding 30% of rainfall, simulating moderate drought. As part of these rainout shelters, a tubing system has been installed to drain the water away from the site, ensuring all drought plots remain as such. For Drought Net, 6 extra plots were added, three nutrient controls (i.e., no addition) and three NPK plots in which shelters were. Including these additional 6 Drought-Net plots makes for 30 plots total in this experiment, split across 3 blocks. Each of these blocks contain one of each treatment type, including shelter plots, making for 10 plots per block.

Within this experimental design, my sampling has been structured to examine the effect of time at two temporal scales. First, this experiment began with limited pre-treatment sampling in 2019 focused on the plant community (species composition and ANPP). As the nutrient and drought treatments began in 2020, so did peak season (July) herbivore damage sampling and

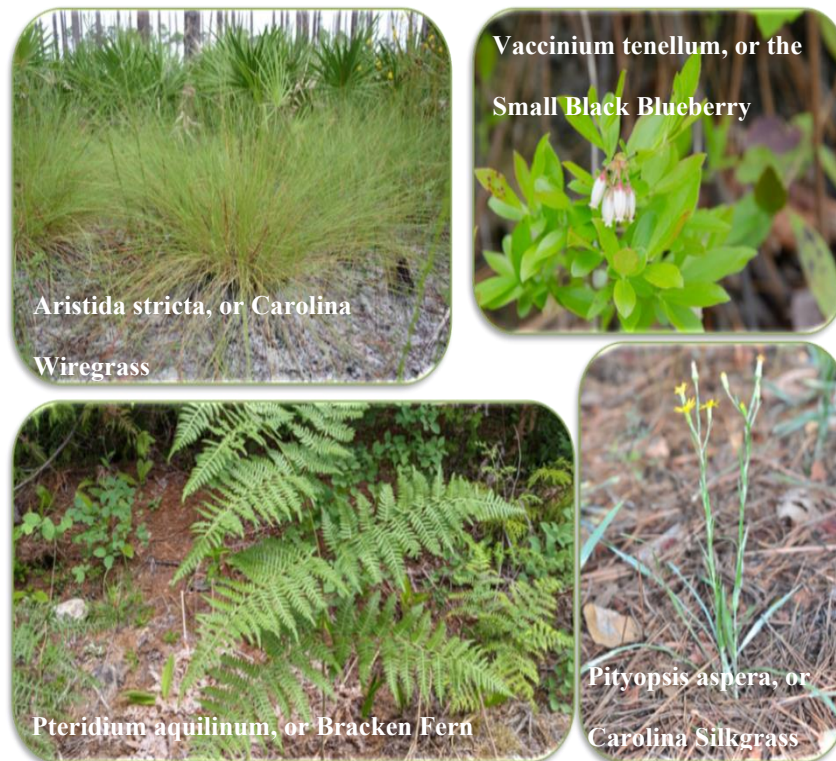
insect community sampling. This peak season insect sampling (community and herbivore damage), as well as plant community sampling in early (community) and late season (community and ANPP), occurred yearly from 2020 to 2023. Secondly, in 2022 only, I also conducted seasonal sampling in early (April), middle (July – which corresponds with yearly sampling), and late summer (September) of herbivore damage and insect community.

### **Data collection**

Herbivore damage – Herbivore damage was studied on 4 key understory species (**Fig. 3**) in the LLP savanna ecosystem in July of every year (2020-2023) as well as seasonally in 2022 (April, July, September).

**Figure 3: Four key longleaf pine understory plants selected for herbivore damage study.**

*Note:* Two forb species (*Vaccinium tenellum*, *Pityopsis aspera*), a grass species (*Aristida stricta*), and a fern (*Pteridium aquilinum*). All species native to the longleaf pine savanna range



These species were chosen for their abundance (top 10) during the first two years of studying plant species composition, and 3 of them flower throughout the growing season. *Vaccinium tenellum* blooms in the early season and both *Aristida stricta* and *Pityopsis aspera* flower in the late season (**Fig. 3**). *Pteridium aquilinum* is a non-flowering, rhizomatous fern species. In each of the 30 plots, 5 fully expanded leaves of each species were chosen at random, preferentially from different individuals. These leaves were observed and assigned to a category of percent leaf damage, using a marginally altered leaf damage protocol from the Nutrient Network. Using visual estimation, leaf damage type was assessed, and leaves were assigned appropriate damage ranges. The damage ranges were as follows: 0%, 1-5%, 6-25%, 26-60%, and >60% (Castagneyrol et al., 2012). To accurately determine damage category, the leaves were relativized to the observed total leaf area. When working with others, observers synchronized their observations during the first few measurements and periodically throughout the day. For analysis purposes, all damage categories were simplified to their average value (e.g., 1-5% and 26-60% became 3% and 43%, respectively).

### ***Insect community***

Arthropod samples were taken in July of every year (2020-2023) as well as seasonally in 2022 (April, July, September) using SweepNet and D-vac collection methods (**Fig. 4**). The SweepNet method (**Fig. 4A**) consists of a team of two individuals. One person uses a large butterfly net and ‘sweeps’ along the ground in a plot, keeping the net about 1 inch off the ground. The second individual waits with a collection bag until sweeping is finished, wrapping the collection bag around the butterfly net. The two individuals will then carefully maneuver to brush arthropods into the collection bag. In this experiment, the sweeper walked the borders of each plot and crossed the center twice. The D-vac method (**Fig. 4B**) only requires one person but

**Figure 4: Two methods of insect collection used. A) Will Mann (left) preparing to SweepNet with an undergraduate researcher, and (B) Rose Terry (center) performing D-Vac collection.**



is aided by a second. This process enlists the use of a large leaf blower. The flow of air is reversed, and an apparatus is attached to the blower to catch arthropods in fine mesh bags. While SweepNet tends to collect arthropods that dwell on plants, D-Vac tends to collect topsoil-dwelling, smaller arthropods. After collection, arthropod sampling bags are deflated and placed into coolers to limit activity. Once transported back to the lab, they are placed in freezers, sorted by sampling method and year.

Starting from the first sampling year, the arthropod samples are taken from their respective bags, and sorting out the arthropods from soil and litter into a 15ml glass vial. Each sample is checked at least twice by different people. Once the second check has been completed, it is determined if the plot requires a third check or may proceed to the identification stage. If a third check is required, it is completed by senior members of the team. Using published or site-specific identification guides, each arthropod individual is counted and identified to Order, and as close to Family as possible. 5ml glass vials are used to sort arthropods by Order. Once all individuals have been accounted for, plot-level weight is measured at the plot level.

### ***Plant community***

Plant community composition surveys were conducted annually every year (2020-2023) as well as seasonally in 2022 (April, July, September). Aboveground plant biomass is collected in September of every year (2020-2023) as well as seasonally in 2022 (April, July, September). A 0.1m x 1m clip strip was used in each of our 30 plots, placed semi-randomly throughout the plot. In the initial collection in 2020, the clip strip was placed nearest to the center of each plot. For each time point onward, ANPP has been collected about 10 cm away from the previous collection point. This is to ensure that our plots are being measured in the same relative area each year and that each clip is not influence by previous years harvest.

### ***Leaf nutrient content***

A homogenous subsample of the plant community biomass is used for the nutrient content analysis. Once dried and weighed for biomass, these samples were ground and homogenized, and sent to the Soil Testing Lab at Kansas State University for analysis of N, P, and K content.

### **Data analysis**

All data manipulation, statistics, and graphing were conducted in R version 4.3.2. Total herbivore damage was defined as the chewing plus mining/sucking damage types. The data was normalized by log transformation. This log-transformed data was the dependent variable in all models. To detect the effects of nutrient addition and drought on herbivore damage (Aim 1), mixed-effect model ANOVAs were used treatments as fixed effects and both block and plot were included as random effects. Estimated Marginal Means (emmeans) were run for pairwise comparison of ANOVA results with no correction. Separate models were run for three different subsets of data. First, we explored the effects through time using only the July timepoint from all

four years of data collection. For this analysis we dropped the six drought plots. Second, we explored the effect of the season using only data from 2022 when the seasonal sampling occurred. For this analysis, we also dropped the six drought plots. Third, we explored the effects of drought using data from all three seasons in 2022 only. We only kept C, NPK, C+Drought, and NPK+Drought plots. To determine how various mechanisms related to herbivore damage (Aim 2), we ran linear regressions with herbivore damage as the dependent variable and various mechanisms as the independent variable. Separate models were run for each independent variable (see Table 4 for the list of variables). For all regressions, data were subset to only include 2022 July data.



## CHAPTER II: RESPONSE OF HERBIVORE DAMAGE TO NUTRIENT ADDITONS

### **Aim 1: Herbivore damage response to nutrient additions**

Across years, herbivore damage varied greatly by both year and species (**Table 1**). *A. stricta* had the lowest herbivore damage and *P. aquinillum* had the highest (**Fig. 5**). There were numerous significant effects of nutrients in interactions with either species or year. In general, although exceptions were found, P tended to increase herbivore damage (**Fig. 6**) while N lowered it (**Fig. 7**). Species-by-P was significant with only *A. stricta* increasing herbivore damage with P additions although all species trended this way. Species-by-K was significant in the main model however post-hoc tests revealed no significant differences between control and K additions for any species with two species trending towards lower damage and two trending towards higher damage. An N by P by K by species interaction was also found in the main model, with *A. stricta* and *V. tenellum* showing P addition leading to higher herbivore damage compared to N addition while many of the other treatments were not statistically different from either. *P. aquilinum* showed the highest herbivore damage in PK treatments significantly more so than in the P alone.

Across seasons, herbivore damage varied greatly by both season and season by species (**Table 2**). *A. stricta* displayed more herbivore damage early in the season, but the lowest in the late season (**Fig. 8**). *P. aspera* and *P. aquilinum* increase in herbivore damage throughout the season, whereas *V. tenellum* has the highest herbivore damage in both the mid and late seasons. In this subset of data, we saw a N by P by species interaction (**Fig. 9**). Post hoc tests revealed that *P. aspera* was the only species significantly affected with lower herbivory in the P plots and higher herbivory in the NP plots compared to N alone and control plots. The full interaction was also significantly different (Season\*Sp\*N\*P\*K) with post hoc differences being complex (**Fig.**

**10).** Interestingly, all four species showed significant differences in the late season, 3 in the early season, and only 2 in the middle season.

**Table 1: Effect of N, P, K, year, and species as well as their interactions on herbivore damage.**

<b>Independent Variable</b>	<b>df</b>	<b>Chi-square</b>	<b>Pr (&gt;Chi-square)</b>
<b>Yr</b>	<b>3</b>	<b>31.33</b>	<b>&lt;0.001</b>
<b>Sp</b>	<b>3</b>	<b>19.92</b>	<b>&lt;0.001</b>
N	1	0.00	1.000
P	1	0.75	0.387
K	1	0.10	0.747
<b>Yr*Sp</b>	9	12.58	0.182
<b>Yr*N</b>	3	1.65	0.649
<b>Sp*N</b>	3	5.80	0.122
<b>Yr*P</b>	3	1.51	0.680
<b>Sp*P</b>	<b>3</b>	<b>14.31</b>	<b>0.003</b>
<b>N*P</b>	1	0.05	0.819
<b>Yr*K</b>	3	0.50	0.919
<b>Sp*K</b>	<b>3</b>	<b>13.90</b>	<b>0.003</b>
<b>N*K</b>	1	0.05	0.819
<b>P*K</b>	1	0.71	0.401
<b>Yr*Sp*N</b>	9	13.00	0.163
<b>Yr*Sp*P</b>	9	9.83	0.365
<b>Yr*N*P</b>	3	0.62	0.891
<b>Sp*N*P</b>	<b>3</b>	<b>7.33</b>	<b>0.062</b>
<b>Yr*Sp*K</b>	<b>9</b>	<b>19.96</b>	<b>0.018</b>
<b>Yr*N*K</b>	3	1.08	0.782
<b>Sp*N*K</b>	<b>3</b>	<b>9.96</b>	<b>0.019</b>
<b>Yr*P*K</b>	3	0.32	0.957
<b>Sp*P*K</b>	<b>3</b>	<b>17.05</b>	<b>0.001</b>
<b>N*P*K</b>	1	0.10	0.747
<b>Yr*Sp*N*P</b>	9	9.31	0.409
<b>Yr*Sp*N*K</b>	<b>9</b>	<b>17.67</b>	<b>0.039</b>
<b>Yr*Sp*P*K</b>	<b>9</b>	<b>21.03</b>	<b>0.013</b>
<b>Yr*N*P*K</b>	3	0.67	0.880
<b>Sp*N*P*K</b>	<b>3</b>	<b>12.52</b>	<b>0.006</b>
<b>Yr*Sp*N*P*K</b>	<b>9</b>	<b>16.19</b>	<b>0.063</b>

*Note:* Shown are the results from a mixed model anova using the mid-season sampling point across four years (2020-2023).  $p < 0.10$  are shown bolded. See Fig. 5-7 for corresponding visual representations of statistically significant effects.

**Table 2: Effect of N, P, K, season, and species as well as their interactions on herbivore damage.**

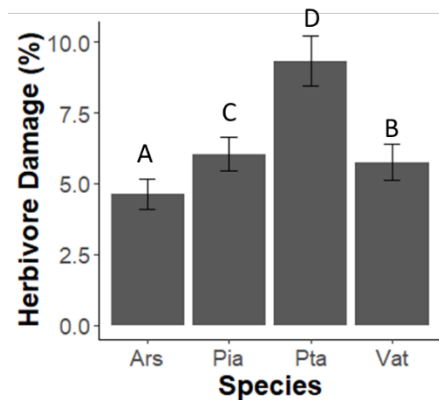
<b>Independent Variable</b>	<b>df</b>	<b>Chi-square</b>	<b>Pr (&gt;Chi-square)</b>
Season	2	2.07	0.356
Sp	<b>3</b>	<b>7.05</b>	<b>0.070</b>
N	1	1.28	0.258
P	1	0.10	0.747
K	1	0.10	0.748
Season*Sp	<b>6</b>	<b>17.08</b>	<b>0.009</b>
Season*N	2	0.02	0.992
Sp*N	3	2.29	0.514
Season*P	2	0.05	0.976
Sp*P	3	2.15	0.542
N*P	1	0.19	0.660
Season*K	2	1.23	0.541
Sp*K	3	0.98	0.805
N*K	1	0.10	0.750
P*K	1	0.03	0.874
Season*Sp*N	<b>6</b>	<b>10.98</b>	<b>0.089</b>
Season*Sp*P	6	6.54	0.365
Season*N*P	2	0.36	0.837
Sp*N*P	<b>3</b>	<b>6.54</b>	<b>0.088</b>
Season*Sp*K	6	6.37	0.383
Season*N*K	2	2.99	0.224
Sp*N*K	3	5.19	0.159
Season*P*K	2	2.86	0.240
Sp*P*K	3	1.31	0.726
N*P*K	1	0.04	0.849
Season*Sp*N*P	6	10.09	0.121
Season*Sp*N*K	<b>6</b>	<b>16.70</b>	<b>0.010</b>
Season*Sp*P*K	<b>6</b>	<b>12.60</b>	<b>0.050</b>
Season*N*P*K	2	3.35	0.187
Sp*N*P*K	3	5.40	0.145
Season*Sp*N*P*K	<b>6</b>	<b>19.68</b>	<b>0.003</b>

*Note:* Shown are the results from a mixed model anova using the early, middle and late-season sampling points across 2022.  $p < 0.10$  are shown bolded. See Fig. 8-10 for corresponding visual representations of statistically significant effects.

Looking at the interaction of NPK with drought (**Table 3**), season-by-species interactions were again seen with this subset of data (**Fig. 11**) that match the differences seen with the above subset of data (**Fig. 8**). Effects of drought (**Fig. 12**) varied by season and by species (**Fig. 13**). For example, drought decreased herbivory in early season for *P. aspera* but increased herbivory in late season for *P. aquilinum*. A season by species by drought by nutrient effect was seen.

**Figure 5: Arthropod herbivore damage on four longleaf pine savanna understory plants**

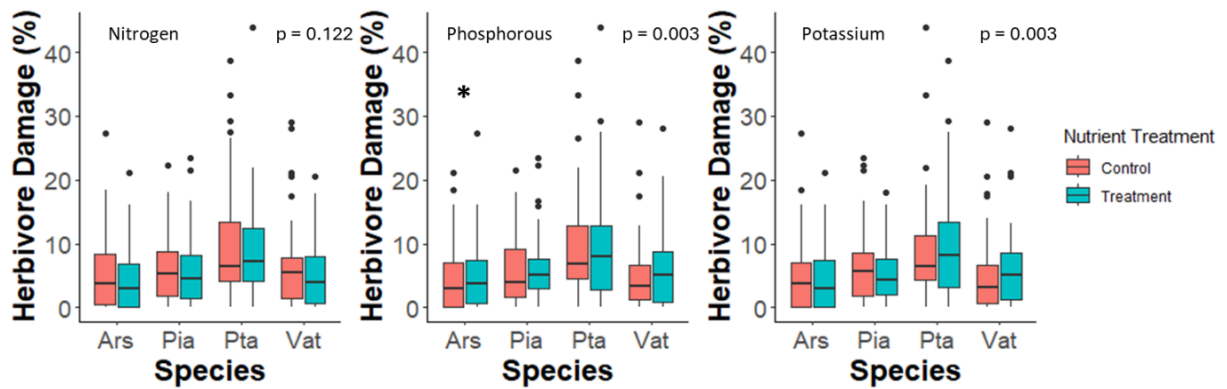
Note: Using the mid-season sampling point across four years (2020-2023), means with standard error are shown (error bars) with letters denoting significant post hoc differences ( $p < 0.10$ ). Note strong species differences. Ars- *A.stricta*, Pia- *P.aspera*, Pta- *P.aquilinum*, Vat- *V.tenellum*



For example, *P. aspera* has lower damage in the NPK + drought (**Fig. 14**) plots compared to the control and drought alone in both the early and middle seasons. Conversely, *P. aquilinum* had higher herbivory in any of the treated plots compared to the control, but only in the late season.

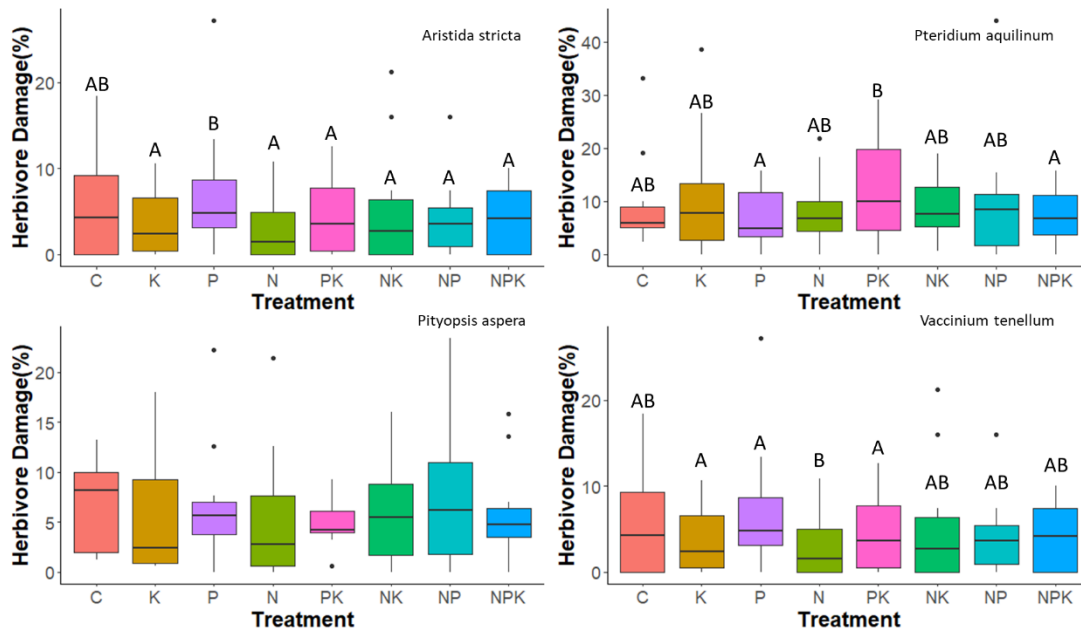
**Figure 6: Effect of leaf nutrients on mean arthropod herbivory for (left) nitrogen, (middle), phosphorous, and (right) potassium**

Note: Species acronyms: Ars- *A.stricta*. Pia- *P.aspera*, Pta- *P.aquilinum*, Vat- *V.tenellum*. Using the mid-season sampling point across four years (2020-2023), means with standard error are shown (error bars) with asterisks (\*) denoting significant post hoc differences within a species due to the nutrient effect ( $p < 0.10$ ).



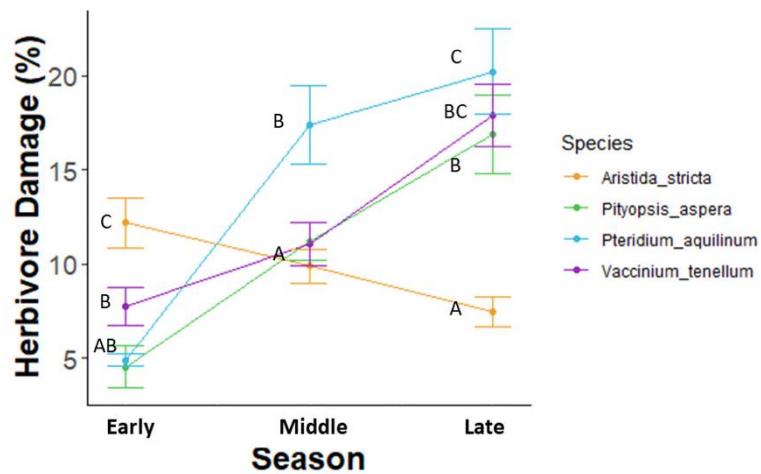
**Figure 7: Effect of treatments on mean arthropod herbivory (%)**

Note: *A.stricta* (top left), *P.aquilinum* (top right), *P. aspera* (bottom left), *V.tenellum* (bottom right). Using the mid-season sampling point across four years (2020-2023), means with standard error are shown (error bars) with letters denoting significant post hoc differences within a species due to the nutrient effect ( $p < 0.10$ ). Treatments left to right: C, K, N, NK, NP, NPK, P, PK



### Figure 8: Plant species-specific arthropod herbivore damage by timepoint

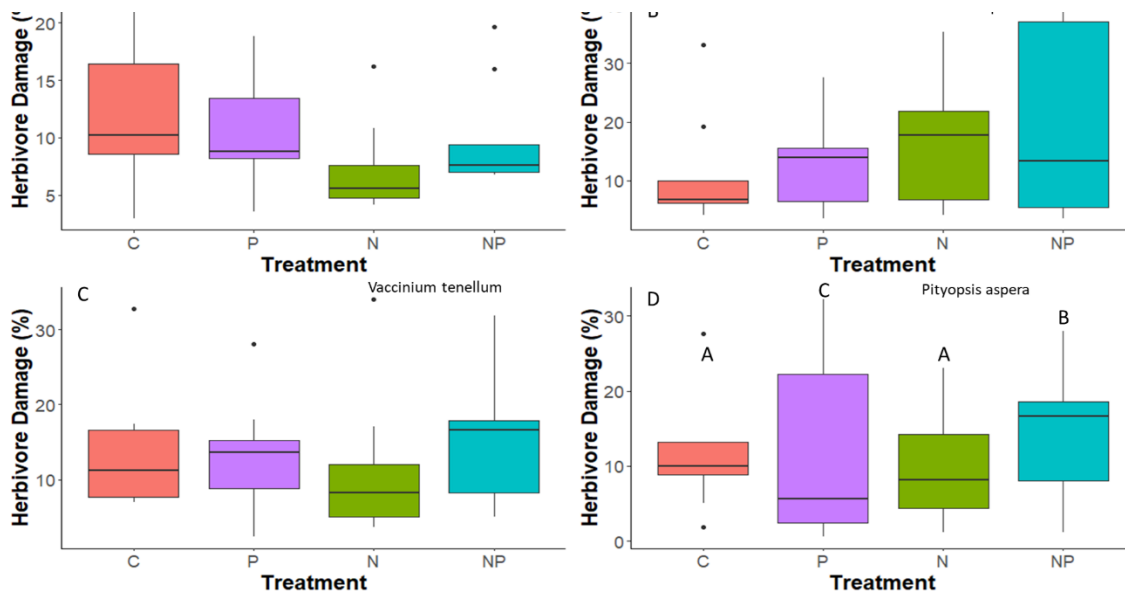
Note: Using 2022 data only across three season, means with standard error are shown (error bars) with letters denoting significant post hoc species differences within a season ( $p < 0.10$ ). *Aristida stricta* is the most herbivorized species in the early season and the least in the late season. This may hint at an interaction with arthropod ontogeny and changing feeding guilds or differences in plant forage quality due to plant ontogeny.





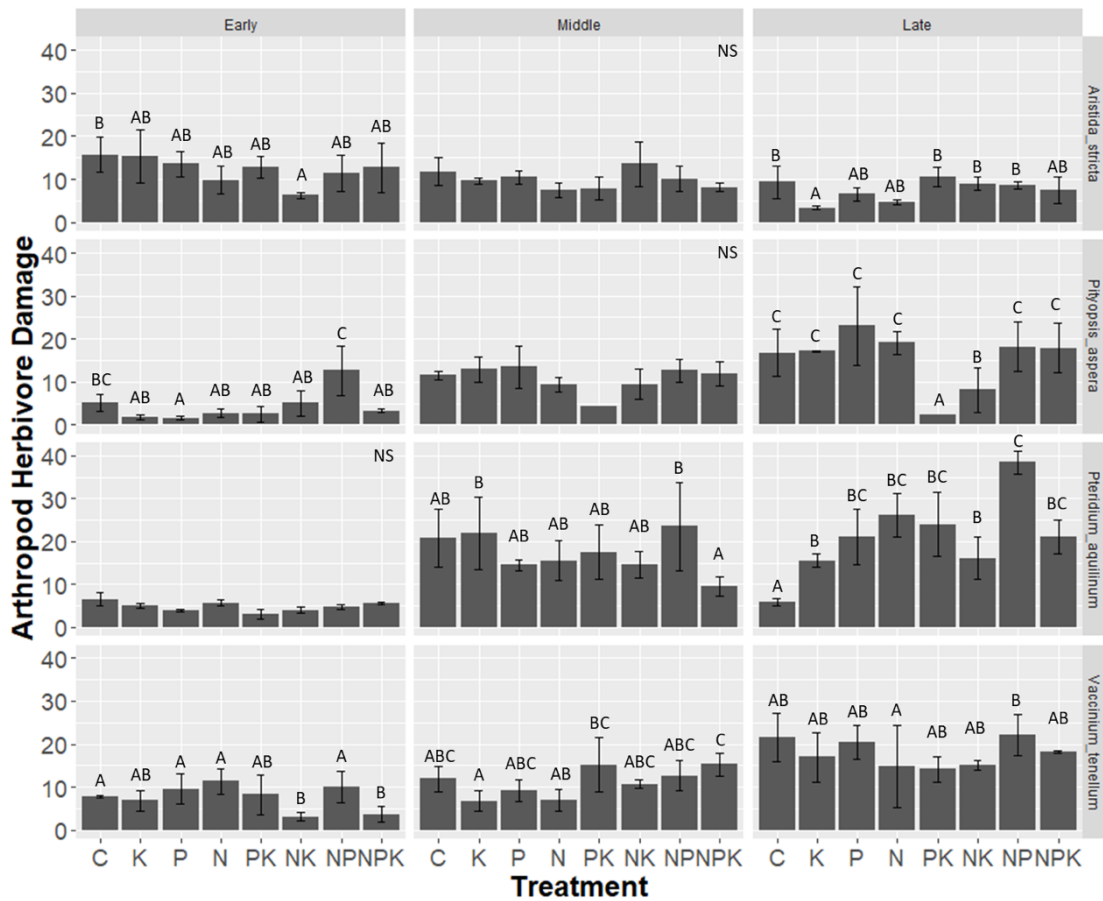
**Figure 9: Effect of treatments on mean arthropod herbivory (%)**

Note: *A.stricta* (top left), *P.aquilinum* (top right), *P. aspera* (bottom left), *V.tenellum* (bottom right). Using the mid-season sampling point across four years (2020-2023), means with standard error are shown (error bars) with letters denoting significant post hoc differences within a species due to the nutrient effect ( $p < 0.10$ ). Treatments left to right: C, P, N, NP.



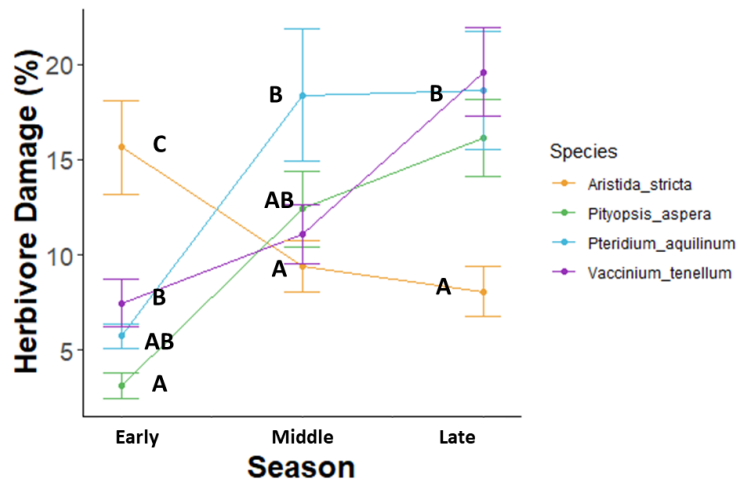
**Figure 10: Herbivore damage by plant species, treatment, and timepoint**

Note: Early, Middle, and Late (left to right). Treatments left to right: C, K, N, NK, NP, NPK, P, PK. Species (top to bottom): *Aristida stricta*, *Pityopsis aspera*, *Pteridium aquilinum*, *Vaccinium tenellum*



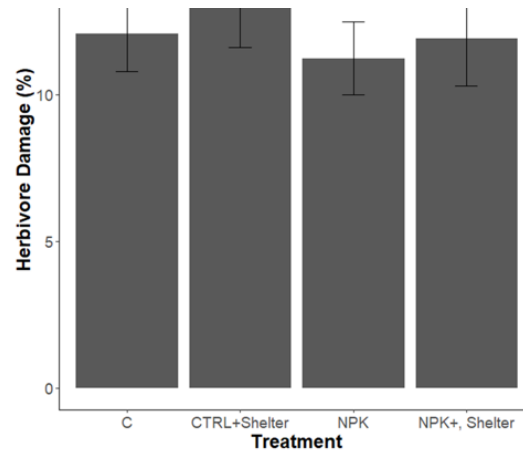
**Figure 11: Plant species-specific arthropod herbivore damage under drought by timepoint**

Note: Using 2022 data only across three seasons, means with standard error are shown (error bars) with letters denoting significant post hoc species differences within a season ( $p < 0.10$ ). *Aristida stricta* is the most herbivorized species in the early season and the least in the late season. This may hint at an interaction with arthropod ontogeny and changing feeding guilds or differences in plant forage quality due to plant ontogeny.



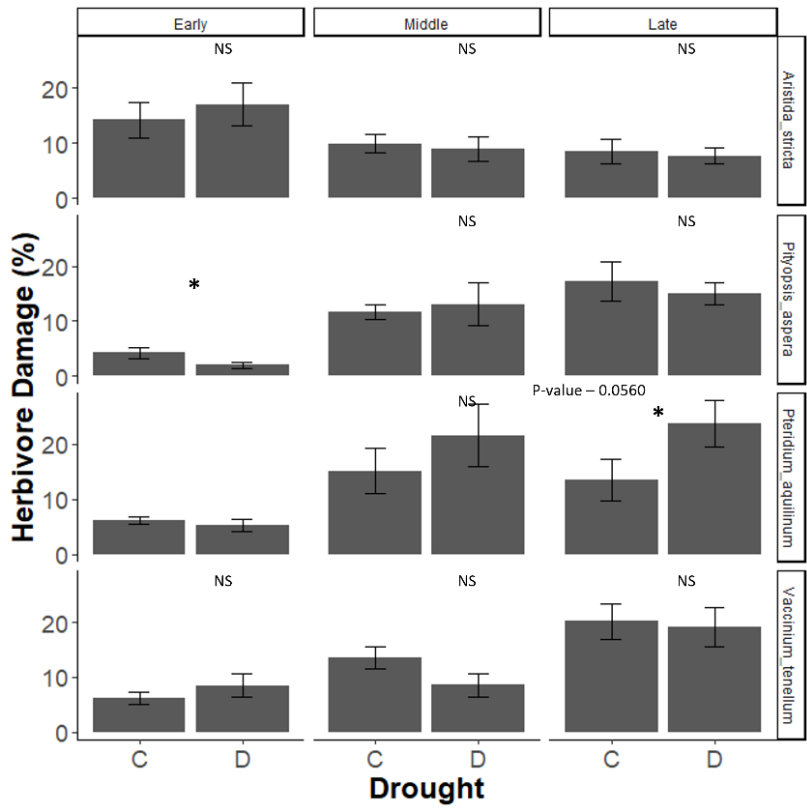
### Figure 12: Mean Arthropod herbivore damage in drought-by-nutrient treatments

Note: Using the mid-season sampling point across four years (2020-2023), means with standard error are shown (error bars) with letters denoting significant post hoc differences ( $p < 0.10$ ).



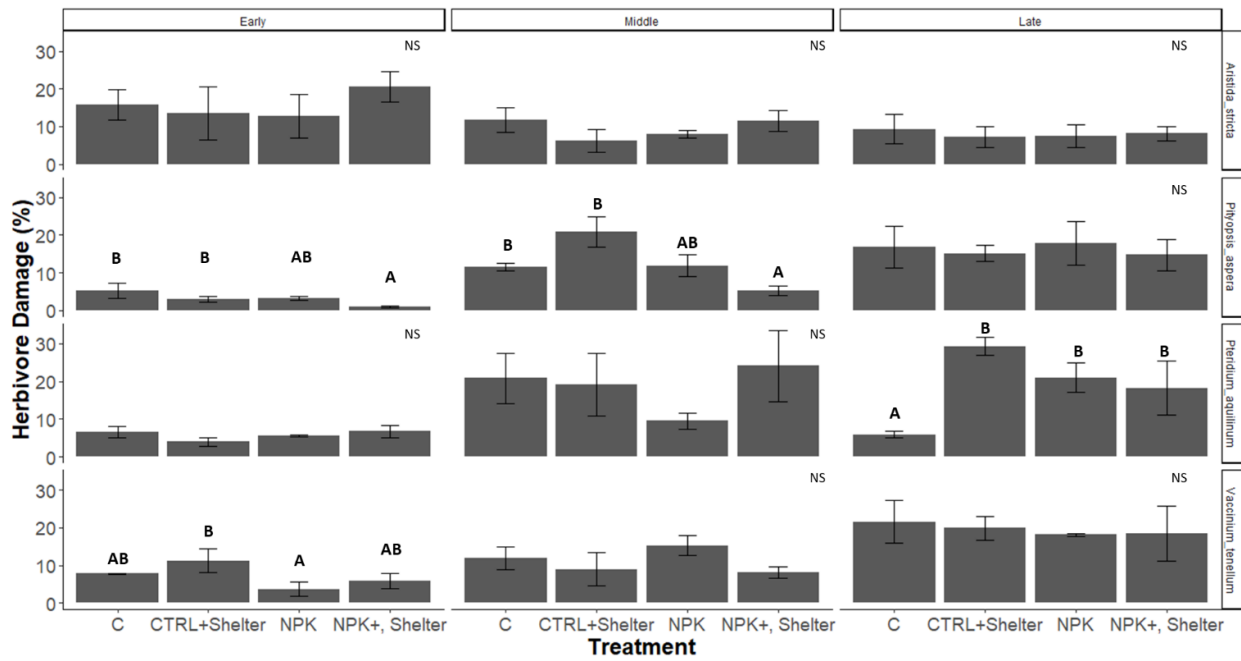
**Figure 13: Mean Arthropod herbivore damage in drought, separated by species**

Note: Using 2022 data only across three seasons, means with standard error are shown (error bars) with asterisks (\*) denoting significant post hoc species differences within a season ( $p < 0.10$ )



**Figure 14: Mean arthropod herbivore damage under drought and nutrient additions by species and timepoint**

Note: Using 2022 data only across three seasons, means with standard error are shown (error bars) with letters denoting significant post hoc species differences within a season ( $p < 0.10$ ). Timepoints: (Early, Middle, and Late, left to right). Treatments left to right: C, K, N, NK, NP, NPK, P, PK. Species (top to bottom): *Aristida stricta*, *Pityopsis aspera*, *Pteridium aquilinum*, *Vaccinium tenellum*.



**Table 3: Effect of NPK, drought, season, and species as well as their interactions on herbivore damage.**

<b>Independent Variable</b>	<b>df</b>	<b>Chi-square</b>	<b>Pr (&gt;Chi-square)</b>
Season	2	1.991	0.36954
<b>Sp</b>	<b>3</b>	<b>6.7896</b>	<b>0.07891</b>
Drought	1	0.7665	0.38131
NPK	1	0.9579	0.32771
<b>Season*Sp</b>	<b>6</b>	<b>16.4545</b>	<b>0.01151</b>
Season*Drought	2	0.6584	0.71949
<b>Sp*Drought</b>	<b>3</b>	<b>1.7144</b>	<b>0.63373</b>
Season*NPK	2	0.2119	0.89945
<b>Sp*NPK</b>	<b>3</b>	<b>1.0424</b>	<b>0.791</b>
<b>Drought*NPK</b>	<b>1</b>	<b>3.1378</b>	<b>0.0765</b>
<b>Season*Sp*Drought</b>	<b>6</b>	<b>12.2702</b>	<b>0.05621</b>
Season*Sp*NPK	6	8.4482	0.20707
Season*Drought*NPK	2	0.8908	0.64057
<b>Sp*Drought*NPK</b>	<b>3</b>	<b>3.3491</b>	<b>0.34086</b>
<b>Season*Sp*Drought*NPK</b>	<b>6</b>	<b>11.3481</b>	<b>0.0782</b>

*Note:* Shown are the results from a mixed model anova using early, middle, and late-season sampling points across 2022.  $p < 0.10$  are shown bolded. See Fig. 11-14 for corresponding visual representations of statistically significant effects.

CHAPTER III: EXPLORING VARIOUS MECHANISM'S EFFECTS ON THE MAGNITUDE  
OF HERBIVORE DAMAGE

**Aim 2: Explore various mechanisms' effects on the magnitude of herbivore damage**

None of the 25 variables that were potential drivers of herbivore damage showed significant relationships (**Table 4; Fig. 15-18**).



**Table 4: Relationship between potential variables and arthropod herbivore damage.**

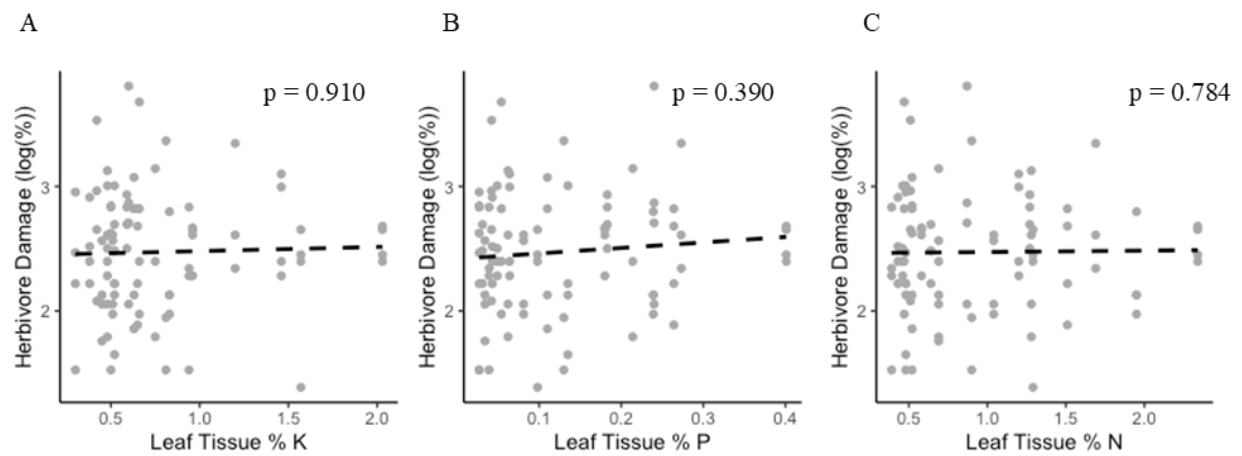
<b>Independent Variable</b>	<b>DF</b>	<b>F-statistic</b>	<b>P-value</b>	<b>Multiple R-square</b>
<b>Leaf % N</b>	1, 90	0.013	0.910	<0.001
<b>Leaf % P</b>	1, 90	0.746	0.390	0.008
<b>Leaf % K</b>	1, 90	0.075	0.784	<0.001
<b>Plant Species Diversity</b>	1, 90	2.493	0.118	0.027
<b>Plant Species Richness</b>	1, 90	2.356	0.128	0.026
<b>Plant Species Evenness</b>	1, 90	0.556	0.458	0.006
<b>Plant Species Dominance (BP)</b>	1, 90	0.837	0.363	0.009
<b>Wiregrass Cover</b>	1, 90	<0.001	0.998	<0.001
<b>Grass Cover</b>	1, 90	0.031	0.861	<0.001
<b>Forb Cover</b>	1, 90	1.805	0.183	0.02
<b>Dominant Plant Species Cover</b>	6, 85	0.302	0.934	0.499
<b>Forb Biomass</b>	1, 86	0.186	0.667	0.002
<b>Graminoid Biomass</b>	1, 86	0.276	0.601	0.003
<b>Legume Biomass</b>	1, 78	0.028	0.867	<0.001
<b>Litter Biomass</b>	1, 86	0.007	0.936	<0.001
<b>Arthropod Family Dominance (BP)</b>	1, 86	0.077	0.782	<0.001
<b>Arthropod Family Richness</b>	1, 86	0.361	0.550	0.481
<b>Arthropod Family Evenness</b>	1, 86	0.170	0.682	0.002
<b>Arthropod Family Diversity</b>	1, 86	0.461	0.499	0.005
<b>Arthropod Plot Biomass</b>	1, 21	0.350	0.560	0.016
<b>Grasshopper Abundance</b>	1, 86	0.062	0.804	<0.001
<b>Wolf Spider Abundance</b>	1, 86	0.571	0.452	0.007
<b>Leafhopper Abundance</b>	1, 86	0.153	0.697	0.002
<b>Ant Abundance</b>	1, 86	0.167	0.684	0.002
<b>Seed Bug Abundance</b>	1, 86	0.361	0.550	0.004

*Note:* Shown are results from linear regression using data from mid-season sampling in 2022

only. Note no variable was significantly related to arthropod herbivore damage. See Fig. 15-18 for visual representation.

**Figure 15: Relationship between leaf tissue nutrient content and arthropod herbivore damage (log-transformed) for potassium, phosphorous, and nitrogen**

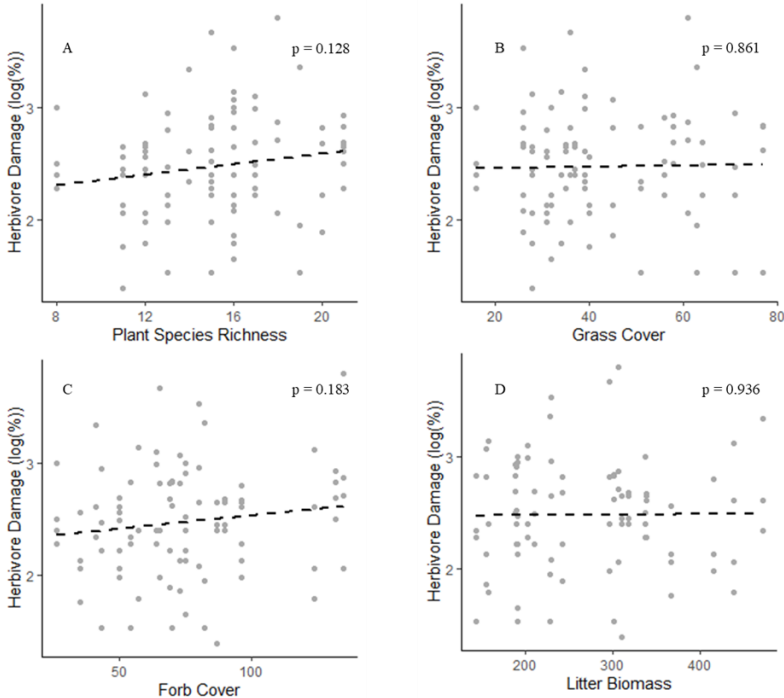
Note: Only 2022 middle season data were used for regression analysis. For full statistics see Table 4.



**Figure 16: Relationship between selected plant community metrics and arthropod herbivore damage (log transformed)**

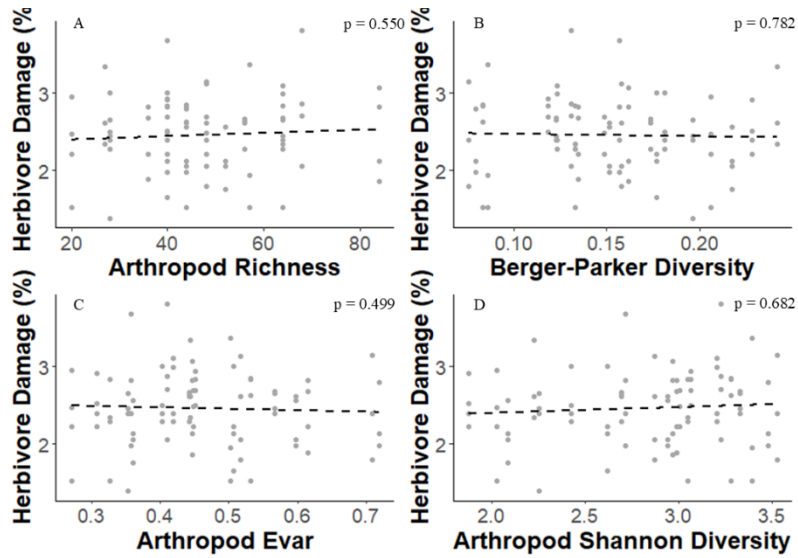
Note: (A) plant species richness, (B) grass cover, (C) litter biomass, and (D) forb cover.

Only 2022 middle season data were used for regression analysis. For full statistics and additional plant community metrics see Table 4.



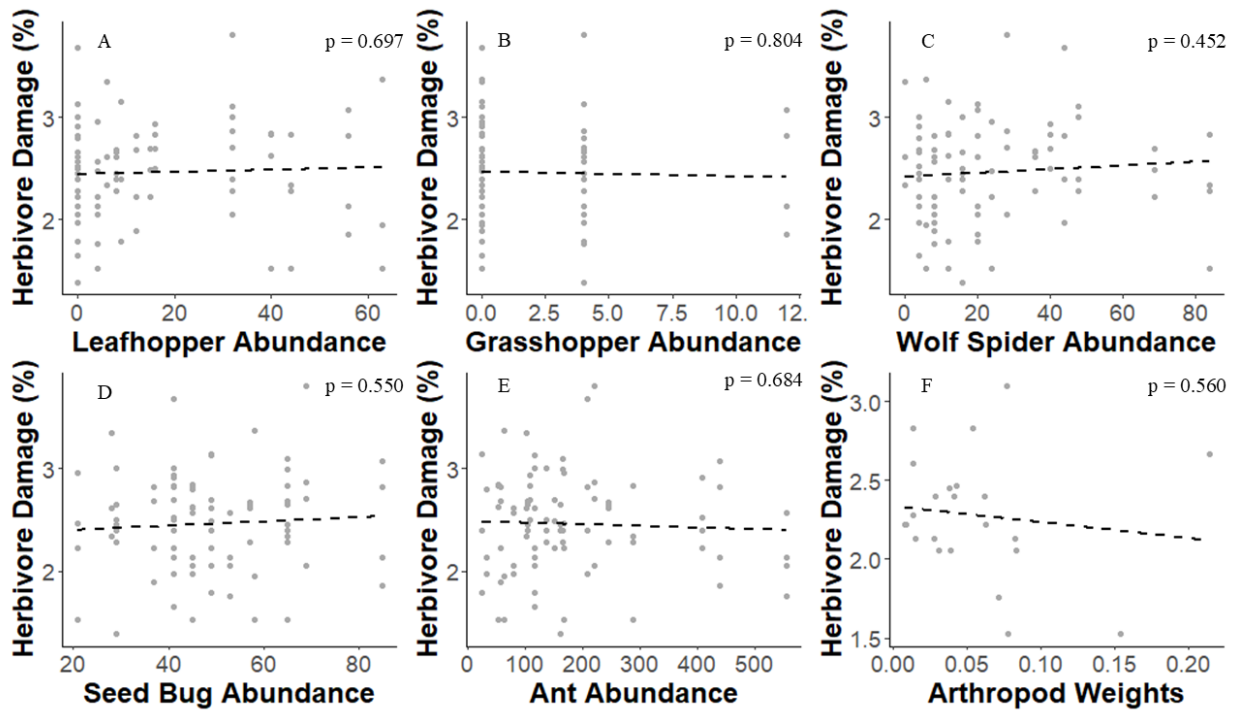
**Figure 17: Relationship between selected arthropod community metrics and arthropod herbivore damage (log transformed)**

Note: (A) Arthropod Family Richness, (B) Berger-Parker Diversity, (C) Arthropod Evar, and (D) Arthropod Family Shannon Diversity. Only 2022 middle season data were used for regression analysis. For full statistics and additional plant community metrics see Table 4.



**Figure 18: Relationship between selected arthropod community metrics and arthropod herbivore damage (log transformed)**

Note: (A) Leafhopper Abundance, (B) Grasshopper Abundance, (C) Wolf Spider Abundance, and (D) Seed Bug Abundance, (E) Ant Abundance, (F) Arthropod Plot Weight. Only 2022 middle season data were used for regression analysis. For full statistics and additional plant community metrics see Table 4.



## CHAPTER IV: THESIS DISCUSSION

Overall, we found herbivore damage to be extremely variable, through time (year and season) and across species, and little clear directional shifts were seen with either nutrient additions, drought, or their interaction. Additionally, of all the mechanisms explored, none showed significant correlations with herbivore damage. While this might suggest that we did not measure the correct variables, rather we believe this is due to the extreme variability seen in herbivore damage and the complex nature of likely interacting mechanisms controlling damage (Hochuli, 2001; Huberty & Denno, 2004; Stout, et al. 2006; Castagneyrol, et al. 2014; Castagneyrol, et al. 2018; Barnes, et al. 2020; Rusman, et al. 2020; Welty, et al. 2020; Welty, et al. 2020; Robinson, et al. 2023). For example, light availability and water stress interact to impact gypsy moth larvae performance and therefore their damage to birch trees increased (Castagneyrol et al. 2018), or how plant ontogeny interacts with other effects on herbivory, especially during early season damage events (Rusman et al, 2020).

The interaction of year and plant species reveals that *P. aquilinum*, a large, conspicuous fern species, displayed the most herbivore damage across years between study species (Figure 5). Plant size has been noted as a possible determinant of herbivory, and may contribute to between-species differences (Robinson, et al. 2023). *A. stricta*, the most common study species, was herbivorized the least across years. This may be due to low forage quality or late bloom (Lewis, et al. 1975). More likely, this is because of the emergence of more attractive forage such as *P. aspera* and *V. tenellum*. Grassland forb species attract many arthropod herbivores, seemingly in contrast to co-occurring grass species (Komatsu, et al. 2015). Responses to precipitation, temperature, and community assemblage will be species-specific, enhancing differences between years (Cowles, et al. 2018; Garcia, et al. 2020; Van Dyke, et al. 2022). Study species vary

greatly in growth form, phenology, and the arthropod herbivores they attract, leading to strong differences in herbivore damage on the four studied species.

When moving into season-specific (**Table 2**) interactions of herbivore damage on the different species, it is important to highlight the dynamic interactions of plant phenology, insect ontogeny, as well as yearly and seasonal differences in plant/arthropod communities (Bandeili & Muller 2010; Novotny, et al. 2010; Mora. et al., 2020; Wetzal, et al. 2023). The dominant grass species, *A. stricta*, is herbivorized nearly 30% more than other study species in the early season, but ends as the least herbivorized at the end of the season (Figure 8). Several reasons could contribute to this switch in most herbivorized species. For example, grasses tend to have their highest forage quality early in the growing season, which might attract herbivores. However, as their tissue becomes tough and as they get bigger and more nutrient diluted, herbivores may switch to other available forage like forbs and shrubs. Additionally, as life stages change throughout the season, arthropods such as caterpillars, who herbivorize the leaves they emerge from, change feeding guilds (Bandeili & Muller 2010). This change in host plant use may cause herbivory to decrease in a single plant species as leaf chewers become nectarivores (Novotny, et al. 2010). Peak season appears to be the most similar in community-wide arthropod herbivore pressure (Figure 8, Figure 10). However, by the end of the season, *A. stricta* is the lowest herbivorized species with nearly 50% less damage than the other three studied species. Leaf-chewing instars of pollinator species during the early season contribute to herbivore damage (Deyrup, et al. 2002) of *P. aspera* and *V. tenellum*, replaced by later emerging leaf-chewers in the peak and late seasons (Poelman, et al. 2008; Stam, et al. 2014; de Bobadilla, et al. 2021). The four plant species are different at every point during the season (**Fig. 8**), and future sampling should consider this variability.

Because of these strong species differences and strong season-by-species interactions, it is not surprising that many of the nutrient and drought effects were species and season-specific. Both P-by-species and K-by-species interactions were significant; however, post hoc tests revealed the only significant species difference was greater herbivory in *A. stricta* with added P. *V. tenellum* and *P. aquilinum* both showed trends towards increased herbivore damage with P additions and K additions. Similarly, when looking at the full species by N by P by K interaction (**Fig. 7**), post hoc tests revealed that herbivore damage of *A. stricta* and *V. tenellum* increased with P alone addition compared to N alone addition; *P. aquilinum* also showed increased herbivory in the PK treatment compared to P or NPK. Behmer (2009) theorized that N is not a limiting resource for insects. Komatsu & Smith (2015) expand on this theory, claiming P is a greater limiting resource than N for arthropods. This would explain increased herbivore damage in P and its factorial plots. Greater herbivore damage may also be explained by shifts in plant community assemblage and variability (Avolio, et al. 2014; Koerner, et al. 2016), caused by increased P. Formerly common plant species may decrease in abundance, forcing arthropod herbivores to concentrate herbivore damage on a few remaining individuals. While these results are a bit complicated, it appears that P is leading to increased herbivory.

Additionally, in the seasonal analysis, we see evidence that N and P additions together might lead to greater herbivore damage than P alone. Per capita herbivore damage increased in N by P treatment plots in the tallgrass prairie (Komatsu & Smith 2015), and in the LLP savanna experiment, may occur via increased arthropod abundance or compensatory feeding. Similar to P-alone treatment, paired N and P treatment may increase the variability of plant species, causing a concentration of herbivore damage (Avolio, et al. 2014; Koerner, et al. 2016) on a small number of individuals. It has also been found that higher P nutrition allows for greater abscission



rates of cotton buds (Forbes & Rosenheim 2011). Perhaps this interactive effect displays an acclimation to higher nutrient availability and concentration of inducible defenses. If more N universally allows for lower herbivore susceptibility via defense chemicals, plants may be able to modulate areas for defense and herbivorization (Chen 2008; Moreira, Zas and Sampedro, 2012). To attract herbivores, a plant may lower the concentration of defense chemicals on some leaves, protecting other leaves and its sexual organs. Once leaves are sufficiently herbivorized, higher P allows for plants to abscise the damaged leaves, preventing them from becoming an energy sink (Forbes & Rosenheim 2011). This allows for plants to either benefit from the effects of herbivore damage or limit its negative effects, while not losing photosynthetic function

Of note, this NxP additive interaction was not detected in the yearly sampling. This could be due to the fact that when seasonal differences were detected, post hoc tests revealed significance most often in the early and late seasons, with mid-season showing few differences. Seasonal changes in environmental conditions likely play a large part in plant productivity and nutrient use (Garcia, et al. 2020). Peak season appears to be the most similar in community-wide arthropod herbivore pressure (Figure 8). In the future, studies should focus on early and late seasons instead of peak season. These sampling times reveal the greatest amount of difference and have important roles in determining seasonal and yearly variation (Lian, et al. 2021; Wu, et al. 2021).

Drought increased herbivore damage, particularly for *P. aquilinum*; however, these patterns were weak and inconsistent. While the leaves in drought plots would be worse for chewing arthropods, sap-suckers may jump at the opportunity to capitalize on N-dense xylem/phloem (Huberty & Denno, 2004) thus the drought plots having higher herbivory. Similarly, the plants may have invested resources in water acquisition (i.e., root growth). This

may lead to lower availability of resources for developing plant defense and higher water use efficiency (Guo, et al. 2024). This could also lead to higher herbivory in the droughted plots. Interestingly though, drought with nutrient additions combined seemed to cancel out the negative effects of drought, with drought + NPK plots not being significantly different from the control plots. This supports the second hypothesis above, with increased nutrients allowing plants to simultaneously invest below ground while still investing in plant defences, which are frequently high in N demand herbivorization (Chen 2008; Moreira, Zas and Sampedro, 2012; Vega, et al. 2015). However, responses were again species-specific, and in *P. aquilinum*, late-season herbivory in C+Shelter plots may be due to increased susceptibility to herbivores via water stress. Increased herbivory of *P. aquilinum* in NPK plots may be due to the preservation of plant productivity or leaf nutrients in the late season or (Guo, et al. 2021).

This minimal response to drought treatments could be due to the low level of drought reduction applied – 30% rainfall reduction. LLP savanna is more homogenous and higher in its MAP than many other savannas across the world (Pau, et al. 2023), occupying a unique climate niche. This savanna is maintained through frequent burning, receiving enough rainfall to turn into a forest if regular burning does not occur (Frost 1993). Therefore, this savanna is not water-limited. Thus a 30% rainfall exclusion may not be enough to limit plant growth here. Additionally, movement of soil moisture across the soil surface or accessing deep soil moisture pools may have allowed understory plants to compensate for reduced direct precipitation (Hartmann & Niklaus 2012) alleviating what was already a moderate drought. Additionally, biodiversity can lead to stability and resistance to drought (Isbell, et al. 2015; Chaves et al. 2021; Liu, et al. 2022). LLP savanna is a highly diverse system and therefore might also require a large magnitude of drought to yield effects.

Overall, none of the mechanistic variables studied were significantly correlated with herbivore damage. We had three major groups of mechanisms – changes in plant tissue nutrient content, changes in plant community structure, and changes in arthropod community structure. We hypothesize that there are methodological mismatches or ecological reasons to explain the null results rather than these drivers not affecting herbivore damage.

First, nutrient concentration in the leaf tissue was measured at the community level, not at the individual plant level. We hypothesize that had we measured plant-level leaf nutrient content significant relationship would have been seen. However, at the plot level, as we measured, no correlation to nutrients might exist because of the strong species-level responses we saw. For example, if *A. stricta* was herbivorized less when its N content was higher, but *A. stricta* decreased in abundance in the N addition plots, that would change the plot level nutrient content. If similar leaf nutrient analysis were performed on each of the study species instead, some trends may present themselves. Many arthropods perform selective feeding in the presence of increased nutrient availability (Behmer 2009; La Pierre and Smith 2016). Nutrient-enriched leaf tissue may attract nearby arthropods (Lu, et al. 2020), thereby keeping per capita herbivory the same.

Second, we were surprised that plot-level plant community metrics didn't yield significant changes in herbivore damage. For example, we hypothesized the increases in plant diversity or richness would cause decreases in herbivore damage. The resource concentration hypothesis (Barnes, et al. 2020) states that arthropods are less likely to encounter preferred plant species in high-diversity patches, and thus are more likely to leave. With added nutrients and larger plant individuals (i.e., increased productivity), oftentimes biodiversity decreases (Isbell, et al. 2013). Another hypothesis, the enemy hypothesis, states that high-diversity plots provide habitat for predator species, leading to greater control of the herbivore population (Barnes, et al.

2020). Barnes, et al. (2020) theorize that, while high biodiversity results in more biomass consumed, this is because high-diversity plots produce more plant material, not because of increased herbivore pressure. However, we saw no relationship. We hypothesize this lack of response though is because the plant community metrics were too plot-focused and not locally focused on our study individuals. Or rather our herbivore damage metric was too individual-focused and therefore did not give a good estimate of plot-level herbivory. Seeing as we saw strong differences in species with herbivore damage, it would stand to reason that plots with greater *A. stricta* cover would experience less plot-level herbivore damage compared to plots dominated by *P. aquilinum*. Perhaps plot-level herbivore damage would be related to plot-level richness, but individual damage is pre-determined by the species being sampled.

Finally, no arthropod herbivore metric predicted herbivore damage. Even incredibly abundant arthropod herbivore families such as *Acrididae* or *Cicadellidae* displayed no response. This failure to predict damage may be due to the resource concentration hypothesis (Barnes, et al. 2020). Increasing the variance of the plant community by P nutrition decreases the chances an herbivore encounters one of its host plants (Avolio, et al. 2014; Koerner, et al. 2016). This variability, along with the likelihood of multiple arthropod herbivores (Stam, et al. 2014) on a single host plant, may create too much biological noise to detect any signals for predicting herbivore damage. However, this increase of variability fits with Robinson's Gini coefficient hypothesis on uneven feeding and explains why we were not able to detect any arthropod herbivore signal (Robinson, et al. 2023). If a small number of plant individuals display a large amount of herbivore damage, community-wide damage levels remain consistent. In future experiments, insect uptake will need to be measured to determine the true cause of herbivore damage alteration.

Numerous studies have shown that arthropod abundance and diversity is a response to multiple mechanisms (La Pierre and Smith 2016; Castagneyrol, et al. 2018; Barnes, et al. 2020; Lewthwaite, et al. 2024). For example, a study in a desert urban system showed that arthropod abundance was mainly driven by water availability, but those effects only emerged when seen through complex interactions with habitat type and bird predation (Bang et al. 2022). Another study shows increasing abundance and species richness of arthropods with increasing plant species richness, but contrasting patterns of dominant herbivore and predator species (Hertzog, et al. 2016). These relationships are nuanced, interactive, and inter-reactive. Our approach of exploring mechanisms through bivariate relationships may not capture the incredibly complex interacting mechanisms controlling herbivore damage.

## CHAPTER V: THESIS CONCLUSIONS

This experiment investigated the effects of nutrient deposition and drought on an important ecosystem process, herbivory, in an imperiled ecosystem, the LLP savanna. Changing climate (Welti, et al. 2020) and the intensification of agriculture (Brudvig, et al. 2013) threaten this once-sprawling ecosystem. However, the general lack of response to treatments indicates that herbivory in the Sandhills is somewhat protected against such change, particularly with N or K additions and moderate drought. The increase in herbivore damage in response to P additions is slightly alarming, as longleaf pine trees are often thought to be P-limited from an agriculture standpoint focused on timber production (Jokela, et al. 1991). Frequently, foresters and land managers looking to support a multi-functional landscape with timber sales will add P to their stands. Our results suggest that land managers may need to carefully think about the effects of phosphorous on the herbivory of the understory and weigh their management targets accordingly.

## REFERENCES

- Agrawal, Anurag A., Amy P. Hastings, Marc T.J. Johnson, John L. Maron, and Juha Pekka Salminen. 2012. "Insect herbivores drive real-time ecological and evolutionary change in plant populations." *Science* (American Association for the Advancement of Science) 338 (6103): 113-116.
- Argens, Laura, Wolfgang W. Weisser, Anne Ebeling, Nico Eisenhauer, Markus Lange, Yvonne Oelmann, Christiane Roscher, et al. 2024. "Relationships between ecosystem functions vary among years and plots and are driven by plant species richness." *Oikos* (John Wiley and Sons Inc) 2024 (1).
- Avolio, Meghan L., Ian T. Carroll, Scott L. Collins, Gregory R. Houseman, Lauren M. Hallett, Forest Isbell, Sally E. Koerner, Kimberly J. Komatsu, Melinda D. Smith, and Kevin R. Wilcox. 2019. "A comprehensive approach to analyzing community dynamics using rank abundance curves." *Ecosphere* (John Wiley & Sons, Ltd) 10 (10): e02881. <https://onlinelibrary.wiley.com/doi/full/10.1002/ecs2.2881>.
- Avolio, Meghan L., Sally E. Koerner, Kimberly J. La Pierre, Kevin R. Wilcox, Gail W.T. Wilson, Melinda D. Smith, and Scott L. Collins. 2014. *Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie*. Vol. 102.
- Bandeili, Babak, and Caroline Müller. 2010. *Folivory versus florivory—adaptiveness of flower feeding*. Vol. 97. <http://link.springer.com/10.1007/s00114-009-0615-9>.
- Barnes, A D, C Scherber, U Brose, E T Borer, A Ebeling, B Gauzens, D P Giling, et al. 2020. "Biodiversity enhances the multitrophic control of arthropod herbivory." *Sci. Adv* 6: 6603-6609. <https://www.science.org>.
- Barton, Kasey E., and Julia Koricheva. 2010. "The ontogeny of plant defense and herbivory: Characterizing general patterns using meta-analysis." *American Naturalist* ( The University of Chicago Press ) 175 (4): 481-493. <https://www.journals.uchicago.edu/doi/full/10.1086/650722>.
- Behmer, Spencer T., and Anthony Joern. 2008. "Coexisting generalist herbivores occupy unique nutritional feeding niches." *Proceedings of the National Academy of Sciences of the United States of America* 105 (6): 1977-1982. <https://doi.org/10.1073/pnas.0711870105>.
- Belovsky, G. E., and J. B. Slade. 2000. "Insect herbivory accelerates nutrient cycling and increases plant production." *Proceedings of the National Academy of Sciences of the United States of America* ( The National Academy of Sciences ) 97 (26): 14412-14417. <https://www.pnas.org/doi/abs/10.1073/pnas.250483797>.
- Berendse, Frank, Rob H E M Geerts, Wim Th Elberse, Martijn Bezemer, Paul W Goedhart, Wei Xue, Erik Noordijk, Cajo J F Ter Braak, and Hein Korevaar. 2021. "A matter of time." *Diversity and Distributions* 27 (7): 1180-1193.
- Betway, Katlyn R., Robert D. Hollister, Jeremy L. May, and Steven F. Oberbauer. 2021. *Species-specific trends and variability in plant functional traits across a latitudinal gradient in northern Alaska*. Vol. 32. John Wiley and Sons Inc.
- Bista, Deepesh R., Scott A. Heckathorn, Dileepa M. Jayawardena, and Jennifer K. Boldt. 2020. "Effect of drought and carbon dioxide on nutrient uptake and levels of nutrient-uptake proteins in roots of barley." *American Journal of Botany* 107 (10): 1-9. doi:10.1002/ajb2.1542.

- Bista, Deepesh R., Scott A. Heckathorn, Dileepa M. Jayawardena, Sasmita Mishra, and Jennifer K. Boldt. 2018. "Effects of Drought on Nutrient Uptake and the Levels of Nutrient-Uptake Proteins in Roots of Drought-Sensitive and -Tolerant Grasses." *Plants* 7 (28). <http://dx.doi.org/10.3390/plants7020028>.
- Borer, Elizabeth T, Eric W Seabloom, Daniel S Gruner, W Stanley Harpole, Helmut Hillebrand, Eric M Lind, Peter B Adler, et al. 2014. *Herbivores and nutrients control grassland plant diversity via light limitation*.
- Bramon Mora, Bernat, Eura Shin, Paul J. CaraDonna, and Daniel B. Stouffer. 2020. *Untangling the seasonal dynamics of plant-pollinator communities*. Vol. 11. <https://www.nature.com/articles/s41467-020-17894-y>.
- Brockway, Dale, Kenneth Outcalt, Donald Tomczak, and Everett Johnson. 2006. "Restoration of Longleaf Pine Ecosystems." *United States Department of Agriculture Forest Service* (SRS-83): 1-44.
- Brudvig, Lars A, Emily Grman, Christopher W Habeck, John L Orrock, and Joseph A Ledvina. 2013. "Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands." *Forest Ecology and Management* (Forest Ecology and Management) 310: 944-955. <http://dx.doi.org/10.1016/j.foreco.2013.09.053>.
- Burger, Jutta C, Michael A Patten, John T Rotenberry, and Richard A Redak. 2005. "Patterns and Processes of Arthropod Community Succession after a Fire." *USDA Forest Service Gen. Tech Rep* 249-251.
- Burghardt, Karin T., and Douglas W. Tallamy. 2013. "Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods." *Diversity and Distributions* 19 (12): 1553-1565.
- Cardoso, Pedro, Philip S. Barton, Klaus Birkhofer, Filipe Chichorro, Charl Deacon, Thomas Fartmann, Caroline S. Fukushima, et al. 2020. "Scientists' warning to humanity on insect extinctions." *Biological Conservation* (Elsevier) 242.
- Castagneyrol, Bastien, Hervé Jactel, Corinne Vacher, Eckehard G. Brockerhoff, and Julia Koricheva. 2014. "Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization." *Journal of Applied Ecology* 51 (1): 134-141.
- Castagneyrol, Bastien, Xoaquín Moreira, and Hervé Jactel. 2018. "Drought and plant neighbourhood interactively determine herbivore consumption and performance." *Scientific Reports* 8 (1): 5930. <https://www.nature.com/articles/s41598-018-24299-x>.
- Cavender-Bares, Jeannine, Kenneth H Kozak, Paul V A Fine, and Steven W Kembel. 2009. "The merging of community ecology and phylogenetic biology." *Ecology Letters* 693-715. <https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2009.01314.x>.
- Cecil, Eric M., Marko J. Spasojevic, and J. Hall Cushman. 2019. "Cascading effects of mammalian herbivores on ground-dwelling arthropods: Variable responses across arthropod groups, habitats and years." *Journal of Animal Ecology* (John Wiley & Sons, Ltd) 88 (9): 1319-1331. <https://onlinelibrary.wiley.com/doi/full/10.1111/1365-2656.13033>.
- Chaves, Rocío, Pablo Ferrandis, Adrián Escudero, and Arantzazu L Luzuriaga. 2020. *Diverse phylogenetic neighborhoods enhance community resistance to drought in experimental assemblages*. Vol. 11. <https://doi.org/10.1038/s41598-021-01991-z>.
- Chen, Ming Shun. 2008. *Inducible direct plant defense against insect herbivores: A review*. Vol. 15.



- Christopher M. Oswalt, Jason A. Cooper, Joan L. Walker Horace W. Brooks, and and Roger C. Conner Sonja N. Oswalt. 2012. "History and Current Condition of Longleaf Pine in the Southern United States." Asheville, NC, 1-51.  
[https://www.srs.fs.usda.gov/pubs/gtr/gtr\\_srs166.pdf](https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs166.pdf).
- Christopher M. Oswalt, Jason A. Cooper, Joan L. Walker Horace W. Brooks, and and Roger C. Conner Sonja N. Oswalt. 2012. "History and Current Condition of Longleaf Pine in the Southern United States." Asheville, NC, 1-51.  
[https://www.srs.fs.usda.gov/pubs/gtr/gtr\\_srs166.pdf](https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs166.pdf).
- Coleman, J S, and A S Leonard. 1995. "Why it matters where on a leaf a folivore feeds Optimal defense 9 Plant-insect interactions." *Oecologia* (Springer-Verlag) 101: 324-328.
- Coleman, James S. 1986. "Leaf development and leaf stress: increased susceptibility associated with sink-source transition." *Tree Physiology* 2 (1-2-3): 289-299.  
<https://doi.org/10.1093/treephys/2.1-2-3.289>.
- Cowles, Jane, Bazartseren Boldgiv, Pierre Liancourt, Peter S. Petraitis, and Brenda B. Casper. 2018. *Effects of increased temperature on plant communities depend on landscape location and precipitation*. Vol. 8. John Wiley and Sons Ltd.
- Crawley, Michael J. 1989. "INSECT HERBIVORES AND PLANT POPULATION DYNAMICS Distinguishing Performance and Dynamics." [www.annualreviews.org](http://www.annualreviews.org).
- Cronin, James Patrick, Stephen J. Tonsor, and Walter P. Carson. 2010. "A simultaneous test of trophic interaction models: which vegetation characteristic explains herbivore control over plant community mass?" *Ecology Letters* (John Wiley & Sons, Ltd) 13 (2): 202-212.  
<https://onlinelibrary.wiley.com/doi/full/10.1111/j.1461-0248.2009.01420.x>.
- Ding, Shuting, Xiangqi Shao, Jianxin Li, Golam Jalal Ahammed, Yanlai Yao, Jian Ding, Zhangjian Hu, Jingquan Yu, Kai Shi, and Correspondence Kai Shi. 2021. *Nitrogen forms and metabolism affect plant defence to foliar and root pathogens in tomato*.  
<https://onlinelibrary.wiley.com/doi/10.1111/pce.14019>.
- Dinnage, Russell, Marc W. Cadotte, Nick M. Haddad, Gregory M. Crutsinger, and David Tilman. 2012. "Diversity of plant evolutionary lineages promotes arthropod diversity." *Ecology Letters* (John Wiley & Sons, Ltd) 15 (11): 1308-1317.  
<https://onlinelibrary.wiley.com/doi/full/10.1111/j.1461-0248.2012.01854.x>.
- Dunn, Peter O., Insiyaa Ahmed, Elise Armstrong, Natasha Barlow, Malcolm A. Barnard, Marc Bélisle, Thomas J. Benson, et al. 2023. "Extensive regional variation in the phenology of insects and their response to temperature across North America." *Ecology* (John Wiley & Sons, Ltd) 104 (5): e4036. <https://onlinelibrary.wiley.com/doi/full/10.1002/ecy.4036>.
- Engstrom, R Todd. 1993. "Characteristic Mammals and Birds of Longleaf Pine Forests." Tallahassee, 127-138.
- Feeley, K. J., C. Bravo-Avila, B. Fadrique, T. M. Perez, and D. Zuleta. 2020. *Climate-driven changes in the composition of New World plant communities*. Vol. 10. Nature Publishing Group. <https://www.nature.com/articles/s41558-020-0873-2>.
- Ferguson, Brett J, Céline Mens, April H Hastwell, Mengbai Zhang, Huanan Su, Candice H Jones, Xitong Chu, and Peter M Gresshoff. 2019. "Legume nodulation: The host controls the party." *Plant Cell and Environment* (Blackwell Publishing Ltd) 42 (1): 41-51.
- Fernández De Bobadilla, Maite, · Roel, Van Wiechen, Gerrit Gort, and Erik H Poelman. 2022. *Plasticity in induced resistance to sequential attack by multiple herbivores in Brassica nigra*. Vol. 198. <https://doi.org/10.1007/s00442-021-05043-1>.

- Forbes, Andrew A., and Jay A. Rosenheim. 2011. *Plant responses to insect herbivore damage are modulated by phosphorus nutrition*. Vol. 139. <https://onlinelibrary.wiley.com/doi/10.1111/j.1570-7458.2011.01125.x>.
- Forrest, Jessica RK. 2016. "Complex responses of insect phenology to climate change." *Current Opinion in Insect Science* (Elsevier) 17: 49-54.
- Foster, Claire, Phillip Barton, and David Lindenmayer. 2014. "Effects of large native herbivores on other animals." *Journal of Applied Ecology* 51 (4): 929-938. <https://www.jstor.org/stable/24032493>.
- Frost, Cecil C. 1993. "Four Centuries of Changing Landscape Patterns in the Longleaf Pine Ecosystem." 18: 17-43.
- Garcia, Léo, Gaëlle Damour, Elena Kazakou, Guillaume Fried, Marie Charlotte Bopp, and Aurélie Metay. 2020. *Seasonal and interannual variations in functional traits of sown and spontaneous species in vineyard inter-rows*. Vol. 11. Wiley-Blackwell.
- Gavinet, Jordane, Jean-Marc Ourcival, and Jean-Marc Limousin. 2019. "Rainfall exclusion and thinning can alter the relationships between forest functioning and drought." *New Phytologist* 223: 1267-1279. <https://nph.onlinelibrary.wiley.com/doi/10.1111/nph.15860>.
- Goulson, Dave. 2021. *Silent Earth: Averting the Insect Apocalypse*. Harper.
- . 2021. *Silent Earth: Averting the Insect Apocalypse*. Harper.
- Goulson, Dave. 2019. "The insect apocalypse, and why it matters." *Current Biology* (Cell Press) 29 (19): R967-R971.
- Grelen, Harold E, and Vinson L Duvall. 1966. *COMMON PLANTS OF LONGLEAF PINE-BLUE STEM RANGE*.
- Guo, Haining, Yiran Wang, Guoqing Li, and Sheng Du. 2024. "Effects of Rainfall Exclusion Treatment on Photosynthetic Characteristics of Black Locust in the Sub-Humid Region of the Loess Plateau, China." *Plants* (Multidisciplinary Digital Publishing Institute (MDPI)) 13 (5).
- Guo, Yongfeng, Guodong Ren, Kewei Zhang, Zhonghai Li, Ying Miao, and Hongwei Guo. 2021. *Leaf senescence: progression, regulation, and application*. Vol. 1. BioMed Central. <https://molhort.biomedcentral.com/articles/10.1186/s43897-021-00006-9>.
- Haddad, Nick M., Gregory M. Crutsinger, Kevin Gross, John Haarstad, Johannes M.H. Knops, and David Tilman. 2009. "Plant species loss decreases arthropod diversity and shifts trophic structure." *Ecology Letters* (John Wiley & Sons, Ltd) 12 (10): 1029-1039. <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1461-0248.2009.01356.x>.
- Harpole, W. Stanley, Jacqueline T. Ngai, Elsa E. Cleland, Eric W. Seabloom, Elizabeth T. Borer, Matthew E.S. Bracken, James J. Elser, et al. 2011. "Nutrient co-limitation of primary producer communities." *Ecology Letters* 14 (9): 852-862.
- Harris, James A, Richard J Hobbs, Eric Higgs, and James Aronson. 2006. "Ecological Restoration and Global Climate Change." *Restoration Ecology* 14: 170-176.
- Hartmann, Adrian A, Pascal A Niklaus, A A Hartmann, and P A Niklaus. 2012. "Effects of simulated drought and nitrogen fertilizer on plant productivity and nitrous oxide (N<sub>2</sub>O) emissions of two pastures." *Plant Soil* 361: 411-426.
- Hauser, Thure P., Stina Christensen, Christine Heimes, and Lars P. Kiær. 2013. "Combined effects of arthropod herbivores and phytopathogens on plant performance." Edited by Alison Bennett. *Functional Ecology* 27 (3): 623-632. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12053>.

- Hawkes, Christine V, and Jon J Sullivan. 2001. "THE IMPACT OF HERBIVORY ON PLANTS IN DIFFERENT RESOURCE CONDITIONS: A META-ANALYSIS." *Ecology* 82 (7): 2045-2058. <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/0012-9658>.
- Hochuli, Dieter F. 2001. "Insect herbivory and ontogeny: How do growth and development influence feeding behaviour, morphology and host use?" *Austral Ecology* 26 (5): 563-570. <https://onlinelibrary.wiley.com/doi/10.1046/j.1442-9993.2001.01135.x>.
- Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. "Contrasting sensitivities of two dominant C4 grasses to heat waves and drought." *Plant Ecology* (Kluwer Academic Publishers) 215 (7): 721-731.
- Huberty, Andrea F, and Robert F Denno. 2004. "PLANT WATER STRESS AND ITS CONSEQUENCES FOR HERBIVOROUS INSECTS: A NEW SYNTHESIS." *Ecology* 85 (5): 1383-1398. <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/03-0352>.
- Hunter, Mark D. 2001. "Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics." *Agricultural and Forest Entomology* 3 (2): 77-84. <https://resjournals.onlinelibrary.wiley.com/doi/10.1046/j.1461-9563.2001.00100.x>.
- Hyvarinen, Olli, Mariska Te Beest, Elizabeth le Roux, Graham Kerley, Esther de Groot, Rana Vinita, and Joris P.G.M. Cromsigt. 2021. "Megaherbivore impacts on ecosystem and Earth system functioning: the current state of the science." *Ecography* (John Wiley and Sons Inc) 44 (11): 1579-1594.
- Isbell, Forest, Dylan Craven, John Connolly, Michel Loreau, Bernhard Schmid, Carl Beierkuhnlein, T. Martijn Bezemer, et al. 2015. *Biodiversity increases the resistance of ecosystem productivity to climate extremes*. Vol. 526. <https://www.nature.com/articles/nature15374>.
- Isbell, Forest, Peter B. Reich, David Tilman, Sarah E. Hobbie, Stephen Polasky, and Seth Binder. 2013. *Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity*. Vol. 110.
- . 2013. *Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity*. Vol. 110.
- Jactel, Hervé, Jérôme Petit, Marie-Laure Desprez-Loustau, Sylvain Delzon, Dominique Piou, Andrea Battisti, and Julia Koricheva. 2011. "Drought effects on damage by forest insects and pathogens: a meta-analysis." <https://onlinelibrary.wiley.com/doi/10.1111/j.1365-2486.2011.02512.x>.
- Jia, Shihong, Xugao Wang, Zuoqiang Yuan, Fei Lin, Ji Ye, Zhanqing Hao, and Matthew Scott Luskin. 2018. "Global signal of top-down control of terrestrial plant communities by herbivores." *Proceedings of the National Academy of Sciences of the United States of America* (National Academy of Sciences) 115 (24): 6237-6242. [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1707984115/-/DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1707984115/-/DCSupplemental). [www.pnas.org/cgi/doi/10.1073/pnas.1707984115](http://www.pnas.org/cgi/doi/10.1073/pnas.1707984115).
- Jokela, E. J., E. L. Stone, and W. W. McFee. 1991. *Micronutrient Deficiency in Slash Pine: Response and Persistence of Added Manganese*. Vol. 55. Wiley.
- Jones, B. C., and E. Despland. 2006. "Effects of synchronization with host plant phenology occur early in the larval development of a spring folivore." *Canadian Journal of Zoology* 84 (4): 628-633. <https://cdnsiencepub.com/doi/10.1139/Z06-025>.
- Koerner, Sally E., Meghan L. Avolio, Kimberly J. La Pierre, Kevin R. Wilcox, Melinda D. Smith, and Scott L. Collins. 2016. *Nutrient additions cause divergence of tallgrass*

- prairie plant communities resulting in loss of ecosystem stability*. Vol. 104. Blackwell Publishing Ltd.
- Komatsu, Kimberly J., Meghan L. Avolio, Nathan P. Lemoine, Forest Isbell, Emily Grman, Gregory R. Houseman, Sally E. Koerner, et al. 2019. "Global change effects on plant communities are magnified by time and the number of global change factors imposed." *Proceedings of the National Academy of Sciences* (PNAS) 116 (36): 17867-17873. <https://pnas.org/doi/full/10.1073/pnas.1819027116>.
- Kroes, A., J. M. Stam, A. David, W. Boland, J. J.A. van Loon, M. Dicke, and E. H. Poelman. 2016. *Plant-mediated interactions between two herbivores differentially affect a subsequently arriving third herbivore in populations of wild cabbage*. Vol. 18. Blackwell Publishing Ltd.
- La Pierre, Kimberly J., and Melinda D. Smith. 2016. "Soil nutrient additions increase invertebrate herbivore abundances, but not herbivory, across three grassland systems." *Oecologia* (Springer Verlag) 180 (2): 485-497.
- La Pierre, Kimberly J., Anthony Joern, and Melinda D. Smith. 2015. *Invertebrate, not small vertebrate, herbivory interacts with nutrient availability to impact tallgrass prairie community composition and forb biomass*. Vol. 124. <https://onlinelibrary.wiley.com/doi/10.1111/oik.01869>.
- Lavoie, Bethann, and Karen S Oberhauser. 2004. "Compensatory Feeding in *Danaus plexippus* (Lepidoptera: Nymphalidae) in Response to Variation in Host Plant Quality." *Environ. Entomol* 33 (4): 1062-1069. <https://academic.oup.com/ee/article/33/4/1062/450543>.
- Lawrence, Rachel, Brad M Potts, and Thomas G Whitham. 2003. "Relative Importance of Plant Ontogeny, Host Genetic Variation, and Leaf Age for a Common Herbivore." 84 (5): 1171-1178.
- LeBauer, David S., and Kathleen K. Treseder. 2008. "Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed." *Ecology* 89 (2): 371-379.
- Levey, Douglas J, T Trevor Caughlin, Lars A Brudvig, Nick M Haddad, Ellen I Damschen, Joshua J Tewksbury, and Daniel M Evans. 2016. "Disentangling fragmentation effects on herbivory in understory plants of longleaf pine savanna." <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.1466>.
- Lian, Xu, Shilong Piao, Anping Chen, Kai Wang, Xiangyi Li, Wolfgang Buermann, Chris Huntingford, Josep Peñuelas, Hao Xu, and Ranga B. Myneni. 2021. *Seasonal biological carryover dominates northern vegetation growth*. Vol. 12. <https://www.nature.com/articles/s41467-021-21223-2>.
- Lind, Eric M, Kimberly J La Pierre, Eric W Seabloom, Juan Alberti, Oscar Iribarne, Jennifer Firn, Daniel S Gruner, et al. 2017. "Increased grassland arthropod production with mammalian herbivory and eutrophication: a test of mediation pathways." *Ecology* 98 (12): 3022-3033. <https://www.jstor.org/stable/26602180?seq=8>.
- Lindstedt, Carita, Liam Murphy, and Johanna Mappes. 2019. "Antipredator strategies of pupae: how to avoid predation in an immobile life stage?"
- Liu, Dan, Tao Wang, Josep Peñuelas, and Shilong Piao. 2022. *Drought resistance enhanced by tree species diversity in global forests*. Vol. 15. Nature Publishing Group. <https://www.nature.com/articles/s41561-022-01026-w>.
- Lu, Xiaoming, Xuezheng Zhao, Taiki Tachibana, Kei Uchida, Takehiro Sasaki, and Yongfei Bai. 2022. "Bottom-up effects of plant quantity and quality on arthropod diversity across

- multiple trophic levels in a semi-arid grassland." *Journal of Ecology* 110: 2717-2730. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.13982>.
- Lu, Xiaoming, Xuezhen Zhao, Taiki Tachibana, Kei Uchida, Takehiro Sasaki, and Yongfei Bai. 2020. "Plant quantity and quality regulate the diversity of arthropod communities in a semi-arid grassland." <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13742>.
- Lu, Xiaoming, Xuezhen Zhao, Taiki Tachibana, Kei Uchida, Takehiro Sasaki, and Yongfei Bai. 2021. "Plant quantity and quality regulate the diversity of arthropod communities in a semi-arid grassland." *Functional Ecology* 601-613. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.13742>.
- Lucini, Francesca Arese, Flaviano Morone, Maria Silvina Tomassone, and Hernán A. Makse. 2020. "Diversity increases the stability of ecosystems." *PLOS ONE* (Public Library of Science) 15 (4): e0228692. <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0228692>.
- Luo, Wentao, Robert J Griffin-nolan, Bo Liu, Xiaohan Zuo, Yahuang Luo, Pierre Mariotte, Melinda D Smith, et al. 2021. "Plant traits and soil fertility mediate productivity losses under extreme drought in C 3 grasslands." *Ecology*. <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3465>.
- Luo, Wentao, Taofeek O Muraina, Robert J Griffin-Nolan, Wang Ma, Lin Song, Wei Fu, Qiang Yu, et al. 2023. "Responses of a semiarid grassland to recurrent drought are linked to community functional composition." *Ecology*.
- Martinez-Swatson, Karen, Rasmus Kjølner, Federico Cozzi, Henrik Toft Simonsen, Nina Rønsted, and Christopher Barnes. 2020. "Exploring evolutionary theories of plant defence investment using field populations of the deadly carrot." *Annals of Botany* 125: 737-750.
- Mason, Chase M, and Lisa A Donovan. 2015. "Does investment in leaf defenses drive changes in leaf economic strategy? A focus on whole-plant ontogeny." *Oecologia* 177 (4): 1053-1066. <https://www.jstor.org/stable/43672558>.
- McIntyre, R. Kevin, Barrett B. McCall, and David N. Wear. 2018. "The Social and Economic Drivers of the Southeastern Forest Landscape." *Ecological restoration and management of longleaf pine forests*. 39-67.
- Miller, Joseph T., Garry Jolley-Rogers, Brent D. Mishler, and Andrew H. Thornhill. 2018. "Phylogenetic diversity is a better measure of biodiversity than taxon counting." *Journal of Systematics and Evolution* (Wiley-Liss Inc.) 56 (6): 663-667.
- Mitchell, J. Christina, Daniel M. Kashian, Xiongwen Chen, Stella Cousins, David Flaspohler, Daniel S. Gruner, Jeremy S. Johnson, Thilina D. Surasinghe, Jenny Zambrano, and Brian Buma. 2023. "Forest ecosystem properties emerge from interactions of structure and disturbance." *Frontiers in Ecology and the Environment* (John Wiley and Sons Inc) 21 (1): 14-23.
- Mitchell, Robert J., L. Katherine Kirkman, Stephen D. Pecot, Carlos A. Wilson, Brian J. Palik, and Lindsay R. Boring. 1999. "Patterns and controls of ecosystem function in longleaf pine - wiregrass savannas. I. Aboveground net primary productivity." *Canadian Journal of Forest Research* 743-751.
- Montgomery, Graham A., Robert R. Dunn, Richard Fox, Eelke Jongejans, Simon R. Leather, Manu E. Saunders, Chris R. Shortall, Morgan W. Tingley, and David L. Wagner. 2020.

- "Is the insect apocalypse upon us? How to find out." *Biological Conservation* (Elsevier) 241: 108327.
- Moreira, X, R Zas, and L Sampedro. 2012. *Differential Allocation of Constitutive and Induced Chemical Defenses in Pine Tree Juveniles: A Test of the Optimal Defense Theory*. Vol. 7. [www.plosone.org](http://www.plosone.org).
- Moreira, Xoaquín, Luis Abdala-Roberts, Andrea Galmán, Marta Francisco, María De La Fuente, Ana Butrón, and Sergio Rasmann. 2018. "Assessing the influence of biogeographical region and phylogenetic history on chemical defences and herbivory in *Quercus* species." *Phytochemistry* 153: 64-73. <https://doi.org/10.1016/j.phytochem.2018.06.002>.
- Mortensen, Brent, Brent Danielson, W Stanley Harpole, Juan Alberti, Carlos Alberto Arnillas, Lori Biederman, Elizabeth T Borer, et al. 2018. "Herbivores safeguard plant diversity by reducing variability in dominance." *Journal of Ecology* 106: 101-112. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.12821>.
- Muehleisen, Andrew J, Carmen R E Watkins, Gabriella R Altmire, E Ashley Shaw, Madelon F Case, Lina Aoyama, Alejandro Brambila, et al. 2023. "Nutrient addition drives declines in grassland species richness primarily via enhanced species loss." *Journal of Ecology* 552: 552-563. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.14038>.
- Naumann, G., L. Alfieri, K. Wyser, L. Mentaschi, R. A. Betts, H. Carrao, J. Spinoni, J. Vogt, and L. Feyen. 2018. "Global Changes in Drought Conditions Under Different Levels of Warming." *Geophysical Research Letters* (Blackwell Publishing Ltd) 45 (7): 3285-3296.
- Niu, Decao, Xiaobo Yuan, Arianne J Cease, Haiyan Wen, Chunping Zhang, Hua Fu, and James J Elser. 2018. "The impact of nitrogen enrichment on grassland ecosystem stability depends on nitrogen addition level." *Science of the Total Environment* 618: 1529-1538. <https://doi.org/10.1016/j.scitotenv.2017.09.318>.
- Noss, Reed F., William J. Platt, Bruce A. Sorrie, Alan S. Weakley, D. Bruce Means, Jennifer Costanza, and Robert K. Peet. 2015. "How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain." *Diversity and Distributions* 21 (2): 236-244.
- Novotny, Vojtech, Scott E. Miller, Leontine Baje, Solomon Balagawi, Yves Basset, Lukas Cizek, Kathleen J. Craft, et al. 2010. *Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest*. Vol. 79. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2656.2010.01728.x>.
- Orians, Colin M, and Clive G Jones. 2001. *Plants as resource mosaics: a functional model for predicting patterns of within-plant resource heterogeneity to consumers based on vascular architecture and local environmental variability*. <https://nsojournals.onlinelibrary.wiley.com/doi/10.1034/j.1600-0706.2001.940311.x>.
- Orrock, John L., Lars A. Brudvig, Ellen I. Damschen, W. Brett Mattingly, Jennyffer Cruz, Joseph W. Veldman, Philip G. Hahn, and Angela L. Larsen-Gray. 2023. "Long-term, large-scale experiment reveals the effects of seed limitation, climate, and anthropogenic disturbance on restoration of plant communities in a biodiversity hotspot." *Proceedings of the National Academy of Sciences of the United States of America* (National Academy of Sciences) 120 (7): e2201943119. <https://www.pnas.org/doi/abs/10.1073/pnas.2201943119>.
- Oswalt, Christopher M., Jason A. Cooper, Horace W. Brooks, Joan L. Walker, Sonja N. Oswalt, and and Roger C. Conner. 2012. "History and Current Condition of Longleaf Pine in the

- Southern United States." Asheville, NC, 1-51.  
[https://www.srs.fs.usda.gov/pubs/gtr/gtr\\_srs166.pdf](https://www.srs.fs.usda.gov/pubs/gtr/gtr_srs166.pdf).
- Parker, John D., Deron E. Burkepile, Marc J. Lajeunesse, and Eric M. Lind. 2012. "Phylogenetic isolation increases plant success despite increasing susceptibility to generalist herbivores." *Diversity and Distributions* 18 (1): 1-9.
- Pau, Stephanie, Daniel M. Griffith, Nicole E. Zampieri, and Jennifer Costanza. 2023. "Longleaf pine savannas reveal biases in current understanding of savanna biogeography." *Global Ecology and Biogeography* 32 (11): 2047-2052.  
<https://onlinelibrary.wiley.com/doi/10.1111/geb.13747>.
- Pearse, Ian S, and Andrew L Hipp. 2014. "Native plant diversity increases herbivory to non-natives." *Proceedings of the Royal Society B: Biological Sciences*.  
<http://dx.doi.org/10.1098/rspb.2014.1841> or <http://rspb.royalsocietypublishing.org>.
- Piao, Shilong, Qiang Liu, Anping Chen, Ivan A Janssens, Yongshuo Fu, Junhu Dai, Lingli Liu, Xu Lian, Miaogen Shen, and Xiaolin Zhu. 2019. "Plant phenology and global climate change: Current progresses and challenges." *Glob Change Biol* 25: 1922-1940.  
<https://onlinelibrary.wiley.com/doi/10.1111/gcb.14619>.
- Poelman, Erik H., Colette Broekgaarden, Joop J.A. Van Loon, and Marcel Dicke. 2008. *Early season herbivore differentially affects plant defence responses to subsequently colonizing herbivores and their abundance in the field*. Vol. 17.
- Porter, Ellen M, William D Bowman, Christopher M Clark, Jana E Compton, Linda H Pardo, and Jenny L Soong. 2013. "Interactive effects of anthropogenic nitrogen enrichment and climate change on terrestrial and aquatic biodiversity." *Biogeochemistry* 114: 93-120.
- Prather, Rebecca M., Karen Castillioni, Ellen A.R. Welti, Michael Kaspari, and Lara Souza. 2020. "Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions." *Ecology* (Ecological Society of America) 101 (6).  
<https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecy.3033>.
- Rusman, Quint, Dani Lucas-Barbosa, Kamrul Hassan, and Erik H. Poelman. 2020. "Plant ontogeny determines strength and associated plant fitness consequences of plant-mediated interactions between herbivores and flower visitors." *Journal of Ecology* (Blackwell Publishing Ltd) 108 (3): 1046-1060.
- S. A. PRIOR, G. B. RUNION, R. J. MITCHELL, H. H. ROGERS, and J. S. AMTHOR. 1997. "Effects of atmospheric CO<sub>2</sub> on longleaf pine: productivity and allocation as influenced by nitrogen and water." *Tree Physiology* 17: 397-405.
- Segar, Josiane, Henrique M. Pereira, Lander Baeten, Markus Bernhardt-Römermann, Pieter De Frenne, Néstor Fernández, Frank S. Gilliam, et al. 2022. "Divergent roles of herbivory in eutrophying forests." *Nature Communications* 2022 13:1 (Nature Publishing Group) 13 (1): 1-10. <https://www.nature.com/articles/s41467-022-35282-6>.
- Shan, Liping, Ayub M.O. Oduor, Wei Huang, and Yanjie Liu. 2022. "Nutrient enrichment promotes invasion success of alien plants via increased growth and suppression of chemical defenses." *Ecological Applications* (John Wiley & Sons, Ltd) e2791.  
<https://onlinelibrary.wiley.com/doi/full/10.1002/eap.2791>.
- Sheehan, Thomas N, and Kier D Klepzig. n.d. "Arthropods and Fire Within the Biologically Diverse Longleaf Pine Ecosystem." <https://doi.org/10.1093/aesa/saab037>.
- Sitters, Judith, E. R. Jasper Wubs, Elisabeth S. Bakker, Thomas W. Crowther, Peter B. Adler, Sumanta Bagchi, Jonathan D. Bakker, et al. 2020. "Nutrient availability controls the

- impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands." *Global Change Biology* (Blackwell Publishing Ltd) 26 (4): 2060-2071.
- Smith, Melinda D, Kate D Wilkins, Martin C Holdrege, Peter Wilfahrt, Scott L Collins, Alan K Knapp, Osvaldo E Sala, et al. 2024. "Extreme drought impacts have been underestimated in grasslands and shrublands globally." *Proceedings of the National Academy of Sciences of the United States of America* (National Academy of Sciences) 121 (4): e2309881120. <http://www.ncbi.nlm.nih.gov/pubmed/38190514>.
- Smith, Melinda D., Sally E. Koerner, Alan K. Knapp, Meghan L. Avolio, Francis A. Chaves, Elsie M. Denton, John Dietrich, et al. 2020. "Mass ratio effects underlie ecosystem responses to environmental change." *Journal of Ecology* (Blackwell Publishing Ltd) 108 (3): 855-864.
- Smith, Millicent R., Erik Veneklaas, Jose Polania, Idupulapati M. Rao, Stephen E. Beebe, and Andrew Merchant. 2019. "Field drought conditions impact yield but not nutritional quality of the seed in common bean (*Phaseolus vulgaris* L.)." *PLoS ONE* 14 (9). <https://doi.org/10.1371/journal.pone.0217099>.
- Stam, Jeltje M., Anneke Kroes, Yehua Li, Rieta Gols, Joop J.A. van Loon, Erik H. Poelman, and Marcel Dicke. 2014. *Plant Interactions with Multiple Insect Herbivores: From Community to Genes*. Vol. 65. <https://www.annualreviews.org/doi/10.1146/annurev-arplant-050213-035937>.
- Stanley Harpole, W, Lauren L Sullivan, Eric M Lind, Jennifer Firn, Peter B Adler, Elizabeth T Borer, Jonathan Chase, et al. 2016. "Addition of multiple limiting resources reduces grassland diversity." *Community Ecology* 537: 93-96. <http://www.nutnet.org>.
- Stout, Michael J, Jennifer S Thaler, and Bart P H J Thomma. 2006. "PLANT-MEDIATED INTERACTIONS BETWEEN PATHOGENIC MICROORGANISMS AND HERBIVOROUS ARTHROPODS." *Annu. Rev. Entomol* 51: 663-89. [www.annualreviews.org](http://www.annualreviews.org).
- Takahashi, Daisuke, and Atsushi Yamauchi. 2010. "Optimal defense schedule of annual plants against seasonal herbivores." *American Naturalist* 175 (5): 538-550.
- Throop, Heather L, and Manuel T Lerda. 2004. "Effects of Nitrogen Deposition on Insect Herbivory: Implications for Community and Ecosystem Processes." *Ecosystems* 109-133. <https://www.jstor.org/stable/3658603>.
- Tierney, Julie A., Lars O. Hedin, and Nina Wurzbarger. 2019. "Nitrogen fixation does not balance fire-induced nitrogen losses in longleaf pine savannas." *Ecology* (John Wiley & Sons, Ltd) 100 (7). <https://onlinelibrary.wiley.com/doi/full/10.1002/ecy.2735>.
- Titeux, Nicolas, Klaus Henle, Jean-Baptiste Mihoub, Adrián Regos, Ilse R. Geijzenborffer, Wolfgang Cramer, Peter H. Verburg, and Luís Brotons. 2016. "Biodiversity scenarios neglect future land-use changes." *Global Change Biology* 2505-2515.
- Turcotte, Martin M, T Jonathan Davies, Christina J M Thomsen, and Marc T J Johnson. 2014. "Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants." *Proceedings of the Royal Society B: Biological Sciences*. <http://dx.doi.org/10.1098/rspb.2014.0555> <http://rspb.royalsocietypublishing.org>.
- Van Dyke, Mary N, Jonathan M Levine, and Nathan J B Kraft. 2022. *Small rainfall changes drive substantial changes in plant coexistence*. Vol. 611. <https://doi.org/10.1038/s41586-022-05391-9>.



- Van Lear, David H., W. D. Carroll, P. R. Kapeluck, and Rhett Johnson. 2005. "History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk." *Forest Ecology and Management* 211 (1-2): 150-165.
- Vitousek', Peter M, and Robert W Howarth. n.d. "Nitrogen limitation on land and in the sea: How can it occur?" 87-115.
- Wagner, David L., Eliza M. Grames, Matthew L. Forister, May R. Berenbaum, and David Stopak. 2021. "Insect decline in the Anthropocene: Death by a thousand cuts." *Proceedings of the National Academy of Sciences of the United States of America* (National Academy of Sciences) 118 (2). <https://doi.org/10.1073/pnas.2023989118>.
- Walter, Julia, Roman Hein, Harald Auge, Carl Beierkuhnlein, Sonja Löffler, Kerstin Reifenth, Martin Schädler, Michael Weber, and Anke Jentsch. 2012. "How do extreme drought and plant community composition affect host plant metabolites and herbivore performance?" *Arthropod-Plant Interactions* 15-25.
- Welti, Ellen A R, Karl A Roeder, Kirsten M de Beurs, Anthony Joern, and Michael Kaspari. 2020. "Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore." *Proceedings of the National Academy of Sciences of the United States of America* (National Academy of Sciences) 117 (13): 7271-7275. <http://www.ncbi.nlm.nih.gov/pubmed/32152101>.
- Welti, Ellen A. R., Rebecca M. Prather, Nathan J. Sanders, Kirsten M. de Beurs, and Michael Kaspari. 2020. "Bottom-up when it is not top-down: Predators and plants control biomass of grassland arthropods." Edited by Rebecca Morris. *Journal of Animal Ecology* (Blackwell Publishing Ltd) 89 (5): 1286-1294. <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13191>.
- Welti, Ellen, Chris Helzer, and Anthony Joern. 2017. "Impacts of plant diversity on arthropod communities and plant-herbivore network architecture." *Ecosphere* (Ecological Society of America) 8 (10). <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.1983>.
- Wetzel, William C, Brian D Inouye, Philip G Hahn, Susan R Whitehead, and Nora Underwood. 2023. *Annual Review of Ecology, Evolution, and Systematics Variability in Plant-Herbivore Interactions*. Vol. 54. <https://doi.org/10.1146/annurev-ecolsys-102221->
- Wetzel, William C, Heather M Kharouba, Moria Robinson, Marcel Holyoak, and Richard Karban. 2016. *Variability in plant nutrients reduces insect herbivore performance*. [www.nature.com/reprints](http://www.nature.com/reprints).
- Wiens, John J, David D Ackerly, Andrew P Allen, Brian L Anacker, Lauren B Buckley, Howard V Cornell, Ellen I Damschen, et al. 2010. "Niche conservatism as an emerging principle in ecology and conservation biology." *Ecology Letters* 1310-1324. <https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2010.01515.x>.
- William J. Mattson, Jr. 2003. "Herbivory in Relation to Plant Nitrogen Content." <https://doi.org/10.1146/annurev.es.11.110180.001003> ( *Annual Reviews* 4139 El Camino Way, P.O. Box 10139, Palo Alto, CA 94303-0139, USA ) 11 (1): 119-161. <https://www.annualreviews.org/doi/abs/10.1146/annurev.es.11.110180.001003>.
- Wilson, Jerome Keaton, Laura Ruiz, Jesse Duarte, and Goggy Davidowitz. 2019. "The nutritional landscape of host plants for a specialist insect herbivore." *Ecology and Evolution* (John Wiley and Sons Ltd) 9 (23): 13104-13113.
- Wimp, Gina M., Shannon M. Murphy, Deborah L. Finke, Andrea F. Huberty, and Robert F. Denno. 2010. "Increased primary production shifts the structure and composition of a terrestrial arthropod community." *Ecology* 91 (11): 3303-3311.

- Wu, Minchao, Giulia Vico, Stefano Manzoni, Zhanzhang Cai, Maoya Bassiouni, Feng Tian, Jie Zhang, Kunhui Ye, and Gabriele Messori. 2021. *Early Growing Season Anomalies in Vegetation Activity Determine the Large-Scale Climate-Vegetation Coupling in Europe*. Vol. 126. Blackwell Publishing Ltd.
- You, Chengming, Fuzhong Wu, Youmin Gan, Wanqin Yang, Zhongmin Hu, Zhenfeng Xu, Bo Tan, Lin Liu, and Xiangyin Ni. 2017. "Grass and forbs respond differently to nitrogen addition: a meta-analysis of global grassland ecosystems OPEN." *Scientific Reports* 1563. [www.nature.com/scientificreports](http://www.nature.com/scientificreports).
- Young, Alyssa L, Kathryn J Bloodworth, Morgan T Frost, Curtis E Green, and Sally E Koerner. 2021. "Heatwave implications for the future of longleaf pine savanna understory restoration." *Plant Ecology*.
- Zattara, Eduardo E., and Marcelo A. Aizen. 2021. "Worldwide occurrence records suggest a global decline in bee species richness." *One Earth* (Cell Press) 4 (1): 114-123.
- Zhang, Qi, Yanan Li, Mengru Wang, Kai Wang, Fanlei Meng, Lei Liu, Yuanhong Zhao, et al. 2021. "Atmospheric nitrogen deposition: A review of quantification methods and its spatial pattern derived from the global monitoring networks." *Ecotoxicology and Environmental Safety* 216: 112180. <https://doi.org/10.1016/j.ecoenv.2021.112180>.