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**SIMULATED CLIMATE CHANGE ALTERS PHENOLOGY, COMPOSITION, AND  
STRUCTURE OF POST-HARVEST VEGETATION COMMUNITIES**

A Thesis in

Ecology

by

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## **Abstract**

Models predict that climate change may lead to altered forest community composition as southern species are able to migrate successfully northward. Forest harvesting could facilitate climate-related species migration by creating conditions that favor the establishment of new species. My research investigated the effects of simulated climate change on plant community composition, structure, and phenology in a 2007 mixed hardwood clear cut. In 2009, I conducted 22 biweekly vegetation inventories in a two-factorial randomized block design experiment with treatment factors of 2° C air temperature warming and 20% increased precipitation. I measured the impacts of our climate treatments on species composition, percent cover, leaf area index (LAI) and phenology. I used permutation multivariate analysis of variance (PerMANOVA) on the average cover of observed species over the entire season to assess the relationship between community composition and simulated climate change treatments. LAI and percent cover of the entire community and of different growth forms were analyzed using repeated measures ANOVA while community biodiversity, species richness, and phenological events were assessed using standard ANOVA for different growth forms.

The overall and herbaceous community composition was influenced by water treatments ( $p = 0.05$  for both) while the woody community responded strongly to the interaction of warming and precipitation ( $p = 0.03$ ). Woody community analysis using stem abundance showed a strong reaction to warming alone ( $p = 0.005$ ) and potential canopy species composition may also be affected by a warming\*precipitation interaction ( $p = 0.056$ ). In general, Shannon-Weiner biodiversity, evenness, and total or growth form species richness were not affected by our treatments. At mid-summer, forb cover was lowered by the precipitation treatment and woody vegetation increased with warming. Total cover was generally reduced by the interaction of

warming and precipitation. Even though functional group percent cover responses to treatments were highly variable, both large tree cover and LAI were higher in the spring in warmed treatments. During this time period, the average day of leaf out on canopy tree species and tall forbs and the date of flowering for short forbs were advanced in warming treatments and together may have accounted for increased the spring LAI. Our results indicated that young post-harvest forests may have different species assemblages, cover and phenology under climate change scenarios. These effects of climate change could have large and long-lasting impacts on forest communities in the central Appalachians.

## Table of Contents

<b>List of Figures.....</b>	<b>vii</b>
<b>List of Tables .....</b>	<b>viii</b>
<b>Acknowledgements.....</b>	<b>x</b>
<b>Chapter 1: Project Background and Methods .....</b>	<b>1</b>
1.1. Introduction & Background .....	1
1.2. General Methods.....	4
1.2.a. Forest Regeneration and Climate Experiment Design.....	4
1.2.b. Data Collection and Analysis.....	11
1.3. Thesis Organization .....	13
<b>Chapter 2: Phenology.....</b>	<b>14</b>
2.1. Introduction .....	14
2.2. Methods .....	16
2.3. Results .....	17
2.3.a. Life History .....	17
2.3.b. Species Richness .....	19
2.3.c. Structure .....	24
2.4. Discussion.....	30
2.4.a. Life History .....	30
2.4.b. Species Richness .....	34
2.4.c. Structure .....	35
2.5. Ecological Implications.....	36
<b>Chapter 3: Community Composition and Characterization .....</b>	<b>38</b>
3.1. Introduction .....	38
3.2. Methods .....	40
3.2.a. Species assembly and biodiversity .....	40
3.2.b. Community structure .....	43
3.3. Results .....	43
3.3.a. Community Composition .....	43
3.3.b. Biodiversity .....	47
3.3.c. Structure .....	48
3.4. Discussion.....	51
3.4.a. Composition .....	51
3.4.b. Biodiversity .....	53
3.4.c. Structure .....	54
3.5. Ecological Implications.....	56
<b>Chapter 4: Synthesis .....</b>	<b>58</b>
<b>References.....</b>	<b>62</b>
<b>Appendix A: Species List and Functional Groups.....</b>	<b>68</b>

<b>Appendix B: Dates of Vegetation Inventory and LAI Measurements .....</b>	<b>72</b>
<b>Appendix C: Results of Statistical Tests for Phenology Chapter .....</b>	<b>73</b>
<b>Appendix D: Indicator Species Analysis Results.....</b>	<b>75</b>
<b>Appendix E: Average Cover of Species Used in Community Analyses.....</b>	<b>79</b>
<b>Appendix F: Peak Growing Season LAI and Cover RM-ANOVA Results.....</b>	<b>82</b>

## List of Figures

<b>Figure 1-1:</b> Location of the Forest Regeneration and Climate Experiment in Penn State's Stone Valley Forest. The dashed line is the approximate location of the deer fence.....	5
<b>Figure 1-2:</b> FORCE treatment plot schematic. Infrared heaters provided a target +1°C temperature increased during the day and +3°C at night. Non-heated plots had heater replicas to account for shading and water diversion effects.....	6
<b>Figure 1-3:</b> Daily average temperatures for the growing season 9 March (Julian day 67) – 9 November (Julian day 312). a) Daily average temperature (mean $\pm$ standard error) from ambient treatment plots during the growing season shows average temperatures ranging from almost 0° to >20°C. b) Daily average temperature deviation from ambient temperatures shows effectiveness of warming treatments elevating temperatures above ambient conditions and cooling effect of precipitation treatment. Error bars indicate standard error. ....	10
<b>Figure 2-1:</b> Average leaf out of functional groups relative to ambient leaf out. The Julian date (JD) for average leaf out in the ambient treatment is listed for each functional group and was calculated by averaging the first date of leaf out observation for all species belonging to that group at the plot level. Error bars show standard error and * indicates statistical warming effect at $\alpha = 0.05$ . ....	18
<b>Figure 2-2:</b> Interactive effects of warming and increased precipitation resulted in higher species richness in climate change simulations compared to the ambient treatment (repeated measures ANOVA, $p=0.0180$ ). Values presented are the average total species richness for each treatment $n=4$ ; plot size= 4 m <sup>2</sup> ). ....	20
<b>Figure 2-3:</b> Average entire community leaf area index revealed a strong heat effect that was dependent on day (repeated measures ANOVA, heat*day $p=0.0002$ ). Values depicted for each treatment are the mean ( $n=4$ ) of each treatment $\pm$ standard error. The vertical lines represent the average date of leaf out for the two functional groups that displayed earlier leaf out as a result of warming ( $p < 0.05$ ). Tall forb (TF) leaf out is shown with solid lines and large tree (LT) leaf out is represented by dashed lines. Average date of leaf out date under the two warming treatments (W) is shown in light gray and non-warmed treatments (N) in black. ....	25
<b>Figure 3-1:</b> Non-metric multidimensional scaling ordination of treatment plots (triangles) in species space (crosses). Axis 1 and 2 are based on the distribution of species and correspond to unknown plant traits or an environmental gradient. Treatment plots are labeled with treatments (a=ambient, b=heat+water, h=heat/warming only, w=water/precipitation only) and block (1-4). NMS used a relative Euclidean distance measure and average over of each species during the growing season. PerMANOVA results from a randomized complete block configuration where all four treatments were represented separately (RCB) and then paired by warming treatment (Paired) are shown. A full list of PerMANOVA results and treatment effects may be found in Appendix F. ....	45

## List of Tables

<b>Table 1-1:</b> Average temperature from 9 March (Julian day 67) – 9 November (JD 312) 2009, average temperature deviation from ambient, number of growing degree days (GDD5, average temperature > 5°C), number of days with non-freezing temperatures (T>0), date of last spring freeze (Last T<0), and first fall freeze (First T<0). Dates for first and last T<0 are Julian dates. Values presented are mean temperature ± standard error, n=4 for each treatment.....	8
<b>Table 2-1:</b> Average functional group species richness for different periods during the growing season. Julian dates ranges for surveys included in averages are listed in the left-hand column. Treatment codes are as follows: A = no additional heat or water, HW = +2°C, +20% precipitation, H = +2°C, W = +20% precipitation. Values presented are the treatment mean number of species of all surveys conducted within the time period listed at left ± standard error (n=4 for each treatment). Repeated measures analysis of variance (RM-ANOVA) was conducted using all 22 surveys without averaging (see appendix B for survey dates). Significant treatment and day effects are presented with the following code: W = warming, P = precipitation, D = Day, * = interaction. All effects significant at $\alpha = 0.05$ , see Appendix C for table of p-values. Larch and small tree richness were square root transformed (sqrt) for analysis.....	23
<b>Table 2-2:</b> Average functional group cover for different periods during the growing season. Julian dates ranges for surveys included in averages are listed. Treatment codes are as follows: A = no additional heat or water, HW = +2°C, +20% precipitation, H = +2°C, W = +20% precipitation. Values presented are the treatment mean of richness in all surveys occurring within the time period (n=4) ± standard error. Repeated measures analysis of variance (RM-ANOVA) was conducted using all 22 surveys without averaging (see appendix B for survey dates). Significant treatment and day effects are presented with the following code: H = heat, W = water, D = Day, * = interaction. Effects in () are significant at $\alpha = 0.05$ , all other effects are significant at $\alpha = 0.01$ , see Appendix C for p-values. Large tree and small tree cover were log transformed (log) for analysis. ....	29
<b>Table 3-1:</b> Average species richness and biodiversity for the each treatment based on surveys of 4 m <sup>2</sup> plots where n=4 for each treatment. Values presented are mean ± standard error. H' Index is the Shannon-Weiner biodiversity index and D Index indicates the Simpson's biodiversity index. ....	48
<b>Table 3-2:</b> Average leaf area index and functional group cover during peak season. The average of three leaf area index measurement and five cover observations for each plot between 181-223 were used to generate a single value for each plot for this table but used separately for repeated measures ANOVA (RM-ANOVA). Values presented are the mean ± standard error for each treatment, n=4. All significant effects at $\alpha = 0.05$ from RM-ANOVA are listed with the following treatment codes are as follows W = warming (+1°C day, +3°C night), P = precipitation (+20% long-term average, applied weekly), W*P = interaction of	

warming and precipitation, D = day. Log (large trees) indicates the data was long-transformed for analysis.....	49
<b>Table A-1:</b> List of all species found in research plots along with their functional group classification. All names are according to Rhoads & Block (2007).....	68
<b>Table E-1:</b> Average cover and distribution of all species used in analysis of biodiversity and community composition in Chapter 3. Values presented are the average cover from all observations during the 22 vegetation surveys. Species are listed by Genus or 4-letter codes that represent the first two letters of the genus and specific epithet (Appendix A). .....	79
<b>Table F-1:</b> Permutation multivariate analysis of variance p-values for all tests and community types indicate block and treatment effects vary by functional group class. Randomized complete block (RCB) design used block as a fixed effect and four separate treatment effects while the factorial design did not account for block but allowed analysis of interactive effects of heat and water. Plots were paired based on heat or water as a block effect with the remaining variable as a treatment effect if original RCB or factorial analyses were inconclusive. Values in bold highlight $p < 0.05$ .....	82

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## Chapter 1: Project Background and Methods

### 1.1. Introduction & Background

Central Appalachian forests provide a wide range of ecosystem services and serve as an important economic resource for the eastern United States, mostly through harvesting by the woody products industry. When left intact, forests provide additional economic benefits through ecosystem services such as carbon and nitrogen storage (Rose *et al.* 2000, Nabuur *et al.* 2007, Davidson *et al.* 2003). Understanding the potential long-term impacts of harvesting on eastern U.S. forest ecosystems is important for future forest management and will require consideration of potential climate change scenarios (Mitchell *et al.* 1997, Ross *et al.* 2000, McDermott & Wood 2009). The Appalachians provide a contiguous habitat corridor that is likely be important for species migration in the future as climate change causes suitable growing habitat and species distribution to shift northward (Bachelet *et al.* 2001, Iverson & Prasaad 2001). Climate-related migration could lead to higher biodiversity in some regions, but increased competition for resources could result in localized species extinctions or lower biodiversity (Iverson & Prasaad 2001, Lasch *et al.* 2002, Iverson *et al.* 2004). Ecosystem-level dynamics such as nutrient cycling and carbon storage could also be affected by increased temperatures and changes in vegetation community (Melillo *et al.* 2002).

Forest harvesting over the past century has strongly influenced central Appalachian ecology and will continue to do so in the future (Abrams 1998, Dale *et al.* 2001, Hansen *et al.* 2001, Nabuur *et al.* 2007, Rogers *et al.* 2008). Even though forest area increased at the beginning of the 20<sup>th</sup> century due to agricultural abandonment, intensive forest harvesting over

the past 30 years has created a net loss of forest cover in the eastern United States (Drummond and Loveland 2010). Alterations in the forest environmental brought on by timber harvesting exert selective pressures on species establishment in both the canopy and understory (Duffy & Meier 1992, Swanson *et al.* 2010). Initial floristic composition, stochastic species establishment, and post-harvest environmental conditions control early successional dynamics and control future forest development (Oliver & Larson 1996, Christensen & Gilliam 2003, Gilliam & Roberts 2003, Royo & Carson 2006, Gilliam 2007, Swanson *et al.* 2010). High resource availability following clear cut timber harvesting (i.e. all trees removed at once) may help facilitate the migration and establishment of new species and changes in existing species composition (Gilliam *et al.* 1995, Oliver & Larson 1996, Jenkens & Parker 2000, Small & McCarthy 2002, Iverson *et al.* 2004). Clear cut timber harvesting is a common practice throughout the eastern U.S. Species selection and climate effects on community dynamics early in succession are likely to be important mechanisms for forest response to climate change because young vegetation has been shown to be more sensitive to climate and environmental pressures than mature trees (Jackson *et al.* 2009). In central Appalachian deciduous clear cuts, many trees regenerate from stump or root sprouting. This advanced regeneration gives existing tree species a distinct advantage over species establishing by seed and creates a narrow window in time for new woody and herbaceous establishment (Oliver & Larson 1996). Because of these conditions, the critical period for species establishment is brief with high levels of biotic and environmental interactions including interspecific competition.

Experimental climate change research in forests is a growing field of research, but studies thus far have not occurred in post-disturbance systems. Most manipulative climate studies using open-air, *in situ* heating have focused on low-stature vegetation such as grasslands or alpine

systems (e.g. Price & Wasser 2000, Sherry *et al.* 2008,). Forest response to climate change has mostly been studied by comparing historical data to current systems, using open-top chambers, or computer simulations because of the large stature and long life spans of trees (e.g. McKenna-Easterling *et al.* 2000, Iverson & Prasad 2001, Beckage *et al.* 2008, Gunderson *et al.* 2010, Kardol *et al.* 2010b). Research using open air heating to investigate warming effects on forest succession has focused on old-field succession, which generally occurs more slowly, lacks advanced tree regeneration, and has different nutrient cycling dynamics than clear cut timber harvesting (Oliver & Larson 1996, Kardol *et al.* 2010a). Traditional forest succession research tends to overlook the role of non-tree vegetation that dominates early successional communities and can influence tree regeneration (Gilliam *et al.* 2007). To accurately understand ecosystem dynamics and the long-term implications of climate effects on forests, it is important to look at community-level responses (Gilliam 2007, Swanson *et al.* 2010).

In my thesis, I looked specifically at vegetation community dynamics under simulated climate change in a recent clear cut in central Pennsylvania. The climate simulation was designed to increase air temperature and weekly precipitation. The post-harvest community includes natural woody and herbaceous regeneration that established from root and stump sprouting, existing seed banks, and seed dispersal from the surrounding area. My research focused on two specific areas of community responses to simulated climate change: phenology and community composition and structure. The timing of life history events of individual species plays an important role in structuring a community (Morissette *et al.* 2009). To investigate potential effects of climate change on community phenology, I monitored species' life history events, richness, and community structure measures over the course of an entire growing season. Many of my measures of community change were analyzed on the whole-

community and functional group scales because community responses are likely to be driven by a few species or functional groups that encompass a suite of life history traits. I hypothesized that warming accelerates phenological events such as leaf out to occur which in turn may drive community patterns through altered community structure and interspecific competition. There are many ways to describe a community, but relying on a single measure is often insufficient and may overlook other aspects of community functioning. For this reason, I have used species assembly, biodiversity, balance of functional groups, and leaf area index to describe both the composition and structure of the community. I hypothesized that warming and increasing precipitation will allow certain species assemblages to perform and grow better and others poorly, leading to changes in species composition and the balance of functional groups.

## **1.2. General Methods**

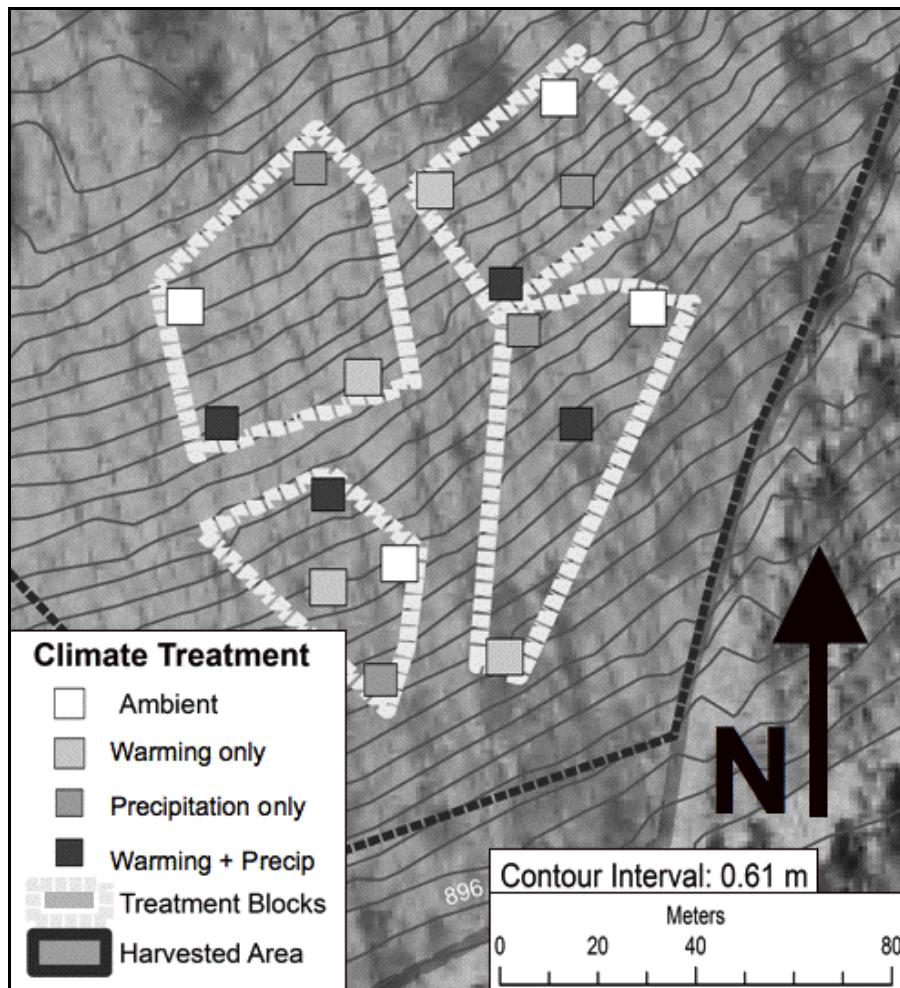
### **1.2.a. Forest Regeneration and Climate Experiment Design**

The Forest Regeneration and Climate Experiment (FORCE) is a set of *in situ* climate manipulations located in the Pennsylvania State University's Stone Valley Forest in Centre Country, PA (40N 85', 77W 83'). A two-hectare (4 acre) block of second growth oak-hickory forest was whole-tree harvested in August 2007. Following timber harvest a deer fence was erected. This is a common practice in central Pennsylvania due to the large deer population and negative impacts of deer browse on regenerating forest (Horsley *et al.* 2003). The site is situated on a southeast-facing slope. Average mean temperature at the site is 9°C with an average maximum of 15°C and minimum of 4°C throughout the year. The annual average maximum temperature is 27 °C and occurs in July, while the average minimum is -8°C in January. Mean

annual precipitation is approximately 100 cm and is evenly distributed throughout the year.

Soils in the site are Berks series with shale, siltstone, and fine grain sandstone origins.

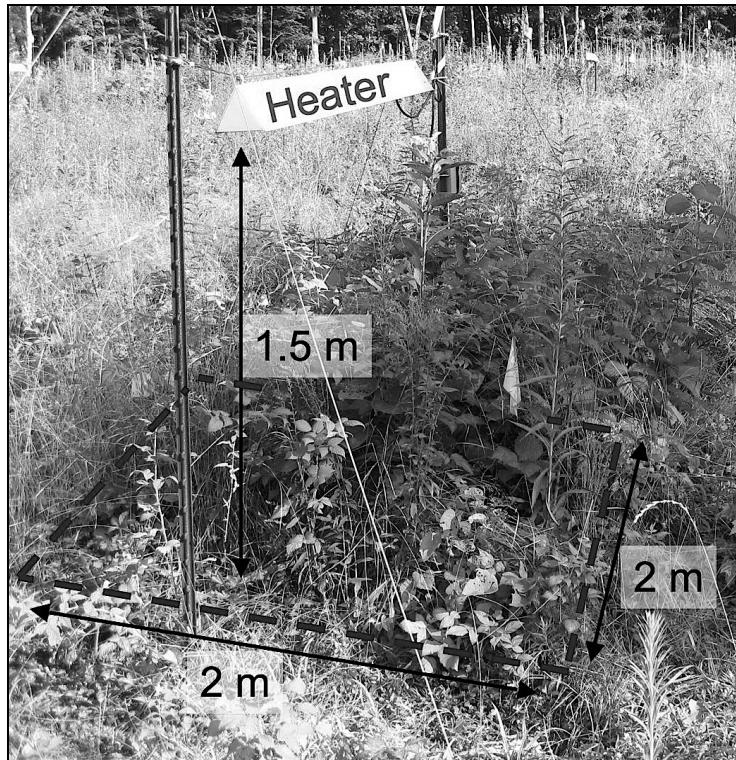
Sixteen 2 x 4 m plots climate treatment plots were established in the two-hectare research site in spring 2008 (Fig. 1-1). A 0.5 m plastic and wire mesh fence that was erected around in plot in spring 2009 to deter plant predation by rodents. Vegetation and soils in one-half of each plot (2 x 2 m) were left undisturbed to allow natural regeneration and vegetation recruitment from the propagule bank.



**Figure 1-1:** Location of the Forest Regeneration and Climate Experiment in Penn State's Stone Valley Forest. The dashed line is the approximate location of the deer fence.

### 1.2.a.i. Climate Treatments:

The experimental design is a 2-factorial randomized complete block design. Plots were arranged into 4 blocks with one plot of each of the following treatments (Fig. 1, described in detail below): ambient, warming only, precipitation only, warming + precipitation. Experimental plots that did not receive warming treatments (ambient and precipitation only) have heater replicas to control for non-heat effects of the structures. Heat treatments began in April 2008 and precipitation treatments began May 2008. The average surface temperature of the center of each plot was continuously monitored using infrared radiometer (IRR) sensors located at the top of posts used to suspend the heaters or heater replicas. Average plot surface temperature was recorded by a central control data logger and checked weekly for proper functioning.



**Figure 1-2:** FORCE treatment plot schematic. Infrared heaters provided a target  $+1^{\circ}\text{C}$  temperature increased during the day and  $+3^{\circ}\text{C}$  at night. Non-heated plots had heater replicas to account for shading and water diversion effects.

- **Ambient** plots served as an experimental control and received neither warming nor increased precipitation treatments, but had heater replicas to mimic installation disturbance and shading effects.
- **Warming only** plots received a constant daytime temperature increase of 1°C and 3°C temperature elevation night. The constant temperature differential was maintained using a real-time proportional-integrative-derivative (PID) feedback system. Temperature of warmed plots were recorded every 15 seconds using IRR sensors and referenced against the temperature of ambient plots to calculate the amount warming needed. Plots were warmed by 2 240V infrared heaters hung 1.5 m above the ground and powered by electricity supplied to the site from the regional electrical grid (Fig. 2, Kimball 2005). Similar methodology has been used in grassland and alpine experiments to study the effects of a warming climate (Price and Waser 2000, Wan et al. 2002, Wan et al. 2005).
- **Precipitation only** received weekly precipitation additions of 20% of the 120-year monthly historical average from State College, PA from the USGS Hydro-Climatic Data Network (<http://daac.ornl.gov/HYDROCLIMATOLOGY/hydroclimatology.shtml>). The amount of precipitation added each week was determined by the historical monthly average and was independent of actual weekly precipitation. April through December precipitation was added in the form of water collected in a series of rainwater catchments distributed throughout the site. In the winter months precipitation was collected in a series of plastic bins and distributed as water, ice, or snow, depending on the state at time of application.

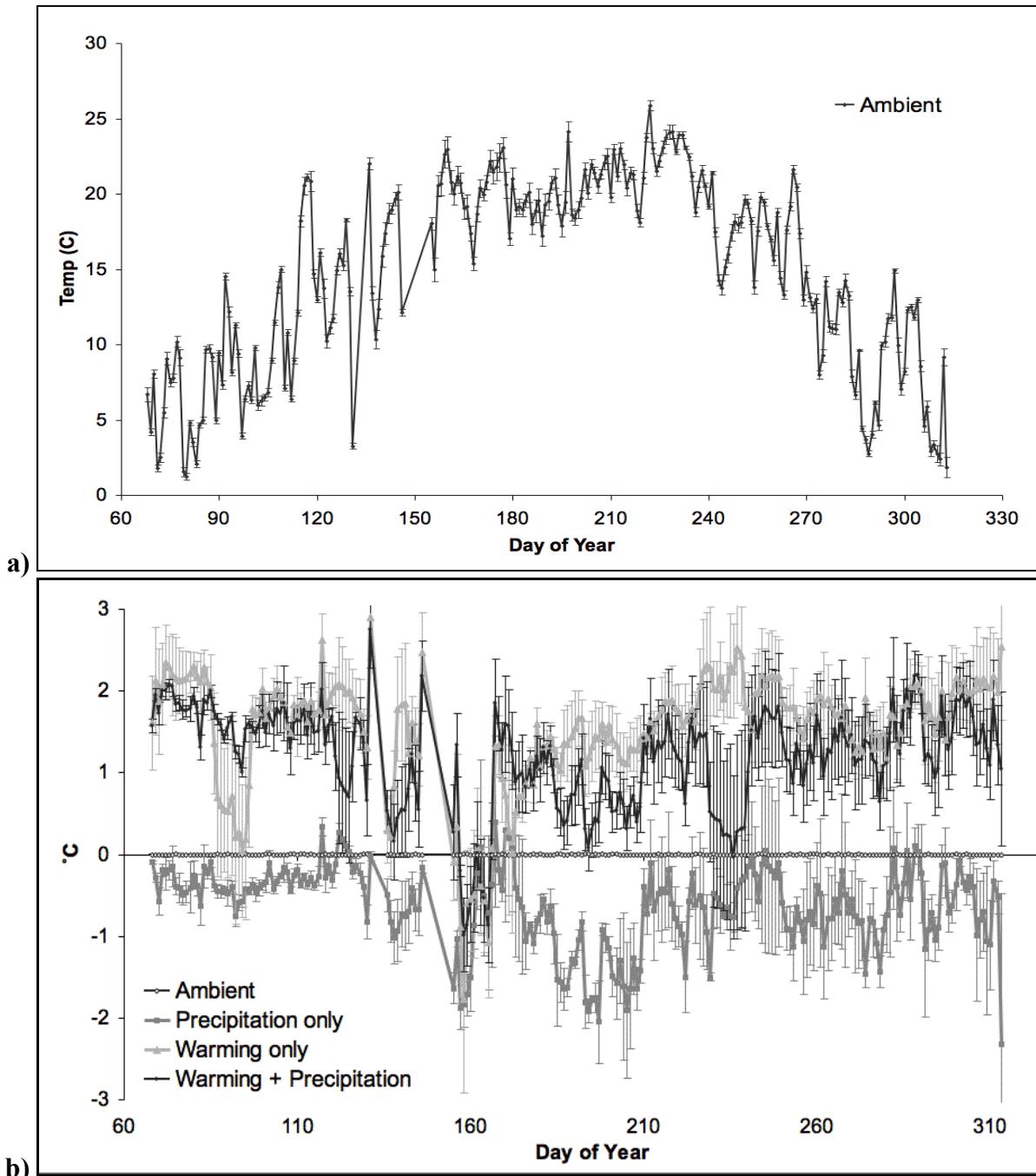
- **Warming + Precipitation** plots received both the warming and increased precipitation treatments. Target heating temperature for warming+precipitation plots was based on temperatures observed in water only plots.

I defined the growing season as early March through early November for my analyses and this period captures most spring leaf out and fall senescence. According to recorded IRR temperatures, the heaters raised the daily average temperature by  $1.23 \pm 0.01$  °C in warming+precipitation plots and  $1.59 \pm 0.01$  °C in warmed only (Table 1-1, Fig. 1-3) during the growing season while the water only treatment resulted in a lower temperature than ambient by 0.59°C. The highest summer temperatures were recorded on 10 August (Julian day 221) and range from an average of 34.6 °C in the water only plots to 38.2°C in the heat only plots. The lowest temperatures during the growing season occurred on 24 March (JD 82), with lows between -11.6°C in the water only plots and -8.2 °C in the heat only plots. Heated treatments had last frost dates 9-23 days earlier than non-heated heated treatments, while first fall frost occurred 5 days earlier than ambient in the water only treatments and 4-5 days later in heated treatments (Table 1-1).

**Table 1-1:** Average temperature from 9 March (Julian day 67) – 9 November (JD 312) 2009, average temperature deviation from ambient, number of growing degree days (GDD5, average temperature  $> 5$  °C), number of days with non-freezing temperatures ( $T > 0$ ), date of last spring freeze (Last  $T < 0$ ), and first fall freeze (First  $T < 0$ ). Dates for first and last  $T < 0$  are Julian dates. Values presented are mean temperature  $\pm$  standard error, n=4 for each treatment.

Treatment	Avg Daily Temp (°C)	Avg Dev from A (°C)	GDD5	Days T>0	Last T<0	First T<0
<i>Ambient</i>	$14.82 \pm 0.01$	$0 \pm 0.0$	$212 \pm 0.7$	$189 \pm 2.5$	$139 \pm 0.0$	$284 \pm 3.0$
<i>Precip only</i>	$14.19 \pm 0.02$	$-0.59 \pm 0.02$	$210 \pm 0.5$	$184 \pm 2.9$	$139 \pm 0.0$	$279 \pm 2.8$
<i>Warming only</i>	$16.36 \pm 0.01$	$1.59 \pm 0.01$	$225 \pm 1.7$	$209 \pm 1.3$	$130 \pm 7.8$	$289 \pm 1.4$
<i>Warm + Precip</i>	$16.01 \pm 0.02$	$1.23 \pm 0.01$	$223 \pm 1.2$	$210 \pm 2.6$	$116 \pm 8.1$	$288 \pm 1.3$

During the 2009 growing season, the research site received 69.86 cm of precipitation. The additional precipitation treatments added another 13.46 cm of rain, resulting in a 19.3% increase in precipitation over the course of the growing season. Weekly precipitation additions ranged from 0.28 – 0.38 cm and corresponded to weekly precipitation increases between 4.8% to >350%. There was only one week in 2009 during which I added precipitation treatment to the plots when no precipitation had fallen on the site.



**Figure 1-3:** Daily average temperatures for the growing season 9 March (Julian day 67) – 9 November (Julian day 312). a) Daily average temperature (mean  $\pm$  standard error) from ambient treatment plots during the growing season shows average temperatures ranging from almost 0° to  $>20^{\circ}\text{C}$ . b) Daily average temperature deviation from ambient temperatures shows effectiveness of warming treatments elevating temperatures above ambient conditions and cooling effect of precipitation treatment. Error bars indicate standard error.

### 1.2.b. Data Collection and Analysis

Between 24 March (Julian day 82) and 4 November (JD 307) 2009, 22 vegetation inventories of all plots were completed. I conducted weekly vegetation surveys from 24 March until 1 June to track emergence and life history during the spring growing season. Vegetation surveys occurred on a biweekly basis after June 1, at which point most species had emerged and established in the plots. All plants were identified according to Rhoads and Block (2007). Plants that were unidentifiable when first observed were flagged, numbered, and identified later in the season. In each survey, I recorded the percent cover and phenophase of all species present and density of woody stems by species. Percent cover was estimated in 1% increments between 1-20% and then in 5% increments above 20%. Estimates of less than 1% were recorded as 0.1%. A phenophase is an observable stage in a plant life cycle (USA National Phenology Network, [www.usanpn.org](http://www.usanpn.org)) and included: budburst (woody only), leaf out, flowering, ripened fruit/seed, and senescence. More details about phenophase criteria will be discussed in with phenology chapter of this thesis (section 2.2).

I identified 106 plants to species, an additional 8 to genus, and 21 “unknowns” remain unidentified (Appendix A) during the growing season. Most of the unknowns remain unidentified because they were not widely present in the research site and plot specimens did not survive to maturity as a result of competition early in the growing season or predation from small herbivores. All grass and sedge species were grouped and labeled as “grass” due to difficulty of identification. For the rest of this thesis I will use the term species loosely to refer to all plants identified in the course of my research, including those identified to the genus level or that remain unidentified. Species were divided into seven functional groups based on growth form to allow better comparison of plant responses across plots with different species composition. The

first division of species was based on general growth form: woody, grass, and forbs. Woody vegetation was divided into the following categories: large tree, small tree, shrub and vine. Forbs were classified as short forbs if maximum height for the species was less than 1m and tall forbs if the maximum height could be 1m or greater. Species were also noted as native, non-native, and invasive according to Rhodes and Block (2007).

Leaf area index (LAI) was measured for each plot at least once a month in full sun using an AccuPAR LP-80 PAR/LAI ceptometer from Decagon Devices, Inc (Pullman, WA). Two measurements offset 0.5 m from the outside plot edges and parallel to the slope were taken per plot and then averaged to obtain a single value per plot per day. LAI was calculated automatically along the 80 cm length of the ceptometer as a function of the average below-above canopy ratio ( $\tau_{au}$ ,  $\tau$ ) of photosynthetically active radiation (PAR, 400-700 nm wavebands), the fraction of beam radiation ( $F_b$ ), a leaf distribution constant ( $chi$ ,  $\chi$ ), and the zenith angle of the sun ( $z$ ) (Decagon Devices, Inc 2008). LAI is a measure of leaf density and can indicate light availability and the amount of competing vegetation above ground level. LAI can also be used as an approximation of above-ground biomass for between-plot comparisons. LAI provides a 3-dimensional assessment of structure, whereas percent cover is limited to 2-dimensions since the maximum cover for a single species is 100% even though it may have many layers of leaves. However, percent cover can be analyzed at the species level while the method used for LAI quantification is a community-level measure. Throughout my thesis, results presented are significant at  $\alpha=0.05$  unless otherwise noted.

### **1.3. Thesis Organization**

The remainder of my thesis has been split into two results chapters and a synthesis. Chapter 2 addresses life history phenology and seasonal patterns of species richness, cover, and leaf area index. Chapter 3 discusses community composition and structure. Each chapter will have a brief introduction, additional methods that primarily describe how data was analyzed, presentation of results and a discussion. The final chapter of my thesis is a synthesis that brings together overarching themes of the two results chapters and the implications of my research.

## Chapter 2: Phenology

### 2.1. Introduction

The study of phenology has recently gained a lot of attention for its role in structuring ecological communities and as a potential mechanism for ecosystem response to climate change (Morisette et al 2009). Climate change over the past century, and in particular the past 30 years, has caused earlier spring green-up in many systems across the globe (Menzel *et al.* 2006, Shwartz *et al.* 2006, Gordo & Sanz 2010). In the eastern United States, spring leaf out has advanced at an average rate of 1.2 days per decade since 1955 (Schwartz *et al.* 2006). Earlier leaf out appears to be driven by increased spring and winter temperatures of as much as 0.6°C per decade during this time period (Schwartz *et al.* 2006). Unlike other organisms, plants are sessile and individuals cannot move to cope with changing environmental stress. Trees face an additional challenge because their long life cycles lead to a slow rate of genetic drift and adaptation to environmental pressures. To compensate, many trees and other taxa have developed phenological plasticity and responses to environmental cues such as temperature to control the timing of leaf out (Schlitzting 1986).

Regulation of plant phenology and developmental plasticity varies by species, so responses to increased temperature will not be uniform and may change community dynamics (Lechowicz 1984, Thompson & Naeem 1996, van der Meer *et al.* 2002). Specifically, species or functional group responses to climate change could alter community composition and structure over the course of the growing season. Altering life history timing could create a mismatch between resource availability and demand, causing cascading effects throughout the ecosystem (Durant et al 2007). For example, if increased temperature causes some plants to flower sooner,

but the phenology of their primary pollinators does not shift at the same time, both plant and pollinator may be negatively impacted by the asynchrony.

Whole-community phenology studies thus far have been rare due to logistical considerations and the difficulty of scaling local observations to a landscape scale. Filling this gap is an essential component to future assessment of community responses to climate change (Morin & Thuiller 2009). My research experimentally increases both temperature and precipitation in a factorial design, allowing direct observation of the effects of these two climate factors and interactions on species and functional group phenology. Impacts of climate on life history events such as leaf out and flowering can then be connected with community-level patterns such as species richness, percent cover and leaf area index.

I hypothesized that warming will cause some life history events such as bud burst, leaf out, and flowering to occur earlier in the season. Based on long-term average temperature, a 2°C increase in temperature should cause events such as the date of last spring freeze to occur two weeks earlier in the warming treatments. If temperature is a driving cue for phenology, plants in warmed plots should complete phenophase transitions two weeks earlier than plants growing in the ambient temperature. I hypothesized that increased water will have little or no effect on phenology. If there is an effect, I expect it to delay phenology due to cooling from evapotranspiration. I also hypothesized that effects of heat will be more apparent early in the growing season than during the summer or fall. In the spring, low minimum temperatures deter growth of many plants. Increasing the temperature of these plots through active heating may remove a temperature-based limitation on growth and allow some species to leaf out sooner or have greater competitive success early in the season. Earlier emergence of at least some plants should result in increased cover, leaf area index and species richness in the heated treatments.

Later in the spring and summer, nighttime temperatures do not typically approach freezing and so the impact of heat will be less apparent.

## 2.2. Methods

All data collected through the growing season was used to analyze the effects of simulated climate change on the phenology of life history events and seasonal community dynamics (see methods, sect 1.2). Functional group and total species richness and cover as well as LAI were analyzed using a PROC MIXED repeated measures analysis of variance (RM-ANOVA) in SAS 9.2 (SAS Institute 2008). In instances where a warming\*day interaction was significant, a least-squares means effect slice was used to determine time frames where treatment effects were significant. All results presented are significant at  $\alpha = 0.05$  unless otherwise noted. The experimental unit for all analyses was plot-level functional group or community data. Analyses were performed on 3-way interactions between warming treatment ( $+1^{\circ}\text{C}$  day,  $+3^{\circ}\text{C}$  night), precipitation treatment ( $+20\%$  long-term monthly average, applied weekly) and day of year (repeated function).

Dates of first observed leaf out and flowering phenophases of forbs and bud burst and leaf out of woody vegetation were used to analyze life history phenology. Leaf out of forbs was determined by the presence of mature, photosynthetically capable vegetation, which usually coincided with the first recorded observation for each forb. Flowering phenophase was defined by having any flowers open for pollination. Woody bud burst phenophase was noted if any vegetation had emerged from the bud scales and the plant did not meet the criteria for being leafed out. Leaf out for woody vegetation was defined by the presence of at least three fully green, partially lignified leaves that appeared capable of photosynthesis. All phenophases

present were recorded for each species. These phenophase definitions are similar to what is used by phenology monitoring organizations such as the USA National Phenology Network ([www.usanpn.gov](http://www.usanpn.gov)).

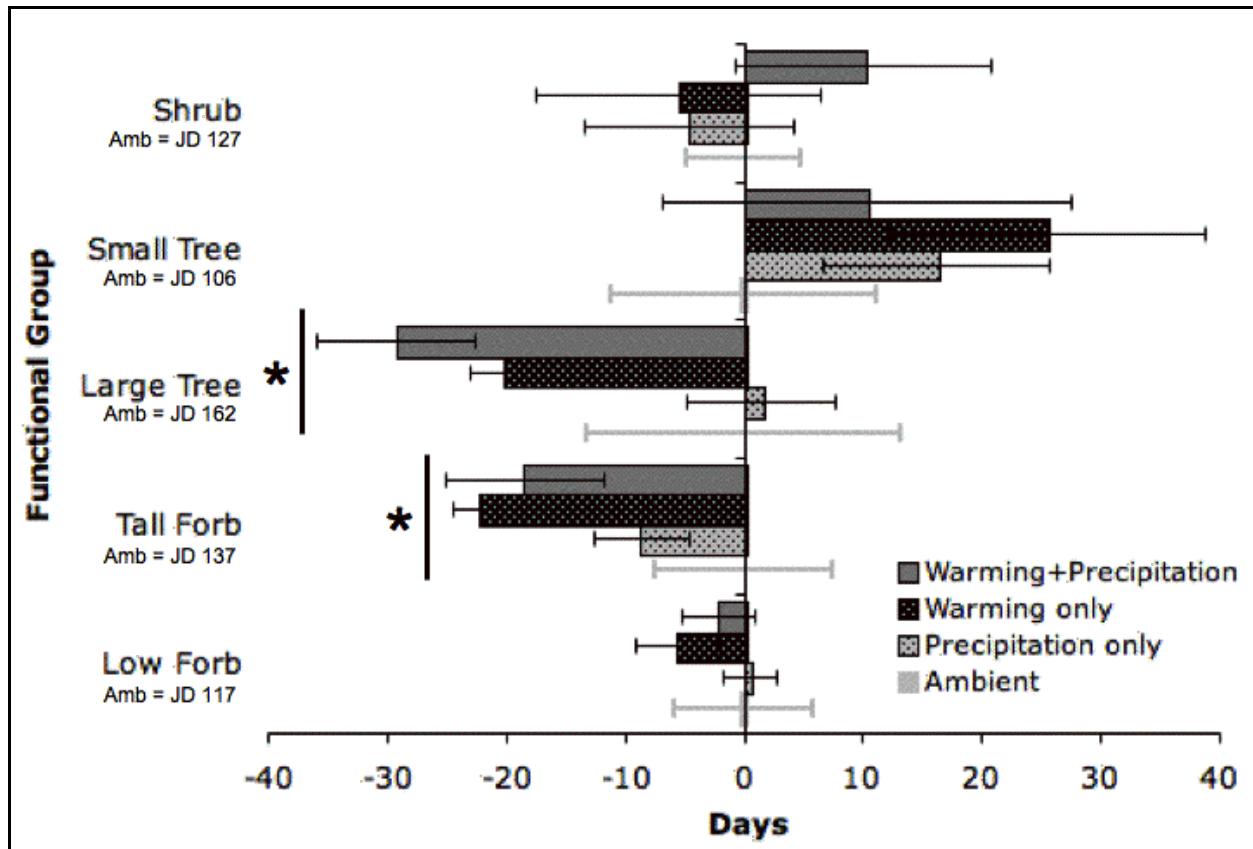
Life history phenology was analyzed at the functional group level. The average date of phenophase onset for each group was calculated by averaging the date of first observation for each species belonging to that group in a plot. I then used ANOVA to analyze treatment effects on the average date of phenophase observation of the functional group using this plot-level data. Because species were unevenly distributed across the landscape, I was unable to directly compare changes in phenology of individual species.

## 2.3. Results

### 2.3.a. Life History

Although forbs as a whole emerged 10 days earlier in response to warming ( $p = 0.0225$ ), this response was specifically driven by a strong response of tall forbs (Fig. 2-1,  $p = 0.0238$ ). General forb leaf out observation in ambient averaged 6 May (JD 125)  $\pm$  13.26 days (mean  $\pm$  standard error) and precipitation only on 3 May (JD122)  $\pm$  3.2 days. Forb leaf out in warming only plots averaged 11 days earlier than ambient, on 25 April (JD 114)  $\pm$  3.8 days, and warming+precipitation plots averaged one day later at 26 April (JD 115)  $\pm$  2.2 days. The tall forb functional group leafed out 2.5-3 weeks earlier than ambient in warming treatments. Tall forb leaf out averaged 25 April (JD 114)  $\pm$  4.5 days in warming only plots and 29 April (JD 118)  $\pm$  13.2 days in warming+precipitation. Short forb leaf out observation occurred slightly early than tall forbs, but was not affected by warming. Average short forb leaf out ranged from 21

April (JD 110)  $\pm$  6.9 days in the warming only treatment to 27 April (JD 116)  $\pm$  4.5 days in precipitation only treatment and was not affected by warming.



**Figure 2-1:** Average leaf out of functional groups relative to ambient leaf out. The Julian date (JD) for average leaf out in the ambient treatment is listed on the left for each functional group and was calculated by averaging the first date of leaf out observation for all species belonging to that group at the plot level. Error bars show standard error and \* indicates statistical warming effect at  $\alpha = 0.05$ .

Only short forbs displayed earlier flowering under warming treatments ( $p=0.0055$ ). The average short forb flowering date was 7 June (JD 157)  $\pm$  5.9 days in ambient plots and 8 June (JD 158)  $\pm$  6.0 days in precipitation only. Flowering in warming plots occurred an average of 10 days earlier, ranging from 28 May (JD 147)  $\pm$  7.3 days in warming+precipitation treatment to 29 May (JD 148)  $\pm$  4.7 days in warming only. In contrast to leaf out, warming did not cause tall forbs to flower noticeably earlier ( $p = 0.2440$ ). Average tall forb flowering began on 26 July (JD

206)  $\pm$  12.1 days in ambient plots and ranged from 11 July (JD 191)  $\pm$  5.9 days in warming+precipitation treatment to 27 July (JD 207)  $\pm$  8.4 days in precipitation only.

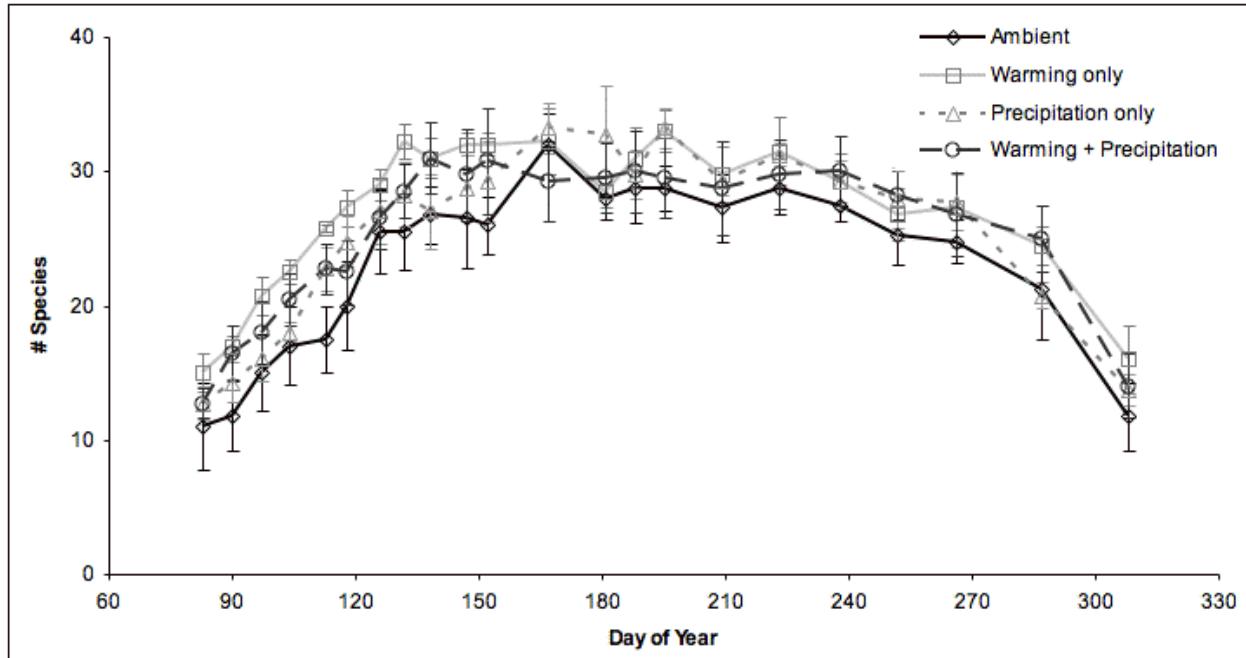
Bud burst of woody plants occurred 3-8 days earlier than ambient in all treatments (warming\*precipitation  $p=0.0498$ ) and was driven by a uniformly moderate response of all functional groups. Bud burst occurred in ambient treatment on 20 April (JD 109)  $\pm$  5.5 days, and was preceded by warming+precipitation (17 April/JD 106  $\pm$  5.2 days) and precipitation only (15 April/JD 104  $\pm$  3.5 days). Warming only treatment had the earliest budburst, averaging 12 April (JD 101)  $\pm$  2.6 days. No individual woody functional groups showed treatment effects on budburst.

Of the three major woody functional groups, only large trees displayed earlier leaf out as a result of increased temperature (Fig. 2-1,  $p = 0.0087$ ). Under ambient temperature conditions, large trees leaf out occurred after shrubs, small trees, and herbaceous vegetation (11 June/JD 161  $\pm$  26.4 days in ambient and 13 June/JD 163  $\pm$  12.5 days in precipitation only). In warmed plots, large tree leaf out occurred 19-28 days earlier than ambient and at the same time as other woody and herbaceous functional group leaf out. Large tree leaf out in warming treatments averaged 14 May (JD 133)  $\pm$  13.3 days in warming+precipitation and 23 May (JD 142)  $\pm$  5.4 in warming only.

### **2.3.b. Species Richness**

Interactive effects of warming and precipitation treatments slightly increased total species richness above what was found in the ambient treatments (Fig. 2-2,  $p = 0.0180$ ). Total species richness during the growing season was relatively low (11-15 species) in the first survey, increased until mid-May, and remained relatively steady at 24-28 species until late summer and

fall (Table 2-1). Average species richness for ambient plots peaked at  $27.5 \pm 2.2$  species (mean  $\pm$  standard error), but generally ranged 24-27 species for most of the growing season. Precipitation only had an average maximum richness of  $29.3 \pm 0.9$  species, warming only plots had a maximum average richness of  $29.8 \pm 1.2$ , and warming+precipitation plots had an average maximum richness of  $28.5 \pm 2.0$  species. The warming only treatment had a trend towards higher species richness, but this did not statistically differ from warming effects at other points in the season. Furthermore, increased temperature and precipitation did not affect cumulative species richness or the rate at which species appeared during the growing season.



**Figure 2-2:** Interactive effects of warming and increased precipitation resulted in higher species richness in climate change simulations compared to the ambient treatment (repeated measures ANOVA,  $p=0.0180$ ). Values presented are the average total species richness for each treatment  $n=4$ ; plot size =  $4 \text{ m}^2$ .

Tall and short forb functional group species richness accounted for roughly two-thirds of the total species richness throughout the growing season (Table 2-1). Even though the warming only treatment had higher species richness than ambient, interactive effects with water resulted in

total forb richness at any point in time to be similar (warming\*precipitation  $p = 0.0003$ ). Tall and short forb functional groups responded differently to warming and precipitation treatments. Short forbs displayed a similar pattern as forbs as a whole where warming increased richness, but interacted with the precipitation treatment, which generally decreased richness (warming\*precipitation  $p = 0.0383$ ). However, species richness was not widely different among treatments and ranged from  $4.8 \pm 1.1$  species in March and had a maximum average richness of  $11.0 \pm 0.8$  species. Tall forb species richness started at  $2.0 \pm 0.6$  species in the beginning of the season in the ambient plots, peaked at  $6.0 \pm 1.7$  species, and was increased by both warming and precipitation treatments (warming\*precipitation  $p = 0.0004$ ). During the growing season, warming or precipitation only treatments had on average 1-2 more species than ambient treatment, while warming+precipitation tall forb richness was similar to ambient.

Total woody species richness was also affected by the combination of warming and precipitation ( $p = 0.0275$ ) and was the result of varying functional group responses. During the growing season, woody species richness in ambient grew from an average of  $2.0 \pm 1.4$  species at the beginning of the season to a peak of  $9 \pm 1.5$  species. Warming+precipitation consistently increased total richness by 1-2 species above ambient throughout the growing season, and warming tended to have a consistent effect of increasing richness only in the spring. As with forbs, species richness of woody functional groups responded differently to warming and increased precipitation. Shrub richness was higher with both increased temperature and precipitation (warming\*precipitation  $p < 0.0001$ ). Warming also resulted in a one species increase in large tree species richness ( $p = 0.0007$ , square root transformed). Small tree richness was showed a statistically significant response to the heat\*water interaction ( $p < 0.0001$ ), but low

functional group species richness (1-2 species, square root transformed for analysis) made it difficult to discern consistent directionality of the effects.

**Table 2-1:** Average functional group species richness for different periods during the growing season. Julian dates ranges for surveys included in averages are listed in the left-hand column. Treatment codes are as follows: A = no additional heat or water, HW = +2°C, +20% precipitation, H = +2°C, W = +20% precipitation. Values presented are the treatment mean number of species of all surveys conducted within the time period listed at left  $\pm$  standard error ( $n=4$  for each treatment). Repeated measures analysis of variance (RM-ANOVA) was conducted using all 22 surveys without averaging (see appendix B for survey dates). Significant treatment and day effects are presented with the following code: W = warming, P = precipitation, D = Day, \* = interaction. All effects significant at  $\alpha = 0.05$ , see Appendix C for table of p-values. Large and small tree richness were square root transformed (sqrt) for analysis.

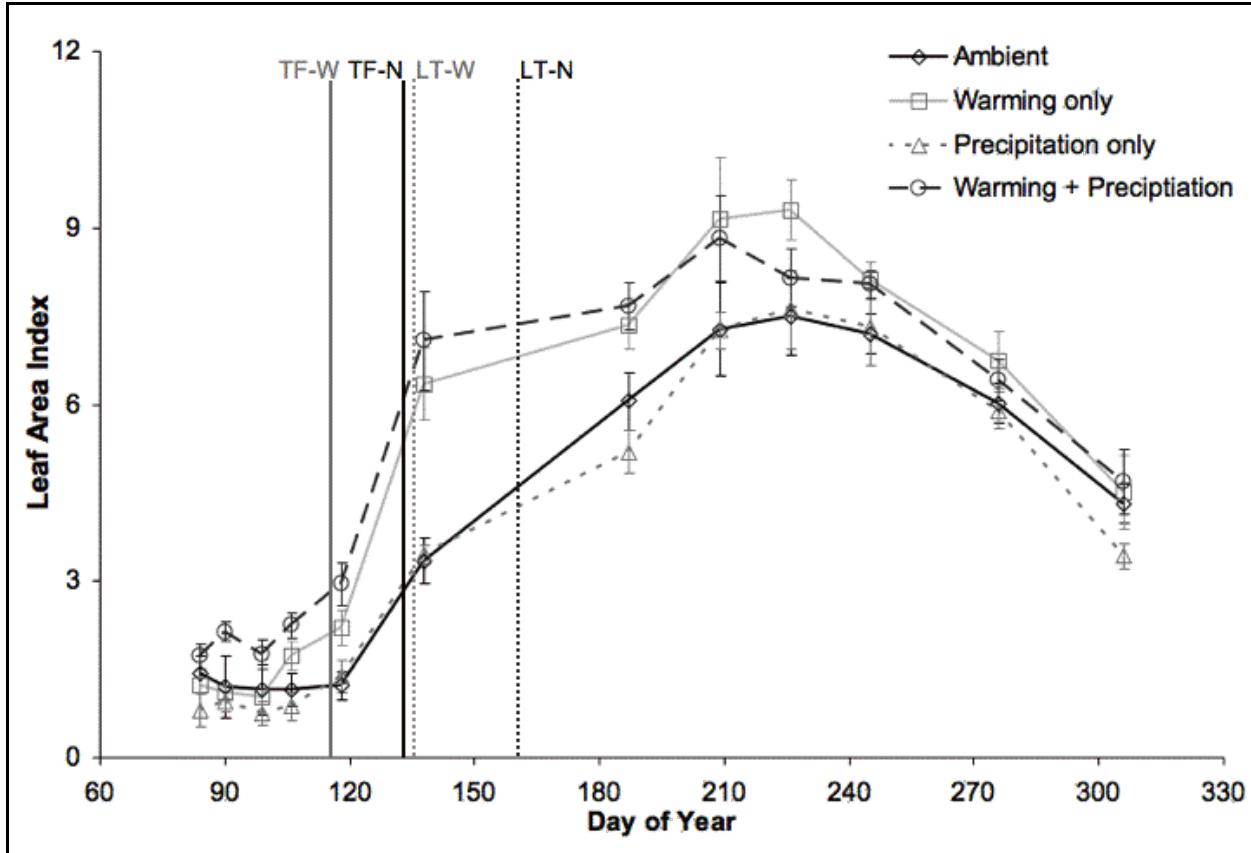
		Total Richness	Forb Total Richness	Tall Forb	Short Forb	Woody Total Richness	Large Tree	Small Tree	Shrub
JD 83- 145	A	14.9 $\pm$ 3.0	10.6 $\pm$ 2.5	3.0 $\pm$ 0.9	7.0 $\pm$ 1.6	3.2 $\pm$ 0.8	1.3 $\pm$ 0.6	1.1 $\pm$ 0.4	1.3 $\pm$ 0.3
	HW	16.5 $\pm$ 1.7	12.0 $\pm$ 1.4	4.4 $\pm$ 1.0	7.4 $\pm$ 0.7	3.4 $\pm$ 0.1	1.8 $\pm$ 0.3	1.1 $\pm$ 0.1	1.7 $\pm$ 0.2
	H	18.3 $\pm$ 1.0	13.1 $\pm$ 1.2	4.7 $\pm$ 0.9	8.3 $\pm$ 1.4	4.2 $\pm$ 0.6	1.7 $\pm$ 0.1	0.8 $\pm$ 0.5	2.3 $\pm$ 0.2
	W	15.3 $\pm$ 0.9	11.3 $\pm$ 0.9	4.0 $\pm$ 0.5	7.3 $\pm$ 0.9	3.0 $\pm$ 0.4	1.9 $\pm$ 0.4	0.0 $\pm$ 0.0	2.4 $\pm$ 0.3
JD 151- 223	A	24.7 $\pm$ 2.9	15.3 $\pm$ 2.1	5.0 $\pm$ 1.6	9.4 $\pm$ 1.3	7.6 $\pm$ 1.5	3.0 $\pm$ 0.7	1.3 $\pm$ 0.5	2.3 $\pm$ 0.5
	HW	25.8 $\pm$ 1.9	15.4 $\pm$ 0.9	5.4 $\pm$ 0.9	9.1 $\pm$ 1.1	9.0 $\pm$ 0.9	4.0 $\pm$ 0.9	1.5 $\pm$ 0.3	2.7 $\pm$ 0.4
	H	28.0 $\pm$ 1.0	18.0 $\pm$ 1.5	6.5 $\pm$ 0.7	10.9 $\pm$ 1.6	8.3 $\pm$ 1.1	3.6 $\pm$ 0.7	1.0 $\pm$ 0.4	2.9 $\pm$ 0.4
	W	24.1 $\pm$ 1.3	16.5 $\pm$ 1.0	6.3 $\pm$ 0.9	9.7 $\pm$ 0.9	6.3 $\pm$ 0.3	2.3 $\pm$ 0.4	0.5 $\pm$ 0.3	3.1 $\pm$ 0.3
JD 226- 308	A	25.5 $\pm$ 1.6	15.4 $\pm$ 1.4	5.0 $\pm$ 1.7	9.8 $\pm$ 0.7	8.3 $\pm$ 1.1	3.4 $\pm$ 0.5	1.3 $\pm$ 0.5	2.3 $\pm$ 0.3
	HW	27.3 $\pm$ 2.4	14.8 $\pm$ 1.2	5.8 $\pm$ 0.8	8.5 $\pm$ 0.8	10.8 $\pm$ 1.2	4.7 $\pm$ 1.1	1.5 $\pm$ 0.3	3.1 $\pm$ 0.3
	H	27.7 $\pm$ 1.5	17.5 $\pm$ 1.7	6.5 $\pm$ 1.3	10.3 $\pm$ 1.3	8.7 $\pm$ 1.2	3.8 $\pm$ 0.8	1.0 $\pm$ 0.4	2.8 $\pm$ 0.3
	W	27.8 $\pm$ 0.9	17.8 $\pm$ 1.0	7.4 $\pm$ 1.1	9.8 $\pm$ 1.6	8.2 $\pm$ 0.2	3.5 $\pm$ 0.4	0.7 $\pm$ 0.4	3.2 $\pm$ 0.3
RM-ANOVA		W*P, D	W*P, D	W*P, D	W*P, D	W*P, D	W*P, D (sqrt)	W, D (sqrt)	W*P, D

### 2.3.c. Structure

Although warming increased leaf area index throughout the growing season, the effects were most pronounced early in the growing season (Fig. 2-3). A warming\*day RM-ANOVA effect ( $p = 0.0002$ ) indicated that effects of heat were not uniform during the growing season, and least squares mean effect comparisons of LAI at individual dates revealed significant warming effects occurred from 16 April (JD 106) through 14 August (JD 226). Even though LAI was greater in warmed treatments, light availability at ground level was low in all treatments after canopy establishment in June. During late spring and summer, photosynthetically active radiation (PAR) at ground level was typically  $<100 \mu\text{mol}/\text{m}^2\text{s}$  in all treatments while PAR above the vegetation canopy was  $>1000 \mu\text{mol}/\text{m}^2\text{s}$ . Percentage of PAR penetration (ground level PAR divided by above canopy PAR) ranged 0-5% among treatments during the summer. Total cover did not show the same day-dependent warming effects as LAI and instead showed increased temperature and precipitation acting independently of day (warming\*precipitation  $p < 0.0001$ ). Total cover in ambient plots started at  $89.8\% \pm 24.1\%$  and peaked at  $344\% \pm 46.4\%$ . Water only had lower total cover than other treatments throughout the growing season (Table 2-2). Warming+precipitation had the highest cover of all treatments in the spring and then ambient had highest cover for the summer and fall.

**Table 2-2:** Average functional group percent cover for different periods during the growing season. Julian dates ranges for surveys included in averages are listed. Treatment codes are as follows: A = no additional heat or water, HW = +2°C, +20% precipitation, H = +2°C, W = +20% precipitation. Values presented are the treatment mean of richness in all surveys occurring within the time period (n=4)  $\pm$  standard error. Repeated measures analysis of variance (RM-ANOVA) was conducted using all 22 surveys without averaging (see appendix B for survey dates). Significant treatment and day effects are presented with the following code: W = warming, P = precipitation, D = Day, \* = interaction. All effects are significant at  $\alpha = 0.05$ , see Appendix C for p-values. Large tree and small tree cover were log transformed (log) for analysis.

		Total Cover	Forb Total	Tall Forb	Short Forb	Woody Total	Large Tree	Small Tree	Shrub	Grass
JD 83- 145	A	101.8 $\pm$ 17.9	56.2 $\pm$ 21.8	6.7 $\pm$ 5.2	50.4 $\pm$ 20.1	3.4 $\pm$ 1.8	1.7 $\pm$ 1.6	0.6 $\pm$ 0.3	1.8 $\pm$ 1.2	42.4 $\pm$ 15.9
	HW	119.6 $\pm$ 13.2	50.7 $\pm$ 17.1	17.5 $\pm$ 4.8	33.1 $\pm$ 21.3	1.7 $\pm$ 0.7	0.9 $\pm$ 0.4	0.1 $\pm$ 0.1	1.2 $\pm$ 0.5	67.2 $\pm$ 11.9
	H	95.1 $\pm$ 17.3	45.8 $\pm$ 17.3	5.4 $\pm$ 2.2	40.3 $\pm$ 15.8	5.6 $\pm$ 1.6	0.3 $\pm$ 0.1	0.0 $\pm$ 0.0	4.7 $\pm$ 1.4	43.5 $\pm$ 5.7
	W	53.0 $\pm$ 3.8	10.8 $\pm$ 2.3	2.7 $\pm$ 0.8	8.1 $\pm$ 2.3	1.4 $\pm$ 0.3	0.1 $\pm$ 0.1	0.0 $\pm$ 0.0	1.4 $\pm$ 0.3	40.8 $\pm$ 4.9
JD 151- 223	A	197.4 $\pm$ 11.4	101.1 $\pm$ 22.7	9.3 $\pm$ 3.8	91.5 $\pm$ 26.3	43.9 $\pm$ 18.8	13.0 $\pm$ 8.4	3.8 $\pm$ 2.0	26.1 $\pm$ 16.4	52.4 $\pm$ 8.8
	HW	198.1 $\pm$ 19.4	93.8 $\pm$ 23.1	41.5 $\pm$ 12.2	50.6 $\pm$ 30.8	36.4 $\pm$ 5.0	12.6 $\pm$ 2.0	4.3 $\pm$ 1.1	17.1 $\pm$ 3.9	67.5 $\pm$ 10.2
	H	184.7 $\pm$ 7.7	87.6 $\pm$ 19.9	23.6 $\pm$ 5.7	63.0 $\pm$ 19.5	55.1 $\pm$ 13.5	11.8 $\pm$ 6.0	0.8 $\pm$ 0.6	34.8 $\pm$ 7.5	42.1 $\pm$ 7.2
	W	132.6 $\pm$ 12.3	52.4 $\pm$ 15.1	20.4 $\pm$ 9.1	31.2 $\pm$ 8.4	27.5 $\pm$ 6.8	2.4 $\pm$ 0.6	0.7 $\pm$ 0.1	24.4 $\pm$ 6.8	52.6 $\pm$ 4.8
JD 226- 308	A	276.2 $\pm$ 29.8	145.0 $\pm$ 36.6	16.3 $\pm$ 6.7	128.1 $\pm$ 41.9	72.8 $\pm$ 19.1	18.8 $\pm$ 6.7	5.8 $\pm$ 3.4	37.8 $\pm$ 17.2	58.4 $\pm$ 14.0
	HW	245.0 $\pm$ 19.0	99.4 $\pm$ 26.3	39.7 $\pm$ 10.4	58 $\pm$ 31.3	71.7 $\pm$ 11.2	22.8 $\pm$ 4.3	8.9 $\pm$ 2.5	30.7 $\pm$ 6.7	87.9 $\pm$ 11.0
	H	252.1 $\pm$ 2.8	115.0 $\pm$ 25.8	32.2 $\pm$ 8.6	81.8 $\pm$ 24.5	99.0 $\pm$ 28.0	23.3 $\pm$ 12.1	1.2 $\pm$ 0.8	49.4 $\pm$ 10.8	39.2 $\pm$ 6.9
	W	209.3 $\pm$ 15.4	89.6 $\pm$ 16.9	38.8 $\pm$ 10.2	40.6 $\pm$ 14.2	68.2 $\pm$ 13.5	15.9 $\pm$ 4.3	1.7 $\pm$ 1.3	49.3 $\pm$ 11.2	51.5 $\pm$ 5.0
RM- ANOVA	W*P, D	W*P, D	W, P, D	W*P, D	W*P, D	W*P, W*D (log)	W*P, D (log)	W*P, D	W*P, D	W*P, D



**Figure 2-3:** Average entire community leaf area index revealed a strong heat effect that was dependent on day (repeated measures ANOVA, heat\*day  $p=0.0002$ ). Values depicted for each treatment are the mean ( $n=4$ ) of each treatment  $\pm$  standard error. The vertical lines represent the average date of leaf out for the two functional groups that displayed earlier leaf out as a result of warming ( $p < 0.05$ ). Tall forb (TF) leaf out is shown with solid lines and large tree (LT) leaf out is represented by dashed lines. Average date of leaf out under the two warming treatments (W) is shown in light gray and the two non-warmed treatments (N) in black.

Forb cover over the entire growing season was generally decreased by interactive effects of warming and precipitation treatments (Table 2-2,  $p = 0.0034$ ). Total forb cover in ambient plots ranged from  $46.0\% \pm 16.6\%$  in the first vegetation survey to a peak  $179.5\% \pm 46.9\%$  at the end of the summer. Even though forb cover was initially similar in ambient and both warming treatments (precipitation only treatment started lower at  $10.0\% \pm 4.3\%$ ), all warming and precipitation treatments had lower forb cover than ambient by early summer. Forbs were generally the dominant functional group, accounting for 25-50% of total cover among treatments

at the beginning of the growing season, and roughly 45% in all treatments by early summer. Although all warming and precipitation treatments tended towards lower relative forb cover than ambient, precipitation treatment had the strongest effect and caused relative cover to drop from  $40.8\% \pm 6.0\%$  to  $28.5\% \pm 10.5\%$  in warming+precipitation over the course of the summer and precipitation only to drop  $46.2\% \pm 6.9\%$  to  $36.4\% \pm 10.7\%$ . Relative forb cover in ambient plots increased from  $45.6\% \pm 10.2\%$  to  $54.9 \pm 9.7\%$  during the summer and fall.

As with phenology and species richness, cover of tall and short forbs responded differently to warming and precipitation treatments (Table 2-2). Short forb cover was consistently decreased by interactive effects of heat and water ( $p = 0.0043$ ). In ambient plots short forb cover accounted for most of total forb cover and ranged from  $34.3\% \pm 14.6\%$  early in the season to a peak of  $158.9\% \pm 51.0\%$ . In contrast, short forb cover ranged  $36.6\% \pm 16.5\%$  to  $108.8\% \pm 35.2\%$  in warming only,  $30.0\% \pm 22.8\%$  to  $66.0\% \pm 41.5\%$  in warming+precipitation, and  $6.4\% \pm 5.1\%$  to  $84.0\% \pm 37.1$  in precipitation only. Warming and precipitation treatments both increased tall forb cover independently ( $p < 0.0001$  each). Precipitation treatments showed the greatest increases in tall forb cover compared to short forbs with peaks of  $46.8\% \pm 10.9$  in warming + precipitation and  $43.0\% \pm 11.0\%$  in precipitation only compared to  $43.6 \pm 10.4\%$  in warming only and  $22.4\% \pm 13.0\%$  in ambient.

Total grass cover was increased by a combination of warming+precipitation, but lowered by warming only or precipitation only treatments (warming\*precipitation  $p < 0.0001$ ). Grass cover did not change throughout the growing season as much as other functional groups and averaged  $50.8\% \pm 11.2\%$  in ambient,  $38.71 \pm 2.87$  in warming only,  $46.3 \pm 1.0$  in precipitation only, and  $39.2 \pm 9.8\%$  in warming+precipitation for the entire growing season. Relative cover of grasses decreased over the course of the growing season as woody and forb functional groups

increased in cover and dominance. Relative cover grass cover was generally increased by precipitation treatments with relative cover dropping over the course of the growing season from  $74.2\% \pm 14.5\%$  in the first survey to  $22.6 \pm 3.1\%$  in October in precipitation only and  $69.7\% \pm 13.0\%$  to  $34.3\% \pm 6.7\%$  in warming+precipitation. Relative grass cover in the ambient treatment started at  $50.1\% \pm 14.1\%$  and ended with  $14.4\% \pm 5.0\%$  during this time period, while warming only dropped from  $69.3\% \pm 11.8\%$  to  $9.8\% \pm 3.9\%$ .

Total woody cover was generally increased by warming only treatment, but was moderated and had interactive effects with precipitation treatment (warming\*precipitation  $p = 0.0508$ ). All woody cover began at 0% in the spring before leaf out, but peaked at  $94.5\% \pm 35.3\%$  in ambient plots,  $101.0\% \pm 17.3\%$  in warming+precipitation, and  $91.7\% \pm 14.9\%$  in precipitation only. Warming only had the highest total woody cover with a peak of  $136.8\% \pm 37.0\%$ . Like total cover, relative cover of woody vegetation was increased by interactive effects of warming and precipitation ( $p = 0.0013$ ). Relative cover of woody vegetation started at 0% in all treatments before spring before leaf out and then remained relatively stable following canopy establishment in mid-summer. Maximum relative cover of woody vegetation in ambient plots was  $34.5\% \pm 12.4\%$ ,  $38.9\% \pm 5.1\%$  in warming+precipitation,  $43.2\% \pm 8.4\%$  in precipitation only, and  $46.6\% \pm 10.6\%$  in warming only.

Woody functional groups also displayed highly varied cover responses to increased temperature and precipitation, but generally showed increased cover with warming only or warming+precipitation treatments (Table 2-2). Large tree cover showed a similar pattern as LAI, where warming increased cover early in the growing season (warming\*day  $p = 0.0001$ , log transformed data). Throughout the rest of the growing season, warming appeared to generally increase large tree cover while interactive effects with precipitation appeared to lower cover

(warming\*precipitation  $p = 0.0018$ , log transformed data). Large tree cover peaked at  $28.3\% \pm 11.0\%$  in the ambient treatment,  $23.3\% \pm 6.1\%$  in precipitation only,  $28.6\% \pm 5.2\%$  in warming+precipitation, and  $30.25\% \pm 14.0\%$  in warming only. Small tree cover was generally lowered by warming or precipitation alone, but raised by the combination of the two factors (warming\*precipitation  $p = 0.0004$ , log transformed data). Small tree cover in ambient plots peaked at only  $11.4\% \pm 5.7\%$ , whereas precipitation only peaked at  $3.0\% \pm 2.0\%$ . The maximum cover for small trees in warming+precipitation was  $11.3\% \pm 3.5\%$ , which is lower than ambient, but throughout most of the growing season, warming+precipitation plots had higher small tree cover. Shrubs, like other functional groups, also showed interactive effects of warming and precipitation ( $p = 0.0023$ ), but contrasted with small trees in that warming or precipitation had higher cover than ambient, whereas the combination warming+precipitation had lower cover. Maximum shrub cover in the ambient treatment was  $57.8\% \pm 28.0\%$ , while warming only peaked at  $66.0\% \pm 14.0\%$ , precipitation only  $73.0\% \pm 18.6\%$ , and warming+precipitation peaked at  $47.5\% \pm 9.4\%$ .

## 2.4. Discussion

I hypothesized that warming would accelerate the onset of important phenological events and alter seasonal patterns of community characteristics such as species richness, vegetation cover, and leaf area. In general, I expected events such as leaf out and season progression of plant cover to occur approximately 2 weeks under simulated climate warming. This prediction was based on historical average daily temperatures for the region and the timing of events such as last spring freeze. Warming only plots averaged  $1.59 \pm 0.01$  °C above ambient temperatures and warming+precipitation averaged an increase of  $1.23 \pm 0.01$  °C above ambient (Table 1-1). The warming treatments caused 10-15 more growing degree-days than non-warmed plots and last frost occurring 9-23 days earlier. The increased precipitation only treatment could affect phenology through an average cooling of  $0.59 \pm 0.02$  °C compared to ambient temperatures. This cooling effect translated into fewer growing degree-days, but did not affect the average date of last frost in the spring. In the following sections I will discuss how these treatment effects may be related to plant and community phenology.

### 2.4.a. Life History

My observations of earlier leaf out in a warmer climate supports my hypothesis and the conclusions of other studies, but may indicate greater temperature sensitivity and variability of functional group responses of leaf out than previously documented. General woody and forb leaf out occurred approximately 10 days early with a nearly 2°C temperature increase. Previous phenological studies using satellite imaging suggested that this temperature increase should only

correspond to a four-day advance. While phenological patterns are likely to vary greatly between years based on actual temperature and precipitation, 2009 spring average temperatures and precipitation amounts were very similar on a monthly basis to the long-term averages. My research suggests that functional group or species traits play an important role in controlling community phenological responses to warming. Even though forbs and woody vegetation as a whole exhibited earlier leaf out under warming, this pattern was strongly influenced by specific responses of functional groups within these broad categories. Tall forbs were the only forb functional group to show earlier leaf out even though short forb flowering occurred earlier in warming treatments. Similarly, even though woody leaf out occurred earlier in warmed treatments, large trees were the only functional group to show responses in this way.

The 18-22 day earlier leaf out of tall forbs may be explained by life history characteristics of this functional group. The tall forb functional group was dominated by plants that emerge, grow, and flower later in the season than short forbs. For example, the *Solidago* genus generally possesses these characteristics and was well represented throughout my research plots. In contrast, the short forb functional group includes most spring ephemerals and early season flowering plants and showed no effect of heat on timing of emergence. Several common members of the short forb functional group, such as *Veronica officinalis*, *Geum canadensis*, and *Potentilla canadensis*, were able to maintain mature green vegetation (a leafed out phenophase) through the winter or produce leaves very soon after snow melt and before I started monitoring vegetation. As a result, my estimates of warming effects on short forb leaf out do not include accurate assessment of these evergreen or semi-evergreen species and may be an incomplete measure of the potential impacts on early season phenology for this functional group. It is also possible that many short forb species that do not maintain green leaves through the winter

may rely more on light cues to determine spring green up. This could be an adaptation to avoid some of the disadvantages of phenotypic plasticity such as emerging during an unusual warm spell and then be killed by a subsequent frost (Morin *et al.* 2009). Spring ephemerals have a narrow window of high light availability to complete most of their life-history cycle. Frost damage during this time could be more detrimental to plants with short, early season life cycles than species that will complete most of their lifecycles over the course of the summer and fall. Tall forbs typically emerge later in the season, often after the last frost, and therefore may not depend on light-based growth cues but rely more on temperatures. Over time, earlier leaf out of tall forbs would reduce the temporal niche that short forbs fill and could reduce the success of short forbs through increased competition for light and nutrients earlier in the season. Even though light and temperature based controls of plant growth are known to exist, little progress has been made in classifying such physiological mechanisms in the wide diversity of central Appalachian forests and my proposed mechanisms for my observed phenological responses to warming are highly speculative (Lechowicz 1984).

Altered timing of flowering was also observed and could influence long-term community dynamics. In contrast to patterns in leaf out, short forbs flowered 10 days earlier with increased temperature, even though leaf out was not affected. There are several possible explanations for why flowering of short forbs responded to treatments without a similar shift in emergence. As mentioned above, one explanation may be that at least some short forb species are able to retain green vegetation through the winter and as a result do not show changes in timing of spring leaf out. Flowering signals may also be independent of the environmental cues for leaf out and may rely on stored energy for flowering production. Increased temperatures after leaf out may allow more efficient photosynthesis and result in less time to accumulate the necessary energy for leaf

out than plants growing under ambient conditions. Long-term reproductive success and population viability of short forbs will rely on photosynthesis efficiency and pollinator availability during the earlier flowering. If the timing of leaf-out, flowering, and pollinator availability are decoupled, species that flower earlier could have lower levels of reproduction and will potentially be at risk under climate change scenarios. Other research has found increased temperature to cause earlier flowering of species that bloom before the peak summer temperature and later flowering of species that flower in late summer (Sherry *et al.* 2007). I did not observe either earlier or later flowering of tall forbs in response to warming to support the hypothesis of delayed late-season flowering in response to increased temperatures. This may have been the result of reduced sampling later in the growing season if it was too infrequent to accurately capture late-season phenology.

Earlier leaf out of large trees deters the growth of species that rely on a high light environment and reduced competition early in the growing season to succeed. Even though seedling and sprouts of large trees may be small early in succession, they can rapidly dominate the canopy upon leaf out and shade out other plants for most of their lifespan. Under ambient climate conditions, most understory vegetation emerges before tree leaf out and can take advantage of a narrow window of high light availability and suitable growing temperatures before tree canopy development. An advance in the rate of large tree leaf out would lower light levels on the forest floor, inhibit low-stature plant growth, and could result in accelerated transition from an open, herbaceous-dominated community to a woody-dominated self-thinning forest. Earlier leaf out may benefit large trees by extending their growing season, but it may also put them at greater risk for frost damage from a hard spring freeze (Morin *et al.* 2009).

## 2.4.b. Species Richness

Warming and increased precipitation did not clearly affect the phenology of species richness. The rate at which new species were added to the community and the cumulative species richness were not significantly different among treatments, nor was there higher species richness in the spring. However, the trend towards increased spring woody species richness in warming treatments is easily explained by earlier budburst observed in the warming treatments. Even though the phenology of community species richness was not affected by warming or precipitation treatments, general patterns of treatment effects on species richness over the course of the growing season still provide useful ecological information. Most functional groups showed treatment effects on species richness throughout the season, but the direction of treatment effects varied highly by functional group. Some functional groups such as tall forbs and large tree had higher species richness in plots receiving heat treatments. Earlier leaf out of these two functional groups may have allowed more species to establish than is normal due to less competition and greater resource availability during establishment. Short forb species richness was consistently lower in water treatments. Lowered richness could be the result of increased competition inhibiting species establishment or that the area was no longer suitable growing habitat for some species because of altered environmental conditions such as increased soil moisture or cooler spring soil temperatures.

Unfortunately, low plot-level species richness of some functional groups calls into question the ecological significance of statistical treatment effects on species richness. Monitoring species richness in 4 m<sup>2</sup> may not accurately reflect large-scale community patterns for some large stature and low-density functional groups such as large and small trees. It is likely that I would need a larger study to adequately capture and assess the relationship between

of biodiversity, climate change, and ecosystem functioning for functional groups with such low plot-level diversity.

### **2.4.c. Structure**

The seasonal pattern of leaf area index shows the strongest evidence in support of the hypothesis that warming is more important during the spring “buffer season” when daily temperatures are slightly lower than optimal for leaf expansion. The observed warming\*day interaction indicates non-linear, time-dependent effects increased LAI more in the spring than in the summer or fall. Increased spring LAI is likely driven by the earlier leaf out of large trees and tall forbs. Increased spring cover of large trees provides evidence that these species may gain a competitive advantage through earlier leaf out, especially because they do not face as much pressure for vertical growth to establish in the canopy as other functional groups and can allocate growth accordingly. Tall forb cover may not have been affected by warming early in the growing season because many tall forbs grow from a large basal rosette in a very columnar form that does not expand in area until flowering occurs much later in the season. As a result, percent cover of tall forbs does not change greatly even though they may help drive the warming-based LAI increase as they grow vertically and add dense leaf area. However, separate warming and precipitation treatments may have phenology-based reasons for increasing tall forb cover. Warming may have provided a growth advantage in the spring through earlier growth that was able to persist throughout the season. Increased precipitation may have helped alleviate water limitation, particularly in the summer when water stress is more common.

Earlier leaf out of tall forbs and large trees may also be driving changes in functional group dominance (relative cover) and community structure during the growing season. Warming

appeared to increase tall forb and large tree cover and is likely the result of earlier leaf out. Increased cover of these groups may have lowered relative forb cover through lowered short forb cover, the dominant forb functional group, through competition. Dominance of woody vegetation was increased by warming and precipitation treatments and corresponded to a decrease in forb dominance with these same factors. Higher relative cover of grass due to increased precipitation may also have contributed to relative forb cover or filled an empty niche that developed through reduced forb cover. However, I cannot determine whether greater competition from woody vegetation and grasses under simulated climate change is driving lower forb cover or if altered environmental conditions reduces forb habitat quality.

## **2.5. Ecological Implications**

Simulated climate change alters several aspects of early successional community phenology and may have important long-term implications. Earlier leaf out of large trees and tall forbs appears to drive increased LAI, especially early in the growing season and may be key factors controlling community development. Greater success of these two functional groups may also cause reduced success of other functional groups such as short forbs. Temperature appears to be the most important factor controlling the onset of life history events, although water is important for other community dynamics, and in particular forbs. Many short forbs such as *Viola spp.* and *Veronica spp.* may be more sensitive to precipitation because they possess shallow rooting systems that may predispose them to early onset of water stress. My results indicating that water availability is the dominant organizing force for forb communities supports similar climate change research in other community types (Sherry *et al.* 2007, Kardol *et al.* 2010). I observed a 10-day advance in leaf out in response to warming, which is less than my predicted 2

week advance, but is greater than the 4 day advance of green-up that would be expected based on historically observed rates for the eastern United States (Shwartz *et al.* 2006). This suggests that changes in phenology in response to warming may be stronger than previously expected and could have large consequences for plant communities. I did not explicitly analyze late season phenology, but other research has indicated that increased temperature may also cause an extended fall growing season (Schwartz *et al.* 2006, Sherry *et al.* 2007).

My results indicate temperature as a primary mechanism driving phenological responses, but related environmental conditions such as soil nutrient availability could also be involved (Cleland *et al.* 2006). Nutrient availability may be affected directly by both warming and precipitation, but will likely be mediated by vegetation responses such as the timing of demand and community composition (Neufeld & Young 2003, Lovett *et al.* 2004, Donath & Eckstein 2008). However, components that play a role in ecosystem functioning are tightly linked and it may be impossible to say that climate affects on one component drive the responses of the others. Effects of future climate change will likely vary widely among systems and through time as a result of community and region-specific factors that control particular ecosystem characteristics and responses (Zhang *et al.* 2007). Despite this, my research does contribute experimentally tested evidence that climate change is likely to affect community-level phenology and may be an important mechanism driving early successional forest responses to climate change.

## Chapter 3: Community Composition and Characterization

### 3.1. Introduction

Disturbances can result in altered community composition and structure by aiding the establishment of new species through high resource availability and unoccupied niches (Dale *et al.* 2001, Iverson *et al.* 2004). Early successional community dynamics can provide valuable insight into long-term ecosystem processes and forest development (Swanson *et al.* 2010). For example, biodiversity is often used as an indicator of ecosystem health and the loss of even a few species could result in important changes in ecosystem function (Chapin *et al.* 1997, Naeem *et al.* 1999, McCann 2000, Symstad *et al.* 2003). Species assemblages early in succession can act as ecological filters, selecting for or against certain species, and create different developmental trajectories of vegetation communities (George & Bazzaz 1999a, George & Bazzaz 1999b, George & Bazzaz 2003, Royo & Carson 2006). Species selection by community composition can be created by competition for resources such as light, water, and nutrients, direct inhibition mechanisms such as allelopathy, or facilitation (Lovett *et al.* 2004, Royo & Carson 2006). Forest succession is often defined from the perspective of dominant tree species such as oaks (*Quercus spp.*) and maples (*Acer spp.*), even though early successional communities are high in biodiversity and dominated by non-tree vegetation (Christensen & Gilliam 2003, Gilliam & Roberts 2003, Royo & Carson 2006). Herbaceous vegetation responses to disturbance and climate are often more plastic than woody species and may provide greater information on community-level effects of climate change than focusing solely on woody species (Neufeld & Young 2003).

Subtle changes in succession brought on by a warming climate and altered precipitation regimes could have long-lasting impacts on community composition, biodiversity, and structure. Early successional forests are likely to show greater response to climate change because young vegetation is more sensitive to environmental pressures than a mature forest and there is no single dominant growth form after tree removal (Jackson *et al.* 2010). Models linking climate and current species habitat suitability predict a northward movement of species habitat and will likely cause actual species distributions to shift in response (Bachelet *et al.* 2001, Iverson & Prasaad 2001). Some tree species have already migrated to higher elevations over the past 50 years in response to climate change and others may have already expanded their ranges northward as well (Beckage *et al.* 2008, Woodall *et al.* 2009). However, observational and experimental studies have shown the rates of migration to be slower than models predict (Price & Waser 2000, Beckage *et al.* 2008). Disturbances may be necessary to facilitate migration and catalyze compositional change for long-lived systems like forests (Iverson *et al.* 2004, Dale *et al.* 2001, Nabuur *et al.* 2007, Hansen *et al.* 2001).

My research experimentally investigates the potential impacts of increased temperature and precipitation on early successional community composition, floristic diversity, and structure to understand how forest communities and post-harvest succession may be affected by climate change. I hypothesized that both increased temperature and precipitation will result in unique species assemblages by selecting for species better adapted to the simulated climate. Models have shown tree community composition to be affected by climate change, but herbaceous vegetation in forest succession has thus far not been included in models (Iverson & Prasad 2001, McKenney-Easterling *et al.* 2000). I expected woody community composition to be controlled by the location of stumps and advanced regeneration and not show large compositional

differences on small scales (Ilisson & Chen 2010). Due to the stochasticity of herbaceous community establishment, I expected greater treatment effects on herbaceous community composition. I also hypothesized that increased temperature and precipitation would increase biodiversity because my experiment simulated a moderate climate change that might not be dramatic enough to inhibit the establishment of already thriving species. Similarly, I hypothesized that increased temperature and precipitation would result in higher total vegetation cover and leaf area index, but with woody and herbaceous functional groups responses controlled by different climate factors.

### **3.2. Methods**

Data collected from the weekly and biweekly vegetation surveys (see sect. 1.2) were used to analyze community composition, biodiversity, and structure. Community species assemblages and biodiversity were calculated using a subset of data from the entire season to reduce observer error (sect. 3.2.a, below). Community structure included total percent cover and leaf area index as well as cover of tall forbs, short forbs, large trees, small trees, and shrubs for the peak growing season (30 June – 14 August, see sect. 3.2.b)

#### **3.2.a. Species assembly and biodiversity**

Species that were not consistently identified in each plot in sequential vegetation surveys were eliminated from analysis of species assembly and biodiversity. For each experimental plot, I removed all species that were found in less than two surveys or were found with more than one survey gap between observations if only observed twice. For example, if a species was found in

the third and fourth or fifth surveys of the season it remained in the data matrix. If the species was only observed in one survey or on the third and sixth surveys, it was removed and not included in analyses of community composition and biodiversity. At the end of this trimming process there were 118 species remaining, representing 83 genera (Appendix A). Eighty-five species were herbaceous, 11 of which remain unidentified, and 33 were woody. After trimming the data to reduce observer error, percent cover for each species in a plot was averaged to create a single value for use in composition and biodiversity analyses (Appendix E). This cover value for each species creates both presence-absence data and an indicator of average dominance during the growing season. The end of season stem density (23 September/Julian day 265) for each species was used as an additional method of analyzing the woody community. Stem density is a more common method of analyzing woody communities and complements average cover as a measure of dominance.

Non-metric multidimensional scaling (NMS), permutation multivariate analysis of variance (PerMANOVA), and indicator species analysis were used to analyze the effect of treatments on community species assembly. NMS is a non-parametric ordination method that provides a graphical representation of the similarity in community composition among experimental units in multi-dimensional space. NMS is preferred to other ordination methods such as canonical correspondence analysis or redundancy analysis because it works well with high diversity systems, can use a variety of distance measures for different approaches to community analysis, and does not assume normal continuous distribution of species or linear relationships between variables (Clarke 1993, McCune & Grace 2002). PerMANOVA is a non-parametric method used to quantitatively analyze treatment effects on overall community composition. As with NMS, PerMANOVA is better suited for analyzing community data than

discriminant analysis or MANOVA because most community data is inherently non-normal and relationships between variables is often non-linear. Indicator species analysis complements PerMANOVA by using presence-absence and dominance (average cover) of each species to determine if the presence or dominance of one or more species is indicative of a particular treatment (McCune & Grace 2002).

Biodiversity was analyzed using four different measures in order to provide a more robust analysis of community biodiversity properties. The following four measures were used to indicate different properties of total community biodiversity: Shannon-Weiner biodiversity ( $H'$ ), Simpson's biodiversity (D), evenness and species richness. Species richness indicates how many total species belong in the community or each functional group while evenness provides a measure of how equally distributed dominance is among the number of species. Shannon-Weiner biodiversity index uses both species richness and evenness to provide a single number that is commonly used to indicate biodiversity and is calculated using the equation  $H' = \sum p_i * \ln p_i$  where  $p_i$  represents the fraction of the community (relative cover) represented by each species. Simpson's biodiversity index is typically used to indicate community beta-diversity and is calculated using  $D = \sum p_i^2$ .

Community species assembly and biodiversity were calculated using PC-ORD and statistically compared using a Proc Mixed ANOVA in SAS 9.2. I used a relative Euclidean distance measure, which is commonly used in ecological community analysis, for NMS and perMANOVA analyses. PerMANOVA analysis was performed using a randomized complete block design (RCB-PerMANOVA with four treatments) and two-factorial (heat\*water) PerMANOVA configurations. In cases where neither one of these configurations yielded

significant results, the blocks were split into pairs based on one treatment factor (heat or water) and the complete block configuration was run again to test for the remaining treatment effect.

### **3.2.b. Community structure**

For analysis of community structure I only used data from field observations during the peak growing season (30 June/Julian day 180 – 14 August/JD 225) to reduce time-dependent treatment effects and make the results comparable to most plant community composition research that is based on data collected only during the summer. I used 30 June – 14 August as the peak season because this period maintained relatively high and stable species richness, percent cover, and leaf area index. This period includes five vegetation surveys and three measurements of leaf area index (Appendix B). Stem abundance for woody functional groups is based on data from 23 September (JD 265) when stem density was highest. Percent cover and LAI were analyzed using repeated measures analysis of variance (RM-ANOVA) in SAS 9.2.

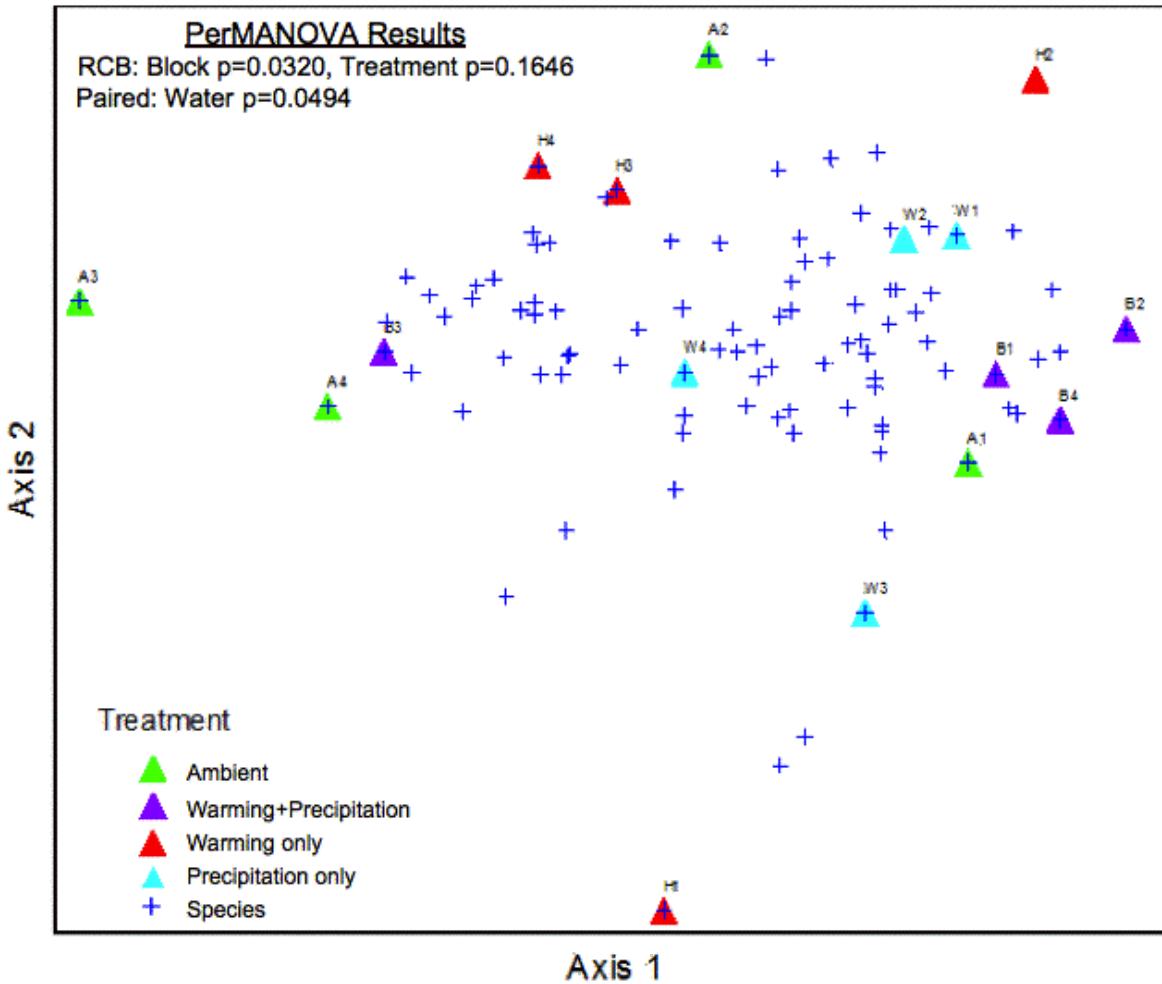
## **3.3. Results**

### **3.3.a. Community Composition**

Few of the 118 species found in the treatment plots had sufficient distribution and treatment responses to act as indicator species. Only 4 of 85 herbaceous species and 2 of 33 woody species were useful indicator species. Grass ( $p = 0.0508$ ) and *Prunus serotina* ( $p = 0.0270$ ) were more common in the warming+precipitation treatment, while *Sympyotrichum lavae* ( $p = 0.0140$ ) and *Vitis spp.* ( $p = 0.0478$ ) were associated with warming only. More

broadly, increased cover of *Vitis spp.* could indicate the presence of warming ( $p = 0.0498$ ), *Amphicarpa bracteata* (0.0202), and *Symphyotrichum laeve* ( $p = 0.0050$ ) were associated with plots that do not receive increased precipitation treatment, and *Erechtites hieraciifolia* ( $p = 0.0488$ ) was associated with increased precipitation. A few other species that tended towards higher cover in certain treatments included *Epilobium ciliatum* ( $p = 0.0748$ , no warming), *Taraxacum officinale* ( $p = 0.0820$ , increased precipitation) and *Vitis spp.* ( $p = 0.0736$ , no precipitation increase). Indicator species scores for all species can be found in Appendix D as well as average cover and distribution in Appendix E.

NMS ordination of the overall community showed stronger grouping of our climate manipulation treatments than ambient, but clustering by treatment was generally not very tight (Fig. 3-1). A randomized complete block (RCB) design PerMANOVA using average cover of species over the course of the growing season revealed that block had an strong influence on community composition ( $p = 0.0320$ ). Community composition was altered by the precipitation treatment, within the context of these block effects ( $p=0.0494$ ).



**Figure 3-1:** Non-metric multidimensional scaling ordination of treatment plots (triangles) in species space (crosses). Axis 1 and 2 are based on the distribution of species and correspond to unknown plant traits or an environmental gradient. Treatment plots are labeled with treatments (a=ambient, b= warming+precipitation, h=heat/warming only, w=water/precipitation only) and block (1-4). NMS used a relative Euclidean distance measure and average over of each species during the growing season. PerMANOVA results from a randomized complete block configuration where all four treatments were represented separately (RCB) and then paired by warming treatment (paired) are shown. A full list of PerMANOVA results and treatment effects may be found in Appendix F.

The herbaceous community represented the majority of species found in my research and strongly influence patterns observed at the whole-community level. The most common herbaceous species include *Galium aparine*, *Galium triflorum*, *Geum canadense*, *Potentilla canadensis*, *Solidago canadensis*, *Veronica officinalis*, and *Viola spp.* None of these species

displayed any treatment effects on their distribution or average cover. Even though block influence on herbaceous community composition is weaker than for the whole community ( $p = 0.0676$ ), block and warming treatment must be accounted for to detect the weak effect of increased precipitation on herbaceous composition ( $p=0.0540$ ).

The most common and well-represented woody taxa include *Fraxinus spp.*, *Rubus spp.*, and *Vitis spp.*, of which only *Vitis* performed better in a single treatment (warming only). Most species of common economic and ecological interest unfortunately had poor distribution among treatments and were often absent from at least one treatment combination. For example, no *Acer spp.* were found in plots receiving only increased precipitation, while *Quercus spp.* only appeared in half of the warming+precipitation and warming only plots and one ambient plot. *Acer rubrum* tended towards higher cover in warming only ( $2.8\% \pm 2.1\%$  in warming only versus  $1.3\% \pm$  no standard error in ambient) while *Acer saccharum* had highest cover in ambient with  $3.5\% \pm 2.6\%$  compared to  $3.0\% \pm 1.0\%$  in warming+precipitation and  $2.7\% \pm 2.1\%$  in warming only. However, both species had insufficient distributions to make definitive comparisons. Similarly, the *Quercus* genus tended towards higher cover in warming only ( $4.0\% \pm 1.0\%$  compared to  $3.1\% \pm 0.6\%$  in warming+precipitation and  $2.0\% \pm$  no standard error in ambient), but again lacked power to truly link growth to treatment effects. Only *Prunus serotina* showed significantly higher cover in a treatment as an indicator species for warming+precipitation ( $6.1\% \pm 2.2\%$  versus  $3.27\% \pm 1.6\%$  in ambient and  $1.9\% \pm 1.5\%$  in warming only), but was also absent from all precipitation only plots.

Woody community composition analyzed using the same average cover data as the herbaceous community did not show any strong associations by block ( $p=0.5106$ ) but were highly influenced by individual treatment combinations ( $p=0.0406$ , Appendix F). Further

analysis revealed that interactive effects of warming and precipitation had strong influences on community composition that were able to overcome any inherent block effects ( $p=0.0322$ ).

Analysis of the woody community using stem abundance showed a slightly different trend.

PerMANOVA using stem abundance indicated that warming altered woody community composition ( $p=0.0052$ ) enough to be detectable without including block-based differences in composition ( $p=0.0300$ ). Large trees follow a similar trend, where the interaction of warming and precipitation may influence community composition ( $0.0556$ ), although block influences are likely to play a role ( $p=0.1047$ ).

### **3.3.b. Biodiversity**

Warming and increased precipitation had no discernable effects on plant community biodiversity (Table 3-1). This includes assessment of the overall community and the woody community alone using several common measures of biodiversity. At the whole-community community level, Shannon-Weiner biodiversity index ranged between  $2.43 \pm 0.16$  (mean  $\pm$  standard error) in warming+precipitation plots to  $2.75 \pm 0.12$  in precipitation only, Simpson's biodiversity was between  $0.84 \pm 0.06$  (ambient) and  $0.88 \pm 0.01$  (precipitation only), evenness ranged  $0.67 \pm 0.03$  (ambient) to  $0.75 \pm 0.03$  (precipitation only), and total species richness ranged  $37.0 \pm 2.3$  (warming+precipitation) to  $41.5 \pm 3.3$  (warming only). Total forb species richness was highest in the warming only treatment ( $28.5 \pm 2.8$  versus  $25.3 \pm 2.3$  in ambient) but did not have a significant treatment effect. Short forbs were the only functional group to show a treatment response: decreased species richness in response to precipitation treatment ( $p=0.0004$ ). Short forb species richness in the ambient treatment was  $12.8 \pm 1.0$  and  $13.8 \pm 1.5$  in warming only and can be compared with  $9.5 \pm 1.0$  in precipitation only and  $9.3 \pm 0.5$  in

warming+precipitation. Species richness of woody vegetation as a whole, large trees, and small trees were not affected by warming or increased precipitation. Shrubs showed a trend towards slightly increased species richness with water treatment, but the effect was relatively weak ( $p = 0.0642$ ).

**Table 3-1:** Average species richness and biodiversity for the each treatment based on surveys of  $4 \text{ m}^2$  plots where  $n=4$  for each treatment. Values presented are mean  $\pm$  standard error. H' Index is the Shannon-Weiner biodiversity index and D Index indicates the Simpson's biodiversity index.

	Ambient	Warm+Precip	Warming only	Precipitation only
Total	$38.8 \pm 3.1$	$37.0 \pm 2.3$	$41.5 \pm 3.0$	$38.5 \pm 1.9$
Forb Total	$25.3 \pm 2.3$	$21.3 \pm 0.6$	$28.5 \pm 2.8$	$25.8 \pm 1.7$
Short Forb	$12.8 \pm 1.0$	$9.3 \pm 0.5$	$13.8 \pm 1.5$	$9.5 \pm 1.0$
Tall Forb	$7.5 \pm 1.7$	$7.0 \pm 0.9$	$8.5 \pm 1.3$	$9.3 \pm 0.8$
Woody Total	$10 \pm 1.1$	$13.0 \pm 1.2$	$10.5 \pm 1.0$	$10.0 \pm 0.6$
Large Tree	$4.8 \pm 0.3$	$6.3 \pm 1.3$	$5.0 \pm 0.7$	$4.5 \pm 0.6$
Small Tree	$1.8 \pm 0.6$	$1.3 \pm 0.3$	$1.3 \pm 0.5$	$0.8 \pm 0.4$
Shrub	$2.3 \pm 0.3$	$3.3 \pm 0.4$	$2.8 \pm 0.3$	$3.5 \pm 0.4$
Evenness	$0.67 \pm 0.03$	$0.72 \pm 0.03$	$0.73 \pm 0.04$	$0.75 \pm 0.03$
H' Index	$2.43 \pm 0.16$	$2.67 \pm 0.12$	$2.73 \pm 0.20$	$2.75 \pm 0.12$
D Index	$0.84 \pm 0.03$	$0.85 \pm 0.03$	$0.88 \pm 0.04$	$0.88 \pm 0.01$

### 3.3.c. Structure

Leaf area index during peak growing season was noticeably higher in warmed treatments during the peak growing season ( $p=0.0007$ , Table 3-2). Average leaf area in ambient over the three surveys ( $6.94 \pm 0.46$ ) and precipitation only were similar ( $6.68 \pm 0.24$ ) while warmed treatments were considerably higher ( $8.60 \pm 0.62$  in warming only and  $8.21 \pm 0.41$  in warming+precipitation). In contrast, total percent cover is highest in the ambient plots (272.0%  $\pm 30.9\%$ ) and decreased by interactive effects of warming and precipitation ( $p=0.0194$ ). Total

plant cover was lowest in the precipitation only treatment ( $209.3\% \pm 15.4\%$ ) while warming+precipitation ( $245.9 \pm 19.0$ ) and warming only ( $252.1\% \pm 2.8\%$ ) were in the middle.

**Table 3-2:** Average leaf area index and functional group percent cover during peak season. The average of three leaf area index measurement and five cover observations for each plot between 181-223 were used to generate a single value for each plot for this table but used separately for repeated measures ANOVA (RM-ANOVA). Values presented are the mean  $\pm$  standard error for each treatment, n=4. All significant effects at  $\alpha = 0.05$  from RM-ANOVA are listed with the following treatment codes are as follows W = warming (+1°C day, +3°C night), P = precipitation (+20% long-term average, applied weekly), W\*P = interaction of warming and precipitation, D = day. Log (large trees) indicates the data was long-transformed for analysis.

	Ambient	Warm + Precip	Warming only	Precipitation only	RM-ANOVA
LAI	$6.94 \pm 0.46$	$8.21 \pm 0.41$	$8.60 \pm 0.62$	$6.68 \pm 0.24$	W,D
Total	$272.9 \pm 30.9$	$245.9 \pm 19.0$	$252.1 \pm 2.8$	$209.3 \pm 15.4$	W*P,D
Forbs Total	$142.5 \pm 38.0$	$99.4 \pm 26.3$	$115 \pm 25.8$	$89.6 \pm 16.9$	P
Short Forbs	$126.0 \pm 43.0$	$58.9 \pm 31.3$	$81.8 \pm 24.5$	$49.6 \pm 14.2$	P
Tall Forbs	$15.8 \pm 6.7$	$39.7 \pm 10.4$	$32.2 \pm 8.6$	$38.8 \pm 10.2$	P
Woody Total	$70.9 \pm 18.9$	$71.7 \pm 11.2$	$99 \pm 28.9$	$68.2 \pm 13.5$	
Large Tree	$20.2 \pm 8.0$	$22.8 \pm 4.3$	$23.3 \pm 12.1$	$15.9 \pm 4.3$	W*P (log)
Small Tree	$5.5 \pm 3.3$	$8.9 \pm 2.5$	$1.2 \pm 0.8$	$1.7 \pm 1.3$	W*P
Shrub	$34.8 \pm 17.6$	$30.7 \pm 6.7$	$49.4 \pm 10.8$	$49.3 \pm 11.2$	W*P
Grass	$130.4 \pm 16.5$	$146.5 \pm 18.7$	$137.1 \pm 27.4$	$119.8 \pm 12.8$	W*P

Cover of forb functional groups all responded to increased precipitation, but in different directions (Table 3-2). Total forb cover was decreased by precipitation treatment ( $p=0.0244$ ), with average total forb cover being highest in the ambient treatment ( $142.5\% \pm 38.0\%$ ) and lowest in precipitation only ( $89.6\% \pm 16.9\%$ ). Decreased total forb cover appears to be driven by reduced cover of short forbs in treatments receiving precipitation treatments ( $p=0.0042$ ). Like total forb cover, short cover was highest in ambient plots ( $126.0\% \pm 43.0\%$ ) and lowest in precipitation only ( $49.6\% \pm 14.2\%$ ). In contrast, increased precipitation raised tall forb cover. Tall forb cover was  $15.8\% \pm 6.7\%$  in ambient compared to  $38.8 \pm 10.2\%$  in precipitation only and  $39.7\% \pm 10.4\%$  in warming+precipitation. Tall cover also tended to be higher in warming

treatments ( $p=0.0697$ ) with an average cover of  $32.2\% \pm 8.6\%$  in warming only. Average relative cover of forbs during the peak growing season was not affected by warming or increased precipitation and accounted for almost half of the total cover, ranging from  $49.5\% \pm 9.4\% \pm 17\%$  in ambient plots to  $39.2\% \pm 8.4\%$  in warming+precipitation.

Grass cover was increased through interactive effects of warming and precipitation ( $p=0.0011$ , Table 3-2). Total grass cover was  $130.4\% \pm 16.5\%$  in ambient, lowest in precipitation only ( $119.8 \pm 12.8$ ), and highest in warming+precipitation plots ( $146.5\% \pm 18.7\%$ ). Relative cover of grasses during the peak growing season was also affected by the interaction of warming and precipitation treatments ( $p=0.0150$ ). In this instance, the combination of warming and precipitation increased relative grass cover to almost a third of total cover ( $31.7\% \pm 6.4\%$  compared to  $22.0\% \pm 5.8\%$  in ambient), while warming alone decreased relative grass cover ( $15.8\% \pm 2.8\%$ ). Relative cover of grass was in precipitation only was similar to ambient ( $24.6\% \pm 1.7\%$ ).

Cover of woody vegetation as a whole during the peak growing season was not affected by warming or increased precipitation even though relative cover and cover of functional groups showed varying treatment responses. Relative cover of woody vegetation was increased by both warming and precipitation treatments (warming\*precipitation  $p = 0.0539$ ). Relative cover of woody vegetation the during peak growing season was lowest in ambient plots, accounting for only a quarter of total vegetation cover ( $28.5\% \pm 9.5\%$ ) and highest in warming only ( $39.1\% \pm 11.0\%$ ). Relative woody cover in warming+precipitation ( $29.1\% \pm 3.4\%$ ) was only slightly higher than ambient, while precipitation only showed a greater increase ( $33.3\% \pm 6.9\%$ ). Large tree cover was not affected by warming or precipitation treatments. Small tree cover responded to the interaction of warming and precipitation ( $p=0.0098$ ) and was higher than ambient ( $5.5\% \pm$

3.3%) in warming+precipitation ( $8.9\% \pm 2.5\%$ ), but lower in warming only ( $1.2\% \pm 0.8\%$ ) and precipitation only ( $1.7\% \pm 1.3\%$ ). Shrubs showed the opposite response pattern, in which the interaction of warming and precipitation ( $p=0.0150$ ) lead to higher shrub cover than ambient ( $34.8\% \pm 17.6\%$ ) in single-factor treatment ( $49.4\% \pm 10.8\%$  in warming only and  $49.3\% \pm 11.2\%$  in precipitation only) but slightly lower than ambient in warming+precipitation ( $30.7\% \pm 6.7\%$ ). Total and functional group stem abundance were not affected by treatments (Appendix F).

### 3.4. Discussion

#### 3.4.a. Composition

Herbaceous plant composition varied greatly among plots, but I was able to detect an influence of increased precipitation on herbaceous species assembly. This finding supports the results of other studies in constructed systems that found water to be the primary driver of herbaceous species assembly (Kardol *et al.* 2010). The relatively weak responses of the herbaceous community composition to simulated climate that I observed may be attributed to my study taking place relatively soon after implementations of the climate treatments. Other research spanning longer time periods in other systems have shown that long-term impacts of simulated climate change can be more pronounced of the short-term effects (Walker *et al.* 2006). Many of the species found in my study also were generalists that have wide distributions and often possess suites of traits that allow them to persist under a variety of conditions, often colonizing ecosystems rapidly after a disturbance. The ability of generalist species to survive in a variety of climate scenarios may indicate that early successional herbaceous community

composition is not likely to be an important mechanism affecting long-term forest succession. Alternatively, the large variability in forb community among plots may have made it difficult to statistically compare community composition. Other studies that have observed stronger effects of simulated climate change, particularly precipitation, on herbaceous community composition have relied on systems with fewer species, suggesting this may have limited the outcome of my study (Kardol *et al.* 2010).

I expected plot-level woody community composition to be highly influenced by the location of stumps and pre-harvest forest composition and show less compositional shift in response to temperature and precipitation than the herbaceous community. Surprisingly, the woody community provided stronger evidence in support of altered community composition as a result of climate change. Although no stumps were centered in my research plots, much of the woody community was the result of advanced regeneration from vegetation established before harvest with established root systems and had greater access to water and nutrients (Ilisson & Chen 2010). This may have facilitated woody species' response by allowing certain species to better take advantage greater resource availability that resulted from warming or increased precipitation. Some species may have been better able than others to use warming and increased water availability to add leaf area or increase number of sprouts, providing the mechanisms behind changes in composition. Increased or decreased germination and establishment of species from seed as a result of habitat suitability may also have influenced overall community composition response to treatments.

Altered community composition early in succession does not directly translate into an altered forest development trajectory, but potential effects of warming and precipitation on large canopy tree species assembly early in succession provide the best evidence supporting altered

future forest composition and structure in a moderate climate change scenario. Even weak effects on large tree species assembly are important to note since their distribution and plot-level assembly is highly influenced by the pre-harvest distribution of tree species and other research suggests that these patterns may become amplified over time.

Correlating environmental variables and life history traits with species distribution and responses may help us to elucidate the underlying factors influencing species selection and refine our hypotheses about potential forest succession under different climate change scenarios. The distribution of individual woody and herbaceous species appeared to be strongly influenced by pre-existing propagule banks or stochastic events in establishment and few species were well represented in all treatments and blocks. *Prunus serotina* was the only indicator species likely to persist and be a major component of a mature forest and may provide insight into potential trends of species responses. *P. serotina* has a wide habitat distribution in the eastern U.S. and is frequently associated with both northern hardwood and southern oak forests. It generally possesses a faster growing rate than many other dominant species such as *Acer spp.* and may indicate that similar fast-growing species will benefit most from increased temperature and water availability. Although some inferences can be made from *P. serotina*, poor distribution of most species makes it hard to fully understand the effects of simulated climate change on community composition.

### **3.4.b. Biodiversity**

Community biodiversity was not affected by warming or increased precipitation despite altered woody and herbaceous species assembly. Only decreased short forb species richness from the precipitation treatment suggests that simulated climate change may have effects on

biodiversity. This result may also suggest that the short forb functional group may be the most sensitive to climate perturbation or increased competition from other functional groups. High site biodiversity and large pools of available species may also have contributed to little treatment effects on biodiversity. If many species are available for establishment, it is likely that all available niches in a plot will be filled, even if by different species in different treatments. My observed shifts in species composition and relatively high biodiversity of our site support this explanation. Ambient treatments had an average Shannon-Weiner biodiversity index ( $H'$ ) of  $2.43 \pm 0.16$  and total species richness of  $38.8 \pm 3.1$  species. Ambient plots appear to have representative biodiversity and species richness for the entire harvest because vegetation surveys of non-study plots produced an average  $H'$  of  $2.45 \pm 0.11$  and total richness of  $29.25 \pm 1.89$  species. A nearby clear cut of similar size that was harvested in the same year as my research site had an  $H'$  index of  $1.97 \pm 0.10$  and a total species richness of  $18.25 \pm 1.70$ . It is possible that less diverse systems, particularly those with low species richness, may be more sensitive to climate change and would show greater changes in biodiversity in response to warming or altered precipitation regimes.

### **3.4.c. Structure**

Short forbs were the functional group to show the greatest response to simulated climate change, and appeared to drive cover responses at the total forb and whole-community levels. Lower short forb cover with increased precipitation supports the observed pattern of decreased species richness in these treatments and may have been caused by reduced habitat quality or increased competition from other functional groups. Increased soil moisture and cooler temperatures caused by simulated increase in precipitation may have created less favorable

growing conditions for many short forb species and resulted in reduced cover. Conversely, lower forb cover may have been the result of competition from other functional groups, such as woody vegetation and grass, which were better able to take advantage of increased water availability. Changes in community dynamics that lead to lower forb cover during the peak growing season are likely related to early season dynamics. Short forbs are among the earliest plants to emerge in the spring (see Chapter 2), so increased water and cooler temperatures may have deterred the growth of these species while other species that emerge later were less affected. For example, tall forb cover was greater in increased precipitation treatments. Many tall forbs are late-season species, such as *Solidago spp.*, that emerge after short forbs and may have benefited more from increased precipitation since they grow most actively later in the summer when water is more limiting. In contrast, short forbs may not be stimulated by increased water during the peak growing season because they complete most of their life cycle early in the season, when soil moisture is often higher, and then remain below the canopy during the summer where temperatures are cooler and water stress may be less.

Woody cover as a whole was not affected by warming or precipitation treatments even though shrubs and small trees displayed opposite responses and large trees were not affected. Small tree cover was highest in the warming+precipitation treatment, but lower in single-factor treatments while shrub cover was lowest in warming+precipitation and higher in warming only and precipitation only. It is possible that small tree growth in heat only plots was limited by water availability and increased water alone was insufficient to promote growth. In contrast, shrubs may have been able to take advantage of increased temperature or water alone, but were outcompeted by other vegetation such as small trees and tall forbs in the warming+precipitation treatment. Large trees may not have shown any effects on cover because they allocate more of

their resources to vertical growth and grow in a columnar form that does not increase in percent cover. Vertical growth can instead greatly increases LAI, as suggested in Chapter 2, by increasing leaf density without increasing horizontal cover.

Relative cover as an indicator of functional group dominance may be a better indicator of changes in community structure and composition than total cover since it standardizes differences in total cover. In general, treatment effects on the relative cover of forbs, woody, and grass functional groups were not as strong as those seen with total cover. Increased cover of grasses and woody vegetation in warming and precipitation treatments suggests that these two functional groups may grow better in simulated climate change scenarios than co-occurring forbs. Long-term consequences of this shift in functional group dominance could include altered nutrient cycling and light availability (Donath & Eckstein 2008). Although relative forb cover was not greatly reduced by warming or increased precipitation like total forb cover, the slightly lower cover may still have ecological significance since the relative cover of woody vegetation and grasses cannot both increase without lowering the relative cover of the remaining functional group.

### **3.5. Ecological Implications**

Climate change has the potential to alter both early successional and long-term forest communities. I observed shifts in community composition and functional group dominance as a result of increased precipitation and temperature. Individual species responses to a warmer climate with more frequent precipitation likely drive functional group and community level shifts. The increased cover of certain species and functional groups to warming and precipitation treatments may increase competition for resources and reduce growth of other functional groups

(forbs) through competition and may cause shifts in species composition. Observed effects of simulated climate change on large tree species assembly provides evidence that long-term forest development can be influenced by community- and climate-based selection early in succession. Furthermore, increased total and relative cover of woody functional groups in simulated climate change scenarios may indicate faster accumulation of woody biomass and accelerated succession in the future.

## Chapter 4: Synthesis

Natural community assemblies are highly variable due to localized environmental conditions and a moderate climate change scenario could have subtle effects on community dynamics even in constructed communities. Furthermore, effects of climate change may take several years to manifest themselves (Walker *et al.* 2006). However, natural community assembly and *in situ* experiments contain intact vegetation and soil communities that provide real-world feedback loops that may lead to stronger community-level responses to climate perturbation and are important in understanding the potential effects of climate change on natural ecosystems. My research demonstrated that a 1.6°C increase in temperature and a 20% increase in precipitation can affect early successional community composition, structure and phenology. Effects of simulated climate change on community dynamics are likely to vary heavily between years and sites, but my results support models that show that even conservative estimates of climate change could alter vegetation community dynamics, affect phenology, and have long-term consequences on forests (Iverson & Prasad 2001, Schwartz *et al.* 2006).

I observed changes in community composition and structure during the peak summer growing season and over the course of the entire growing season in response to simulated climate change. Surface temperatures from March through early November were raised an average  $1.59 \pm 0.01$  °C in warming only plots and  $1.23 \pm 0.01$  °C in warming+precipitation plots. Warmer temperatures caused tall forbs and large trees to leaf out around 3 weeks earlier than non-warmed controls. Earlier leaf out of these two functional groups may have been the primary cause of increased leaf area index (LAI) in the spring and early summer, but other functional groups may have added leaf area in ways that were not detected in cover or life history analyses. Earlier leaf out may also have caused increased cover of large trees and tall forbs over the course

of the entire growing season. However, during the peak growing season tall forbs only showed increased cover in response to increased precipitation treatments while large tree cover was not affected by any treatments. Grasses and small trees had higher cover during the peak growing season with increased heat and water, while short forbs had lower cover in precipitation treatments and shrubs only showed increased cover in single-factor treatments (e.g. warmed only and precipitation only). Lower short forb cover in simulated climate change treatments may be the result of increased competition from other functional groups, particularly tall forbs, early in the growing season. Alternatively, lower short forb cover and increased tall forb cover in increased precipitation treatments could indicate decreased habitat quality for many short forb species and more favorable growing conditions for several tall forb species.

Increased precipitation influenced community composition, supporting the hypothesis that decreased cover resulted from a shift in forb habitat suitability. Importance of precipitation in structuring herbaceous communities supports other research that reported similar shifts in community composition in response to increased precipitation (Kardol *et al.* 2010a). Shifts in woody composition and increased cover were dominated by the effects of warming alone or an interaction of warming and increased precipitation. Surprisingly, shifts in woody and herbaceous community composition were not accompanied by increased or decreased biodiversity. Repeated sampling throughout the growing season revealed treatment effects on functional group species richness, but community biodiversity was generally unaffected by simulated climate change. Differential responses of woody and herbaceous vegetation to increased temperature and precipitation indicate that community response to climate change will depend on species or functional group response.

Over time, feedbacks between phenology, composition, and community structure may compensate and mediate what appears to be the beginnings of community divergence or may create a positive feedback cycle and result in markedly different mature forests. Feedbacks are essential for regulating ecosystem functioning and one of the greatest challenges of understanding potential large-scale and long-term effects of climate change (Shaver *et al.* 2000, Kardol *et al.* 2010). Community response to climate change will depend upon localized site conditions such as nutrient and light availability as well as inter-annual weather variability and co-varying climate change factors such as CO<sub>2</sub> concentration (Kardol *et al.* 2010, Morecroft *et al.* 2004, Dukes *et al.* 2005). Recently, concerns have been expressed about potential threshold and non-linear responses to climate change and it is possible that community response to more dramatic climate scenarios will vary greatly from what I observed (Fischlin *et al.* 2007).

Advanced regeneration of woody plant species played an important role in controlling community dynamics and the strong response of woody vegetation to climate treatments. Advanced regeneration following forest harvest strongly influences the community composition and developmental pathway of forest succession (Ilisson & Chen 2009). Thus far, there have been no published experimental climate change studies that have considered active forest management or focused on trees that have resprouted using existing rootstocks. My research observed a shift of both tree and non-tree community composition and dominance that supports previous research suggesting the impacts of climate change can act early in succession to restructure the community and have long-term effects on forest development (Jackson *et al.* 2010). Having established root systems appeared to allow regenerating stems to take advantage of increased temperatures and precipitation to increase their growing season and community dominance.

Attempting to infer long-term forest succession trajectories from early successional dynamics is difficult, but is one of the few practical field-based methods for inferring the potential effects of climate change on forests. Examination of natural community assembly has been largely overlooked in both succession and climate change research because it often yields highly variable data with weak treatment effects. Understanding individual species-level physiological responses to climate pressures will improve researchers' ability to extrapolate long-term forest development from early successional dynamics. Further examination of the life history traits and physiological adaptations of functional groups and species that showed strong responses to simulated climate change will be a valuable starting point for the future. Even though I cannot use my data to draw clear mechanistic explanations for observed community dynamics, my research is a valuable first step that can guide future research in climate change and forest succession.

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## Appendix A: Species List and Functional Groups

**Table A-1:** List of all species found in research plots along with their functional group classification. All names are according to Rhoads & Block (2007).

<b>Species</b>	<b>Common Name</b>	<b>Family</b>	<b>Functional Group</b>	<b>Native Status</b>
<i>Actaea racemosa</i>	black cohosh	Ranunculaceae	tall forb	native
<i>Acer rubrum</i>	red maple	Sapindaceae	large tree	native
<i>Acer saccharum</i>	sugar maple	Sapindaceae	large tree	native
<i>Allium vineale</i>	wild garlic	Alliaceae	short forb	non-native
<i>Ambrosia artemisiifolia</i>	common ragweed	Asteraceae	short forb	native
<i>Amphicarpa bracteata</i>	hog peanut	Fabaceae	vine	native
<i>Anemone americana</i>	liverleaf	Ranunculaceae	short forb	native
<i>Asclepias quadrifolia</i>	four-leaved milkweed	Apocynaceae	short forb	native
<i>Betula lenta</i>	black birch	Betulaceae	large tree	native
<i>Boehmeria cylindrica</i>	false nettle	Urticaceae	short forb	native
<i>Carya spp.</i>	hickory	Juglandaceae	large tree	native
<i>Ceanothus americana</i>	New Jersey tea	Rhamnaceae	shrub	native
<i>Celastrus orbiculatus</i>	Oriental bittersweet	Celastraceae	vine	non-native invasive
<i>Cirsium arvense</i>	Canada thistle	Asteraceae	tall forb	non-native invasive
<i>Circaea canadensis</i>	enchanter's-nightshade	Onagraceae	short forb	native
<i>Cirsium vulgare</i>	bull thistle	Asteraceae	tall forb	non-native invasive
<i>Clematis virginiana</i>	virgin's bower	Ranunculaceae	vine	native
<i>Clinopodium vulgare</i>	wild basil	Lamiaceae	short forb	non-native
<i>Conyza canadensis</i>	horseweed	Asteraceae	tall forb	native
<i>Cornus florida</i>	flowering dogwood	Cornaceae	small tree	native
<i>Cornus racemosa</i>	gray dogwood	Cornaceae	shrub	native
<i>Cornus spp</i>	dogwood	Cornaceae	small tree	native
<i>Crataegus spp</i>	hawthorn	Rosaceae	small tree	native
<i>Desmodium nudiflorum</i>	naked-flowered tick-trefoil	Fabaceae	short forb	native
<i>Desmodium paniculatum</i>	tick-trefoil	Fabaceae	short forb	native
<i>Epilobium ciliatum</i>	willow-herb	Onagraceae	tall forb	native

<b>Species</b>	<b>Common Name</b>	<b>Family</b>	<b>Functional Group</b>	<b>Native Status</b>
<i>Erigeron annus</i>	Daisy fleabane	Asteraceae	tall forb	native
<i>Erechtites hieraciifolia</i>	fireweed, pilewort	Asteraceae	tall forb	native
<i>Erigeron philadelphicus</i>	Daisy fleabane	Asteraceae	short forb	native
<i>Euthamia gramanifolia</i>	grass-leaved goldenrod, flat-topped goldenrod	Asteraceae	tall forb	native
<i>Fraxinus spp</i>	ash	Oleaceae	large tree	native
<i>Fragaria virginiana</i>	wild strawberry	Rosaceae	short forb	native
<i>Galium aparine</i>	bedstraw, cleavers	Rubiaceae	tall forb	native
<i>Galium circaeans</i>	wild-licorice	Rubiaceae	short forb	native
<i>Galium triflorum</i>	sweet-scented bedstraw	Rubiaceae	short forb	native
<i>Geum canadense</i>	white avens	Rosaceae	short forb	native
<i>Geranium maculatum</i>	wild geranium	Geraniaceae	short forb	native
<i>Grass spp</i>	Grass, sedge		grass	
<i>Hackelia virginiana</i>	beggar's-lice, stickseed	Boraginaceae	tall forb	native
<i>Hamamelis virginiana</i>	witchhazel	Hamamelidaceae	small tree	native
<i>Hieracium caepitosum</i>	king-devil	Asteraceae	short forb	non-native
<i>Houstonia longifolia</i>	long-leaved bluets	Rubiaceae	short forb	native
<i>Hypericum punctatum</i>	spotted St. John's-wort	Hypericaceae	short forb	native
<i>Ilex verticillata</i>	common winterberry	Aquifoliaceae	shrub	native
<i>Lactuca serriola</i>	prickly lettuce	Asteraceae	tall forb	non-native
<i>Lepidium campestre</i>	fieldcress	Brassicaceae	short forb	non-native
<i>Lindera benzoin</i>	spicebush	Lauraceae	shrub	native
<i>Liriodendron tulipifera</i>	tulip-poplar, yellow poplar	Magnoliaceae	large tree	native
<i>Lobelia inflata</i>	indian tobacco	Campanulaceae	short forb	native
<i>Lonicera spp.</i>	honeysuckle	Caprifoliaceae	shrub	non-native invasive
<i>Lysimachia quadrifolia</i>	whorled loosestrife	Myrsinaceae	short forb	native
<i>Maianthemum canadense</i>	false soloman's seal	Ruscaceae	short forb	native
<i>Mitchella repens</i>	partridgeberry	Rubiaceae	short forb	native
<i>Microstegium vimineum</i>	Japanese stiltgrass	Poaceae	grass	non-native invasive

<b>Species</b>	<b>Common Name</b>	<b>Family</b>	<b>Functional Group</b>	<b>Native Status</b>
<i>Oenothera perennans</i>	sundrops	Onagraceae	short forb	native
<i>Ostrya virginiana</i>	ironwood, hornbeam	Betulaceae	small tree	native
<i>Oxalis stricta</i>	common yellow wood-sorrel	Oxalidaceae	short forb	native
<i>Parthenocissus quinquefolia</i>	virginia-creeper, woodbine	Vitaceae	vine	native
<i>Phytolacca americana</i>	pokeweed	Phytolaccaceae	tall forb	native
<i>Plantago major</i>	common plantain	Plantaginaceae	short forb	non-native
<i>Potentilla canadensis</i>	cinquefoil	Rosaceae	short forb	native
<i>Populus grandidentata</i>	bigtooth aspen	Salicaceae	large tree	native
<i>Potentilla norvegica</i>	strawberry weed	Rosaceae	short forb	native
<i>Podophyllum peltatum</i>	mayapple	Berberidaceae	short forb	native
<i>Populus tremuloides</i>	quaking aspen	Salicaceae	large tree	native
<i>Prunus serotina</i>	black cherry	Rosaceae	large tree	native
<i>Pseudognaphalium obtusifolium</i>	fragrant cudweed	Asteraceae	short forb	native
<i>Pycnanthemum incanum</i>	mountain-mint	Lamiaceae	short forb	native
<i>Quercus alba</i>	white oak	Fagaceae	large tree	native
<i>Quercus rubra</i>	northern red oak	Fagaceae	large tree	native
<i>Quercus velutina</i>	black oak	Fagaceae	large tree	native
<i>Ranunculus abortivis</i>	small-flowered crowfoot	Ranunculaceae	short forb	native
<i>Rhus glabra</i>	smooth sumac	Anacardiaceae	small tree	native
<i>Rosa multiflora</i>	multiflora rose	Rosaceae	shrub	non-native invasive
<i>Rumex acetosella</i>	sheep sorrel	Polygonaceae	short forb	non-native
<i>Rubus spp</i>	blackberry	Rosaceae	shrub	native
<i>Rubus occidentalis</i>	black raspberry	Rosaceae	shrub	native
<i>Sassafras albidum</i>	sassafras	Lauraceae	large tree	native
<i>Sambucus canadensis</i>	elderberry	Adoxaceae	small tree	native
<i>Sisyrinchium mucronatum</i>	blue-eyed-grass	Iridaceae	short forb	native
<i>Smilax spp</i>	Greenbriar	Smilacaceae	vine	native
<i>Sonchus asper</i>	Common sow-thistle	Asteraceae	tall forb	non-native
<i>Solidago canadensis</i>	Canada goldenrod	Asteraceae	tall forb	native
<i>Solidago caesia</i>	bluestem goldenrod	Asteraceae	tall forb	native

<b>Species</b>	<b>Common Name</b>	<b>Family</b>	<b>Functional Group</b>	<b>Native Status</b>
<i>Solidago nemoralis</i>	gray goldenrod	Asteraceae	short forb	native
<i>Solidago rugosa</i>	wrinkle-leaf goldenrod	Asteraceae	tall forb	native
<i>Symphyotrichum laeve</i>	Aster	Asteraceae	tall forb	native
<i>Symphyotrichum lateriflorum</i>	calico aster	Asteraceae	tall forb	native
<i>Symphyotrichum pilosum</i>	heath aster	Asteraceae	tall forb	native
<i>Taraxacum officinale</i>	common dandelion	Asteraceae	short forb	non-native
<i>Thalictrum thalictroides</i>	rue-anemone	Ranunculaceae	short forb	native
<i>Trifolium aureum</i>	large yellow hop-clover	Fabaceae	short forb	non-native
<i>Trifolium pratense</i>	red clover	Fabaceae	short forb	naturalized
<i>Trifolium repens</i>	white clover	Fabaceae	short forb	non-native
<i>Unknown 20</i>			forb	unknown
<i>Unknown 25</i>			forb	unknown
<i>Unknown 4</i>			grass	unknown
<i>Unknown 52</i>			forb	unknown
<i>Unknown 70</i>			forb	unknown
<i>Unknown 77</i>			forb	unknown
<i>Unknown 80</i>			forb	unknown
<i>Unknown 81</i>			forb	unknown
<i>Unknown 85</i>			forb	unknown
<i>Unknown 86</i>			forb	unknown
<i>Unknown 88</i>			forb	unknown
<i>Uvularia perfoliata</i>	bellwort	Colchicaceae	short forb	native
<i>Veronica officinalis</i>	common speedwell, gypsyweed	Plantaginaceae	short forb	non-native
<i>Veronica serpyllifolia</i>	thyme-leaved speedwell	Plantaginaceae	short forb	non-native
<i>Verbascum thapsus</i>	mullein	Scrophulariaceae	tall forb	non-native
<i>Verbena urticifolia</i>	white vervain	Verbenaceae	tall forb	native
<i>Viola blanda</i>	sweet white violet	Violaceae	short forb	native
<i>Vicia cracca</i>	Canada pea, cow vetch	Fabaceae	tall forb	naturalized
<i>Viola hirsutula</i>	southern wood violet	Violaceae	short forb	native
<i>Viburnum prunifolium</i>	black-haw	Adoxaceae	small tree	native
<i>Viola pubescens</i>	downy yellow violet	Violaceae	short forb	native
<i>Viola soria</i>		Violaceae	short forb	native
<i>Vitis spp</i>	wild grape	Vitaceae	vine	native

## Appendix B: Dates of Vegetation Inventory and LAI Measurements

**Table B-1:** Table with dates and Julian dates of vegetation and ceptometer measurements (leaf area index). The boxes in gray indicate the peak growing season used for analysis of structure in chapter 3.

Vegetation Inventories		Ceptometer Measurements	
Date	Julian Day	Date	Julian Day
24-Mar	83	25-Mar	84
31-Mar	90	31-Mar	90
7-Apr	97	9-Apr	99
14-Apr	104	16-Apr	106
23-Apr	113		
28-Apr	118	28-Apr	118
6-May	126		
12-May	132		
18-May	138	18-May	138
27-May	147		
1-Jun	152		
16-Jun	167		
30-Jun	181		
7-Jul	188	6-Jul	187
14-Jul	195		
28-Jul	209	28-Jul	209
11-Aug	223	14-Aug	226
26-Aug	238		
9-Sep	252	2-Sep	245
23-Sep	266	3-Oct	276
14-Oct	287		
4-Nov	308	2-Nov	306

## Appendix C: Results of Statistical Tests for Phenology Chapter

**Table C-1:** Species richness RM-ANOVA using data from the entire growing season showed that treatment effects varied highly by functional group. Functional groups are broadly defined by mature height class (see methods, sect 1.2 for definitions). Bold highlights statistical significance at  $\alpha = 0.05$ . Up arrows ( $\uparrow$ ) in parenthesis indicate generally increased cover with the presence of the treatment variable while down arrows ( $\downarrow$ ) indicate lower cover with the treatment variable. ( $\uparrow\downarrow$ ) indicates that variable responses were not consistent over time or interactions caused mixed effects.

Response Variable	Transformation	Heat	Water	Day	Heat* Water	Heat*Day
Total		0.0003	0.9677	<b>&lt;0.0001</b>	<b>0.0180</b> ( $\uparrow$ )	0.9549
Forbs		0.1214	0.2792	<b>&lt;0.0001</b>	<b>0.0003</b> ( $\uparrow\downarrow$ )	0.8450
-Short Forbs		0.9046	0.0553	<b>&lt;0.0001</b>	<b>0.0383</b> ( $\uparrow\downarrow$ )	0.8637
-Tall Forbs		0.0368	0.3405	<b>&lt;0.0001</b>	<b>0.0004</b> ( $\uparrow$ )	0.9536
Woody		<0.0001	0.1211	<b>&lt;0.0001</b>	<b>0.0275</b> ( $\uparrow\downarrow$ )	0.8667
-Large Trees	sqrt	<b>0.0007</b> ( $\uparrow$ )	0.3712	<b>&lt;0.0001</b>	0.5709	0.9777
-Small Trees	sqrt	0.0017	0.7009	<b>0.0352</b>	<b>&lt;0.0001</b> ( $\uparrow\downarrow$ )	0.9955
-Shrubs		0.0519	0.0002	<b>&lt;0.0001</b>	<b>&lt;0.0001</b> ( $\uparrow$ )	0.9995

**Table C-2:** Repeated measures analysis of variance of cover and leaf area index (LAI) from all survey points during the growing season showed heat and water effects in almost every functional group, but the ecological significance or direction of results is highly varied. Bold highlights the highest-level interactions with  $p < 0.05$ . Up arrows ( $\uparrow$ ) in parenthesis indicate generally increased cover with the presence of the treatment variable while down arrows ( $\downarrow$ ) indicate lower cover with the treatment variable. ( $\uparrow\downarrow$ ) indicates that variable responses were not consistent over time or interactions caused mixed effects.

Response Variable	Transformation	Heat	Water	Day	Heat* Water	Heat*Day
LAI		<0.0001	0.9830	<b>&lt;0.0001</b>	0.0825 ( $\uparrow\downarrow$ )	<b>0.0002</b> ( $\uparrow$ )
Total Cover		0.0008	0.0003	<b>&lt;0.0001</b>	<b>&lt;0.0001</b> ( $\uparrow\downarrow$ )	0.5832
Forb Cover		0.5739	0.0003	<b>&lt;0.0001</b>	<b>0.0034</b> ( $\downarrow$ )	0.9623
- Rel Cover Forb		0.7527	<b>0.0007</b> ( $\downarrow$ )	0.9940	0.0584 ( $\downarrow$ )	0.9931
-Short forbs		0.1502	<0.0001	<b>&lt;0.0001</b>	<b>0.0043</b> ( $\downarrow$ )	0.9954
-Tall Forbs		<b>&lt;0.0001</b> ( $\uparrow$ )	<b>&lt;0.0001</b> ( $\uparrow$ )	<b>&lt;0.0001</b>	0.9787	0.9232
Woody Cover		0.0094	0.0210	<b>&lt;0.0001</b>	<b>0.0508</b> ( $\uparrow\downarrow$ )	0.9999
- Rel Cover Woody		0.0493	0.2786	<b>&lt;0.0001</b>	<b>0.0013</b> ( $\uparrow$ )	1.0000
-Large Trees	log	<0.0001	0.1471	<0.0001	<b>0.0018</b> ( $\uparrow\downarrow$ )	<b>0.0001</b> ( $\uparrow$ )
-Small Trees	log	0.3716	0.1724	<b>0.0484</b>	<b>0.0004</b> ( $\uparrow\downarrow$ )	0.9944
-Shrubs		0.7922	0.1973	<b>&lt;0.0001</b>	<b>0.0023</b> ( $\uparrow\downarrow$ )	1.0000
Grass Cover		0.0507	0.0002	<b>0.0085</b>	<b>&lt;0.0001</b> ( $\uparrow\downarrow$ )	0.9938
- Rel Cover Grass		0.1793	<b>&lt;0.0001</b> ( $\uparrow$ )	<b>&lt;0.0001</b>	0.4607	0.9583

## Appendix D: Indicator Species Analysis Results

Indicator species analysis was run on all 118 species remaining after data trimming (sect. 3.2). Below are the indicator values calculated according to Defrene & Legendre (1997) and Monte Carlo test of significance generated by PC-ORD (Pullman, WA). Species are listed using 4-letter codes representing the first two letters each of the genus and specific epithet (Appendix A). Species that were only identified to the genus level are listed by genus. "Maxgrp" identifies the treatment in which the species has the maximum observed indicator value according to the following codes: 1=ambient, 2=heat+water, 3=heat only, 4=water only. P\* is the proportion of randomized trials with indicator value equal to or exceeding the observed indicator value. p = (1 + number of runs  $\geq$  observed)/(1 + number of randomized runs)

Column	Maxgrp	Value	IV from randomized groups			
			Observed Indicator	Mean	S.Dev	
1	ACRA	4	20.4	35.3	13.64	0.9290
2	ACRU	3	35.9	30.0	15.42	0.5237
3	ACSA	1	28.6	35.7	12.45	0.6653
4	ALVI	3	34.3	29.0	13.71	0.2603
5	AMAR	4	22.2	27.7	11.07	1.0000
6	AMBR	3	38.6	30.1	11.54	0.1770
7	ANAM	3	25.0	25.0	0.35	1.0000
8	ASQU	3	15.0	26.2	14.92	1.0000
9	BELE	4	38.4	30.4	14.48	0.1948
10	BOCY	3	19.0	31.7	12.48	0.8634
11	Carya	3	23.3	30.9	11.81	0.6379
12	CEAM	4	23.8	44.7	17.10	0.8750
13	CEOB	2	25.0	25.0	0.35	1.0000
14	CIAR	4	33.4	34.9	11.80	0.5671
15	CICA	2	46.3	29.3	15.66	0.2030
16	CIVU	3	17.3	32.4	11.66	0.9740
17	CLVI	4	25.0	25.0	0.35	1.0000
18	CLVU	2	25.0	25.0	0.35	1.0000
19	COCA	2	17.5	32.7	10.18	0.9744
20	COFL	2	25.0	25.0	0.35	1.0000
21	CORA	3	24.1	30.8	13.53	0.5219
22	Cornus	1	25.0	25.0	0.35	1.0000

Column	Maxgrp	Value (IV)	IV from Observed randomized Indicator groups			p *
			Mean	S.Dev		
23	Crataegu	2	47.6	36.4	11.80	0.1778
24	DENU	1	25.0	25.0	0.35	1.0000
25	DEPA	4	25.0	25.0	0.35	1.0000
26	EPCI	1	33.1	28.5	14.76	0.3993
27	ERAN	4	26.8	33.2	9.22	0.7169
28	ERHI	4	39.8	36.5	14.22	0.3379
29	ERPH	3	25.0	25.0	0.35	1.0000
30	EUGR	4	22.7	34.0	11.43	0.8328
31	Fraxinus	1	32.9	39.2	9.35	0.7343
32	FRVI	3	13.9	21.2	14.50	1.0000
33	GAAP	2	67.7	55.0	10.01	0.1450
34	GACI	3	33.0	32.4	11.63	0.4217
35	GATR	1	55.7	48.4	9.86	0.2667
36	GECA	2	26.9	34.3	5.40	0.9210
37	GEMA	1	14.0	33.9	15.48	0.9524
38	grass	2	35.2	30.7	2.66	0.0508
39	HACVI	4	25.0	25.0	0.35	1.0000
40	HAVI	1	25.0	25.0	0.35	1.0000
41	HICA	1	15.1	22.0	13.90	1.0000
42	HULO	1	25.0	25.0	0.35	1.0000
43	HYPU	1	38.1	33.9	12.57	0.3511
44	ILVE	4	25.0	25.0	0.35	1.0000
45	LASE	2	25.0	25.0	0.35	1.0000
46	LECA	3	25.0	25.0	0.35	1.0000
47	LIBE	1	25.0	25.0	0.35	1.0000
48	LITU	4	43.9	37.6	11.24	0.2458
49	LOIN	4	27.7	33.9	8.52	0.7157
50	Lonicera	3	17.6	24.3	13.07	1.0000
51	LYQU	3	27.7	32.3	14.20	0.6297
52	MARA	2	50.0	20.2	15.06	0.2030
53	MIRE	2	25.0	25.0	0.35	1.0000
54	MIVI	1	46.7	44.6	15.81	0.5295
55	OEPE	1	12.5	20.0	15.00	1.0000
56	OSVI	2	25.0	25.0	0.35	1.0000
57	OXST	3	17.8	32.6	13.08	0.9566
58	PAQU	3	16.5	23.3	13.49	1.0000
59	PHAM	3	27.2	34.0	8.51	0.7576
60	PLMA	3	15.3	27.2	11.88	1.0000
61	POCA	1	50.1	39.6	8.94	0.1278
62	POGR	2	13.9	32.1	15.84	0.9814
63	PONO	2	15.3	26.2	14.01	0.8458

Column	Maxgrp	Value (IV)	IV from Observed randomized Indicator groups			p *
			Mean	S.Dev		
64	POPE	3	15.7	29.5	12.33	0.9352
65	POTR	4	50.0	25.7	12.28	0.2038
66	PRSE	2	64.1	34.7	11.86	0.0270
67	PSOB	3	28.1	27.1	13.02	0.5531
68	Pycnanth	4	22.3	27.7	10.98	1.0000
69	QUAL	2	50.0	23.1	14.03	0.2144
70	QURU	2	14.1	21.8	14.74	1.0000
71	QUVE	2	25.3	26.6	13.13	0.5529
72	RAAB	1	12.4	24.9	14.06	1.0000
73	RHGL	4	25.0	25.0	0.35	1.0000
74	ROMU	2	17.5	27.4	14.57	1.0000
75	RUAC	1	25.0	25.0	0.35	1.0000
76	Rubus	4	28.4	31.7	3.02	0.8728
77	RUOC	3	35.5	33.5	4.32	0.3001
78	SAAL	4	13.8	29.6	13.97	0.8556
79	SACA	1	20.8	26.8	11.81	1.0000
80	SIMU	3	23.5	28.6	12.78	0.7117
81	Smilax	3	16.1	23.1	13.68	1.0000
82	SOAS	1	14.3	35.3	15.89	0.9996
83	SOCA	3	30.6	33.7	5.88	0.6795
84	SOLCAE	1	25.0	25.0	0.35	1.0000
85	SONE	3	41.3	28.0	14.51	0.2324
86	SORU	4	30.7	32.5	11.65	0.5171
87	SYFI	3	56.2	31.6	9.30	0.0140
88	SYLA	4	29.4	35.2	9.38	0.7576
89	SYPI	3	17.6	27.9	14.52	1.0000
90	TAOF	4	39.7	33.4	6.82	0.2000
91	thistle	2	25.0	25.0	0.35	1.0000
92	THTH	1	30.2	31.6	12.25	0.4451
93	TRAU	2	23.4	29.2	12.11	0.5195
94	TRPR	4	21.0	30.0	11.46	0.7383
95	TRRE	3	25.0	25.0	0.35	1.0000
96	U20	1	25.0	25.0	0.35	1.0000
97	U35	1	25.0	25.0	0.35	1.0000
98	U4	2	18.5	32.2	11.31	0.9514
99	U52	1	25.0	25.0	0.35	1.0000
100	U70	3	21.6	27.9	11.78	0.7752
101	U77	2	25.0	25.0	0.35	1.0000
102	U80	2	14.3	21.5	14.29	1.0000
103	U81	2	25.0	25.0	0.35	1.0000
104	U85	4	25.0	25.0	0.35	1.0000

Column	Maxgrp	Value (IV)	IV from Observed randomized Indicator groups			p *
			Mean	S.Dev		
105 U86	2	25.0	25.0	0.35	1.0000	
106 U88	2	25.0	25.0	0.35	1.0000	
107 UVPE	3	25.0	25.0	0.35	1.0000	
108 VEOF	1	35.4	41.4	9.10	0.7029	
109 VESE	2	25.0	25.0	0.35	1.0000	
110 VETH	2	26.2	30.2	12.99	0.4437	
111 VEUR	2	20.3	29.5	12.70	0.7756	
112 VIBL	4	25.0	25.0	0.35	1.0000	
113 VICR	3	25.0	25.0	0.35	1.0000	
114 VIHI	3	41.0	48.3	10.11	0.6961	
115 VIPR	2	22.1	27.6	11.13	1.0000	
116 VIPU	1	25.0	25.0	0.35	1.0000	
117 VISO	4	34.5	32.5	4.05	0.3025	
118 Vitis	3	54.8	41.3	7.34	0.0478	

### Appendix E: Average Cover of Species Used in Community Analyses

**Table E - 1:** Average cover and distribution of all species used in analysis of biodiversity and community composition in Chapter 3. Values presented are the average cover from all observations during the 22 vegetation surveys. Species are listed by Genus or 4-letter codes that represent the first two

form	Functional Group	Species	Ambient				Warm+Precip				Warming only				Precipitation only			
			1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
forb	0	U20		0.2														
		U35		0.2														
		U52			0.6													
		U70			0.4		1.0			0.9				0.8	0.9			
		U77							0.3									
		U80					1.1								0.9			
		U81					0.9											
		U85														2.7		
		U86					0.1											
		U88					0.1											
short forb	short forb	ALVI			0.8			0.1					1.7	1.8			0.7	
		AMAR									0.1						0.8	
		ANAM									0.1							
		ASQU	0.9						0.1		1.5							
		BOCY	1.5						2.7	0.4	0.8			1.0	0.6	1.6		
		CICA	0.4			3.6	2.6							0.1				
		CLVU					9.4											
		DENU	1.0															
		DEPA														3.6		
		ERPH							0.1									
		FRVI				3.3								4.2				
		GACI	0.8	1.2			3.5	0.8				2.8	2.4	0.6	1.0			
		GATR	6.7	3.9	44.8	4.6	2.6	4.3	6.3		3.7	0.7	2.1	12.2	4.6	2.7		8.5
		GECA	5.8	2.3	0.6	0.6	1.6	3.0	2.8	2.1	5.2		3.1	3.0	1.3	1.4	2.8	
		GEMA	1.1			5.5			12.1		1.8		1.9				1.2	
		HICA			0.7										0.5			
		HULO			0.3													
		HYPU	1.7	0.7	0.3	0.9			0.7				0.3	1.4			3.4	
		LECA											0.2					
		LOIN			0.3	1.2	1.2			2.3		0.7	0.4	1.5	1.0	1.0	1.2	2.8
		LYQU				0.1					0.4	0.7	0.4		0.1	1.5		

MARA					2.1	2.1																
MIRE					0.2																	
OEPE				0.1									0.1									
OXST		0.7	1.2	2.5			10.8					2.3	8.3						4.1			
PLMA		0.7				0.8			0.6	0.4									0.7			
POCA	3.0	28.5	73.7	85.6	1.3	2.7	70.5	1.9		1.3	37.4	38.0	4.0	7.1					26.0			
PONO				0.8				2.5											0.8			
POPE	2.7	0.8						2.0		2.3			2.5					4.9				
PSOB			1.2								2.5	1.0						1.5				
Pycnanthemum		0.1																	0.8			
RAAB			2.0									0.8						1.3				
RUAC			1.0																			
SIMU				3.0			4.5				1.7	7.2						2.5				
SONE							0.7				4.5	3.1	0.9									
TAOF	0.2	1.3	0.5			2.5	1.8	1.0			2.0	1.0	1.7	1.3	2.4	1.3						
THTH	0.6		0.9	1.4				0.3	0.8	0.8								2.5				
TRAU		1.3					4.7	4.6				4.1			1.0			4.2				
TRPR	2.4				1.6		2.2					1.2			1.1	1.1	0.7					
TRRE												0.1										
UVPE								0.7														
VEOF	17.3	8.0	42.5	34.4	5.6		21.5	0.8	87.2		12.4	8.8	2.2	6.5	28.9	12.5						
VESE							0.4															
VIBL																		0.8				
VIHI	0.6	0.1	0.6	0.7	0.1	0.1		0.9		0.6	1.1	5.0	1.3	0.6	0.1	0.4						
VIPU	0.1																					
VISO	2.4	1.2		1.9	1.4		2.0	1.2	4.0	1.9	1.3	3.0	2.5	1.2	3.7	3.3						
tall forb	ACRA	0.1	6.3			8.0			3.9	2.9	1.0		0.7		14.6							
	CIAR		1.9					9.7	1.2	1.6		5.3	2.7	2.3	3.2	1.7						
	CIVU	4.4	0.8			2.8		2.1		2.1		4.0	1.2			0.3						
	COCA	0.5	1.7		0.1	0.7		1.4	0.8	1.9					1.6	1.0						
	EPCI	0.2	0.5	0.1													1.0					
	ERAN	2.3	0.7	0.6		3.4		1.5			0.1		3.3		1.9	2.3	2.3					
	ERHI	1.2				6.3		1.0		0.3			1.0	0.7	4.0	0.1						
	EUGR		4.0	0.7		1.3			2.5	2.8			8.3	1.6	1.7	5.2						
	GAAP	0.5	0.7	13.1	0.3	0.6	34.5	1.0	17.2	1.9	0.8	2.0	2.0	1.2	0.8	2.1	0.1					
	HACVI																1.0					
	LASE					1.3																
	PHAM		7.1			16.0	9.6		4.8	4.3	17.2	4.5	1.4	9.9	17.8	8.3						
	SOAS	1.3					0.1	0.1			0.3					0.3	0.1					
	SOCA	0.8	3.9	1.5		4.4	1.6	2.4		3.7	0.8	1.3	3.5		2.5	0.9	3.3					
	SOLCAE	2.7																				
	SORU					3.5		0.8		1.0	1.9		1.2	1.0	3.9		1.0					
	SYLA		2.0	2.7	2.6			9.0		2.4	1.5		3.0	0.1	1.8	4.1	3.7					

		SYLAV	1.4	0.8	0.4					1.2	1.0	1.4	1.0	0.5		0.6		
		SYPI				4.0	1.6							13.5				
		thistle						1.0										
		VETH				22.6			8.5	8.5			7.5	4.3		7.9		
		VEUR		0.7			1.1		0.4			0.4			0.3	0.7		
		VICR									0.1							
	vine	AMBR	0.6		0.7	1.5				1.0		1.8	1.2			1.0		
		CLVI													4.4			
grass	grass	grass	82.9	31.2	12.7	44.1	71.7	60.0	45.8	94.0	39.5	38.7	39.2	32.2	45.1	48.1	39.7	45.7
		MIVI	0.8	2.0	50.0			3.5	5.5				9.3		1.0		7.6	5.1
		U4		0.3	0.6	0.7	0.6			1.9		0.5			1.2			0.9
woody	large tree	ACRU			1.3		1.0				5.0		0.7					
		ACSA	8.6	0.1	1.8		1.6	5.1	2.4		0.7	6.8		0.6				
		BELE	0.1	0.1							0.1			0.6	0.4			
		Carya			1.7			1.8	2.3		1.1	0.9	2.5				4.3	
		Fraxinus	13.9	2.8	3.2	1.7	2.6	6.6		1.2		18.0		2.9	3.7	0.6	4.6	3.8
		LITU	2.0	12.9			0.1		1.5			10.0	3.4	1.3	4.0	14.4	5.6	0.5
		POGR							10.2				5.8		1.0		1.0	0.3
		POTR												0.3		1.0		
		PRSE	5.5		4.2	0.1	3.3	9.7	1.4	9.9	3.5		0.4					
		QUAL					2.6		1.5									
		QURU							5.1		3.9							
		QUVE					2.0	2.2	4.1				4.1					
		SAAL		0.9					0.7			2.6		0.6	1.0			
	shrub	CEAM		14.4			0.8	0.7			0.7			0.8	1.0	2.5	0.9	
		CORA				0.6		1.5	4.7		1.9			5.6			1.3	
		ILVE														1.8		
		LIBE			2.3													
		Lonicera							0.4	1.1								
		ROMU		0.1					3.6							1.4		
		Rubus	8.2	23.0	10.5	6.0	14.3	14.9	5.1	7.4	2.8	13.9	7.0	14.5	20.0	13.0	10.9	6.7
	small tree	RUOC	11.9	36.0	6.0		15.6	18.3	2.9	10.7	9.8	35.5	29.0	20.8	25.9	25.9	8.8	11.1
		COFL						1.8										
		Cornus			0.1													
		Crataegus	0.6	2.3	0.4		1.7		3.2	5.0		1.0	0.6	0.3			0.5	
		HAVI	5.9															
		OSVI					5.3											
		RHGL												4.3				
		SACA		7.1							1.4							
	vine	VIPR							3.7				0.0			0.5		
		CEOB					1.1											
		PAQU						1.4				2.8						
		Smilax							0.6	1.0								
		Vitis	1.0	2.7	8.4	10.7	10.2	9.6	1.1	2.7	0.8	20.7	28.1	12.1	1.1	1.5	1.5	0.1

## Appendix F: Peak Growing Season LAI and Cover RM-ANOVA Results

**Table F-1:** Permutation multivariate analysis of variance p-values for all tests and community types indicate block and treatment effects vary by functional group class. Randomized complete block (RCB) design used block as a fixed effect and four separate treatment effects while the factorial design did not account for block but allowed analysis of interactive effects of heat and water. Plots were paired based on heat or water as a block effect with the remaining variable as a treatment effect if original RCB or factorial analyses were inconclusive. Values in bold highlight p < 0.05.

<b>Response Variable</b>	Random Complete Block		Factorial Design			Paired Plots	
	<b>Block</b>	<b>Treatment</b>	<b>Heat</b>	<b>Water</b>	<b>Heat* Water</b>	<b>Heat</b>	<b>Water</b>
Overall Community (Avg Cover)	<b>0.0320</b>	0.1646	0.7996	0.1030	0.4572	0.7802	<b>0.0494</b>
Herbaceous Community (Avg Cover)	0.0676	0.3918	0.9050	0.1072	0.6154	0.8747	<b>0.0540</b>
Woody Community (Avg Cover)	0.5106	<b>0.0406</b>	0.1550	0.2288	<b>0.0322</b>	N/A	N/A
Woody Community (Abundance)	<b>0.0300</b>	<b>0.0014</b>	<b>0.0052</b>	0.8718	0.0568	N/A	N/A
Large Tree (Abundance)	0.1047	0.1202	0.2174	0.8376	0.0556	N/A	N/A

**Table F-2:** Repeated measures analysis of variance results for leaf area index and cover of functional groups. Values in bold highlight  $p < 0.05$ . Numbers in parenthesis are the most significant results from a reduced model where higher-level interactions were removed. Up arrows ( $\uparrow$ ) in parenthesis indicate generally increased cover with the presence of the treatment variable while down arrows ( $\downarrow$ ) indicate lower cover with the treatment variable.

Response Variable	Heat	Water	Heat* Water	Day
LAI	<b>0.0007</b> ( $\uparrow$ )	0.3772	0.8572	<b>0.0012</b>
Total Cover	0.4747	0.0066 ( $\downarrow$ )	<b>0.0194</b> ( $\downarrow$ )	<b>0.0104</b>
Total Forb Cover	0.5174	<b>0.0244</b> ( $\downarrow$ )	0.1878	0.5295
- Relative Cover Forbs	0.4128	0.1182 (.0869) ( $\downarrow$ )	0.9017	0.9614
-Short forbs	0.2393	<b>0.0042</b> ( $\downarrow$ )	0.0820 ( $\downarrow$ )	0.8003
-Tall Forbs	<i>0.0697</i> ( $\uparrow$ )	<b>0.0043</b> ( $\uparrow$ )	0.1001 ( $\uparrow$ )	0.7824
Total Woody Cover	0.1066 ( $\uparrow$ )	0.1226	0.1966	0.5247
- Relative Cover Woody	0.4187	0.5042	.0769 (.0539) ( $\uparrow$ )	0.8930
-Large Trees (log transformed)	0.1186 ( $\uparrow$ )	0.5798	0.4551	0.7375
-Small Trees	0.7571	0.5434	<b>0.0098</b> ( $\uparrow$ )	0.7485
-Shrubs	0.7318	0.7217	<b>0.0142</b> ( $\uparrow\downarrow$ )	0.8241
Total Grass Cover	0.7527	0.0193	<b>0.0011</b> ( $\uparrow$ )	0.7967
- Relative Cover Grass	0.7555	0.0018	<b>0.015</b> ( $\uparrow$ )	0.9292